TOVE BIRKELUND AND HANS JØRGEN HANSEN

SHELL ULTRASTRUCTURES OF SOME MAASTRICHTIAN AMMONOIDEA AND COLEOIDEA AND THEIR TAXONOMIC IMPLICATIONS

Det Kongelige Danske Videnskabernes Selskab
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CONTENTS

Synopsis

The ultrastructures are described of representatives of two lytoceratid genera, *Saghalinites* and *Scaphites* (*Discoscaphites*); one phylloceratid genus, *Hypophylloceras* (*Neophylloceras*); and one coleoid genus, *Groenlandibelus*.

The shell wall of the lytoceratid and phylloceratid ammonites differ significantly in structure. The lytoceratid shell consists of a thin inner prismatic layer, a thick nacreous layer, and a thin outer prismatic layer. The prismatic layers are unilamellar and composed of continuous prisms. The phylloceratid shell consists of a relatively thick, unilamellar, inner prismatic layer, a slender nacreous layer and a very thick multilamellar, quasi-spherulitic outer prismatic layer. The nacreous layer undulates and produces an internal ribbing pattern. The cavities between the nacreous layer and the outer prismatic layer contain small quantities of pigmented matter. The outer prismatic layer differs fundamentally from analogous layers in other ammonites hitherto described.

Hypophylloceras (*Neophylloceras*) also differs from the lytoceratid ammonites here described through the presence of a well-developed prismatic layer on the distal side of the nacreous septa and in its long, nacreous collars connected to the septal necks (false septal necks).

In each of the three ammonite genera the connecting rings are joined together in annular ridges at the septal necks.

In a few specimens of *Saghalinites* the connecting rings of the siphuncle seem to consist of an inner organic tube and an outer calcareous tube with a prismatic fabric.

The first septum distal of the proseptum in *Saghalinites* and *Scaphites* (*Discoscaphites*) is much thinner than the proseptum and is, furthermore, nacreous. It differs in this respect from the "primary septum" as described in many other ammonites.

The ultrastructures of *Groenlandibelus*, referred to Sepiida by JELETZKY (1966), are compared to ultrastructures of other coleoid cephalopods. The calcitic rostrum, built up of radiating prisms, and the nacreous septa ally it to Belemnitida, while the unilamellar, prismatic phragmocone wall allies it to Sepiida.

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Introduction

Ultrastructures of ammonite shells have been studied intensively with the aid of electron microscopy over the last ten years by a number of workers. One of the authors (TB) published a short note in 1967 on early growth stages of *Saghalinites* and *Scaphites* (*Discoscaphites*) and shortly afterwards this work was supplemented by a study on the structures of the septa and the siphuncular tube of *Saghalinites, Scaphites* (*Discoscaphites*) and *Hypophylloceras* (*Neophylloceras*) (Birkelund & Hansen, 1968). Both of these works were based on transmission electron microscope studies. About the same time Erben, Flajs & Siehl (1968, 1969) described the ultrastructures of early growth stages of a great number of ammonite genera based on scanning electron microscopy, and Drushits & Khiami (1970) described early growth stages of two Lower Cretaceous ammonite genera, also by scanning electron microscopy.

Details of the nacre of ammonites have been described first and foremost by Grégoire (e.g. Grégoire, 1958, 1959a, 1959b, 1966; Grégoire & Voss-Foucart, 1970; Voss-Foucart & Grégoire, 1971), but many other recent works on mother-of-pearl, mainly in other mollusc shells, help to throw light also on ammonite nacre (e.g. Wise, 1969, 1970a, 1970b; Mutvei, 1970, 1972a, 1972b; Grégoire, 1962, 1967, 1968, 1972; Erben, 1972a; Towe & Hamilton, 1968; Towe, 1972). Very few recent works based on electron microscopy deal with the ultrastructures of late ontogenetic stages of ammonite shells. Thus, except for works by Erben & Reid (1971) and Erben (1972b) the structures of the late ontogenetic stages have been studied primarily with the light microscope. Without giving a detailed historical account on these early works attention should be drawn to the work of Cornish & Kendall (1888), who stated that the ammonite shell was composed of aragonite, later confirmed in a great number of papers (e.g. Bøggild, 1930; Grandjean, Gregoire & Lutts, 1964; Palframan, 1967). At an early date, Hyatt (1872, p. 107, pl. 4, figs 2–3) had recognized three different layers in the ammonite shell; later Böhmers (1936) and Hölder (1952, p. 25) also mentioned the presence of three layers. Cayeux (1916, p. 492, pl. 54, figs 4–5) described the structure of the outer prismatic layer and the median nacreous layer (= "inner lamellar layer" in *Aegoceras planicosta*), and Bøggild (1930, p. 323, pl. 14, figs 2–4) described the structure of the nacreous layer and the inner prismatic layer in *Harpoceras opalinum* and *Cadoceras elatmae*. The nacreous structure of the septa was described by Bøggild (1930) and later, in *Promicroceras*, by Mutvei (1967) on the basis of light microscopic investigations.

The present work deals with the ultrastructures of all parts of the shell of *Saghalinites*, *Scaphites* (*Discoscaphites*) and *Hypophylloceras* (*Neophylloceras*) in order to throw light on the full ontogeny of the shell structure. An evaluation of similarity and differences between a conservative lytoceratid ammonite, a heteromorph lytoceratid ammonite and a phylloceratid ammonite is also undertaken in order to discern if the evolution of ammonites is reflected in the shell structure. A detailed crystallographic description of the nacre of the ammonites is not within the scope of this work. A separate paper on that subject is under preparation by H. Micheelsen (Copenhagen). It should further be mentioned that Ch. Grégoire (Liége) is investigating the organic remains of the shell of *Saghalinites*.

Phragmocones of Coleoidea are rarely so well preserved that it is possible to study the ultrastructures in detail. One coleoid genus, *Groenlandibelus*, was collected in the same concretions as the ammonites described in the present paper and found to be unusually well preserved. The taxonomic relations of this genus have been the subject of much discussion (Jeletzky, 1966). Its shell structures are here compared with other coleoid cephalopod shells in order to throw further light on its taxonomic position.

Material

All the specimens from Greenland described in this paper derive from calcareous concretions of Maastrichtian age. The concretions occur as boulders in a Danian basal conglomerate in Agatkløft on the peninsula Nûgssuaq, West Greenland. All the material was collected at the localities "Oyster-ammonite Conglomerate" loc. I and II by A. Rosenkrantz and his co-workers (see Birkelund, 1965, p. 18, text-fig. 3). The ammonites were described in the same paper, while the coleoid cephalopod, *Groenlandibelus*, was described by Birkelund (1956) and by Jeletzky (1965, 1966).

Some of the specimens investigated have perfectly preserved shell structures, while others are altered by rescrystallisation or by pyrite impregnation. The chambers are usually filled with brownish, coarse crystalline calcite.

In addition to the material from Greenland, the following material for comparison has been used: Recent material of *Nautilus pompilius* Linné, *Spirula spirula* (Linné) and *Sepia officinalis* Linné; *Spirulirostra* sp. from the Upper Miocene of Karlsgaarde, Denmark; *Belemnitella bulbosa* Meek & Hayden from the Maastrichtian Fox Hills Sandstone, South Dakota, USA; and *Pleuroceras solaris* (Phillips) from the *P. spinatum* Zone, Pliensbachian, Grube Friedericke, Bad Harzburg, DBR.

Preparation

The specimens enclosed within calcareous concretions were cut and ground to the desired level on wet carborundum discs. They were polished with a graded series of diamond pastes and finally etched either with 5 $^0/_0$ HCl or with an aqueous, saturated, un-buffered solution of EDTA. Etching times varied according to wall thickness i.e. the thinner the wall the shorter the etching time. Preparations treated with ultrasonic vibrations were tried but proved unsuccessful. Specimens already freed of the concretions were embedded prior to sectioning in either araldite or epon 812 to prevent the wall layers from flaking off during the grinding process. After etching the specimens were replicated with collodium dissolved in amylacetate. The replicas were exposed to 5 $^0/_0$ HCl to remove adhering crystallites.

For studies in the SEM the replicas were cut into small pieces and mounted on specimen stubs with double adhesive tape. They were plated with about 200 Å pure gold in vacuo under rotation. They were examined in a Stereoscan MK IIa scanning electron microscope at accelerations from 2–30 kv generally in reversed image mode in order to reveal the original topography of the specimen.

For studies in the TEM the replicas were shadowed in vacuo with carbon at an angle of about 45°. The transfer to cut-out grids follows the technique described by HANSEN (1967). The specimens were examined in a Hitachi HU 11C transmission electron microscope at accelerations of 25 or 50 kv. A few specimens were examined in a Philips 75 transmission electron microscope at an acceleration of 50 kv.

The microscopes used in this investigation are all housed in the Laboratory of Electron Microscopy, Geological Institute, University of Copenhagen.

Collodium as replication material was preferred to acetate foil for two reasons: 1. The acetate foil is more easily charred in the SEM than is the collodium. 2. When TEM grids with formvar film are washed in the reflux unit, the acetone used for dissolving the acetate replica often causes the formvar to crack. This phenomenon was less commonly met with using amylacetate.

After replication some of the specimens were re-polished, cleaned and placed in brass-holders in which they were shadowed with 150 Å carbon in vacuo while rotating to ensure a continuous layer. The specimens were studied in a Hitachi XM5 electron microprobe analyser at an acceleration of 20 kv. The wall layer configuration was identified both in reflected light and in reflected electron mode. At magnifications of 1000–2000 times the position of the wall layers was marked on the visual long persistance raster screen with a marker-pen. This enabled the beam spot conducted manually to be kept within the desired layer.

The electron microprobe utilized is housed in the Department of Mineralogy, Geological Institute, University of Copenhagen.

The Principal Layers of the Ammonite Shell Wall

The shell structures of the early growth stages of ammonites have been described by BIRKELUND (1967), BIRKELUND & HANSEN (1968), ERBEN, FLAJS & SIEHL (1968, 1969) and DRUSHITS & KHIAMI (1970).

Our earlier investigations of *Saghalinites* and *Scaphites* (*Discoscaphites*) can be summarized as follows:

First ontogenetic stage. This consists of the protoconch (including the flange), build up of an inner prismatic and an outer irregular sublayer.

Second ontogenetic stage. In the distal part of the protoconch, at the first change in growth, a new layer appears on the inner side which also consists of an inner prismatic and an outer irregular sublayer. This new layer builds up the proseptum and the shell wall to the second change in growth, where it wedges out.

Third ontogenetic stage. At the second change in growth the nacreous layer and the outer prismatic layer of the third ontogenetic stage appear and, a little later, the inner prismatic layer develops. These three layers continue throughout all the later whorls.

The three stages correspond well with the three ontogenetic stages described by ERBEN (e.g. 1964, 1966) on the basis of morphological changes of the shell.

The layers of the two first ontogenetic stages and the prismatic layers of the third ontogenetic stage were called "porcellaneous" in BIRKELUND (1967), in accordance with STENZEL (1964). This term is now abandoned. For the layers of the two first ontogenetic stages no new terms are introduced–purely descriptive terms are preferred to avoid confusion. For the three layers of the third ontogenetic stage a terminology in accordance with BIRKELUND & HANSEN (1968) and ERBEN, FLAJS & SIEHL (1968, 1969) is used (inner prismatic layer–nacreous layer–outer prismatic layer) (pl. 1, fig. 5).

While BIRKELUND & HANSEN (1968) only investigated three Upper Cretaceous genera, ERBEN, FLAJS & SIEHL (1968, 1969) studied a great number of different species (38 belonging to 25 different families) of Carboniferous, Triassic, Jurassic and Cretaceous age. They found remarkably constant shell structures in the early stages, very much in agreement with the structures described by BIRKELUND & HANSEN, although they interpreted the structures in a somewhat different way.

ERBEN, FLAJS & SIEHL suggested a successive formation of the sublayers of the protoconch (a_1 and a_2 in ERBEN, FLAJS & SIEHL, 1969, fig. 5), while we suggested a simultaneous secretion. The formation of the flange is also differently interpreted. ERBEN, FLAJS & SIEHL (1969, fig. 5, p. 2, 29) suggested that the flange is formed late –in connection with the proseptum shortly before the second change in growth– and thus that it belongs to an inner secondary wall of the protoconch, which also formed the early outer part of the whorl following the protoconch (b in ERBEN, FLAJS & SIEHL, 1969, fig. 5). However, BIRKELUND (1967) and BIRKELUND & HANSEN

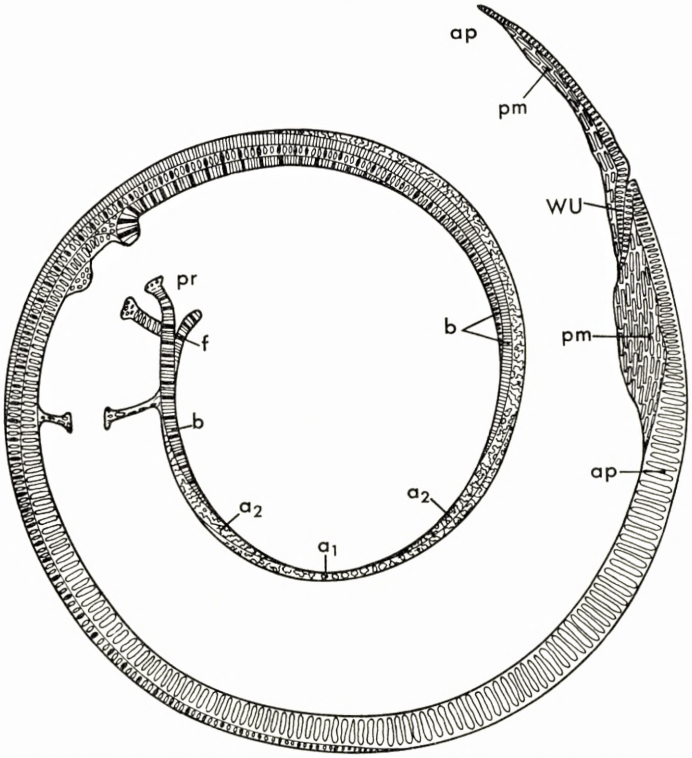

Fig. 1. Ontogeny of shell structure and septa of early growth stages of convolute ammonites. After ERBEN, FLAJS & SIEHL (1969, text-fig. 5). a_1 and a_2: primary shell wall; b: secondary shell wall; f: flange; pr: proseptum; ap: outer prismatic layer; pm: nacreous layer; wu: interruption of growth.

(1968) referred this so-called secondary wall to the second ontogenetic stage. On the other hand, the latest part of the whorl up to the second change in growth is referred to the outer prismatic layer of the third growth stage by ERBEN, FLAJS & SIEHL.

On the basis of a study on two Lower Cretaceous ammonite genera, DRUSHITS & KHIAMI (1970) interpreted the shell layers of the early growth stages in accordance with BIRKELUND & HANSEN.

The two different interpretations are represented in text-fig. 1 and 2 and will receive further comments in connection with the description of the species.

Saghalinites wrighti BIRKELUND, 1965

Plates 1–5, 16; text-figs 2, 3, 5a, 7a–d

Material.

20 specimens prepared for electron microscopical studies.

The first ontogenetic stage (Pl. 1, figs 1–2; pl. 16; text-fig. 2)

The wall of most of the protoconch is extremely thin, about 4 μm. In its most distal part the thickness increases rapidly to 11–12 μm at the point where the layer of the second ontogenetic stage appears.

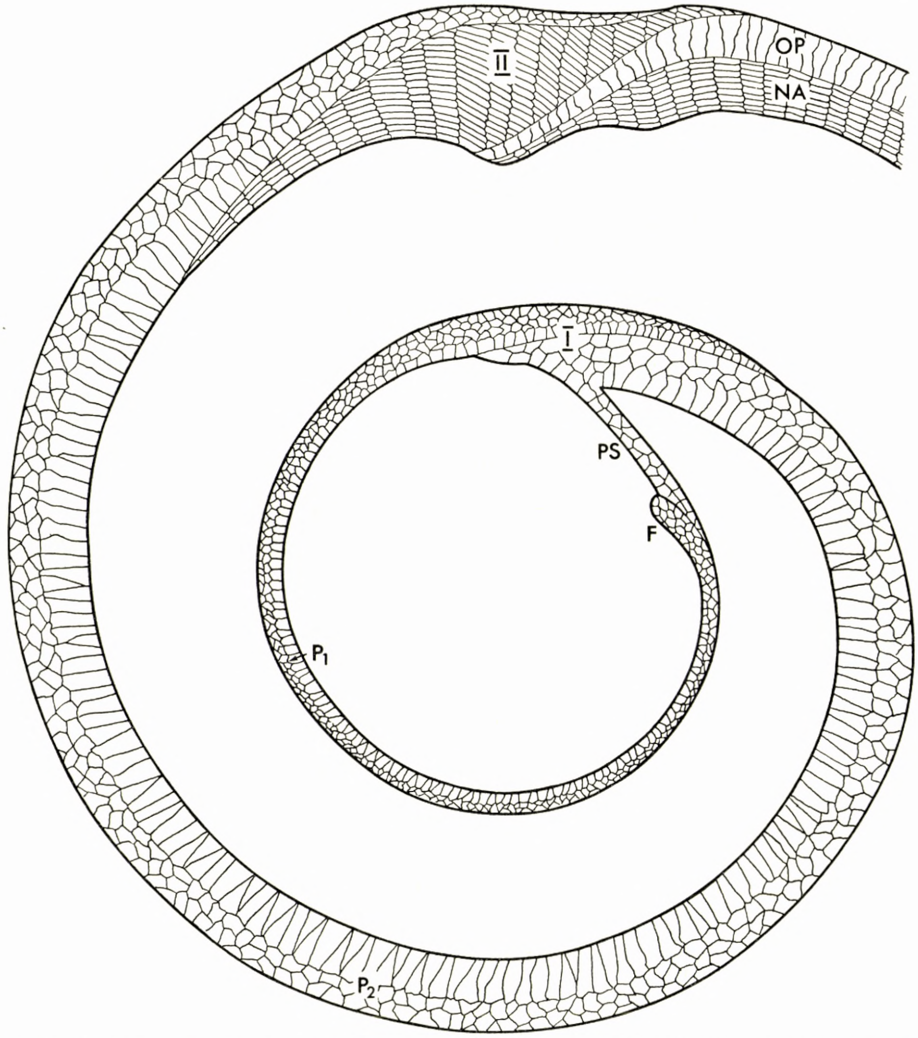

Fig. 2. Ontogeny of shell structure of early growth stages of *Saghalinites wrighti* BIRKELUND. The section is slightly asymmetrical and not to scale. (A symmetrical section, showing the caecum, is figured in pl. 4, fig. 6). P1: prismatic layer of first ontogenetic stage; F: flange; P2: prismatic layer of second ontogenetic stage; PS: proseptum; I: first change in growth; II: second change in growth; OP: outer prismatic layer of third ontogenetic stage; NA: nacreous layer of third ontogenetic stage.

The protoconch consists of two sublayers: the inner always built up of crystal elements coarser than those of the outer sublayer. In the proximal part of the protoconch the crystals are rather irregular, but they become gradually more regularly prismatic towards the distal part of the protoconch. The crystal elements of the outer sublayer are morphologically completely disorganized and retain the same appearance throughout the protoconch. The boundary between the two sublayers becomes gradually more distinct towards the distal end, but is never sharp. Where the boundary can be studied in detail, intermingling crystals can always be seen.

The second ontogenetic stage (Pl. 1, figs 3–4; pl. 16; text-fig. 2).

This stage begins with a remarkable change in growth (1. Wachstumsänderung, Erben, 1964). This is clearly seen on the inner side of the distal part of the protoconch wall, where a new layer appears very abruptly (pl. 16, fig. 1). The layer gradually grows thicker at the expense of the protoconch layer which wedges out close to the ventral part of the proseptum on the distal side. The thickness of the new layer is here 14–16 μm and increases slightly (to 18–19 μm) until it wedges out at the second change in growth.

Almost from the very beginning the layer is differentiated into two sublayers. The inner sublayer is always built of coarser crystal elements than is the outer sublayer. The crystals of the inner sublayer tend to form somewhat regular prisms, while the outer sublayer retains a completely irregular structure. Thus, with regard to structure the second growth stage is remarkably similar to the first growth stage. The boundary between the layers of the two growth stages is distinct (pl. 4, fig. 1; pl. 16, fig. 1).

The two sublayers of the second ontogenetic stage are poorly separated in the early part. Later they become more distinct, but the change is so gradual that the sublayers still must be considered as belonging to a single layer (pl. 1, figs 3–4; pl. 16). Both sublayers can be recognized until the layer wedges out at the second change in growth (pl. 2, fig. 1; pl. 16).

The proseptum belongs to the second stage of growth, the ventral part being continuous with the shell wall of that stage (pl. 4, fig. 1). The dorsal part is connected to the protoconch at the flange. The boundary between the proximal part of the flange and the proseptum is distinct, while the boundary is rather indistinct in the distal part (pl. 2, figs 4–5). It is not evident whether the proseptum wedges out on the outer side of the protoconch as suggested by Palframan (1967) and Birkelund & Hansen (1968), or if the flange is separated from the protoconch proper, supporting Erben, Flajs & Siehl's (1969) interpretation of the flange as a structure formed ontogenetically late and belonging to the second ontogenetic stage (text-fig. 1).

The proseptum has an irregular prismatic structure. It is about 6 μm thick, and thus considerably thicker than the succeeding true septa.

The second change in growth (Pl. 2, fig. 1; pl. 16; text-figs 2, 5a).

The second change in growth of ammonites was already recognized and illustrated by Hyatt (1872, pl. 4, fig. 11). It has been called the "nepionic constriction" (Erben, Flajs & Siehl, 1968; Birkelund & Hansen, 1968), the "premiére varice" (Grandjean, 1910); the "primary constriction" (Shul'ga-Nesterenko, 1926; Bokoslovskaya, 1959); "Anfangseinschnürung" (Böhmers, 1936); "2. Wachstumsänderung" (Erben, 1964; Erben, Flajs & Siehl, 1969), and "primary varix" (Drushits & Khiami, 1970). Currie (1942) also noted a change of growth gradient at this stage. It has the form of a swelling of the shell wall and appears as a marked constriction on the internal cast.

In *Saghalinites* the second change in growth is situated at about 310° from the protoconch (measured as by DRUSHITS & KHIAMI, 1970). At its proximal end the nacreous layer appears on the inner side and thickens gradually, while the thickness of the irregular prismatic layer of the second ontogenetic stage decreases proportionately. The nacre reaches its greatest thickness in the distal part, corresponding to the deepest part of the constriction on the internal cast. Here a thin prismatic layer appears on the inner side and crosses obliquely to the outer side, where it continues as the outer prismatic layer of the third growth stage. As shown in pl. 2, fig. 1; pl. 16 and text-fig. 5 a the structures are widely variable at the crossing prismatic layer, supporting the theory of an important ontogenetic interruption in growth (ERBEN, FLAJS & SIEHL, 1969, p. 7). This is discussed further on p. 22.

The third ontogenetic stage.

The shell wall (Pl. 1, figs 5–8; pl. 2, figs 2–3; pl. 3, figs 1–3; pl. 16). The thickness of the ventral wall increases from 20–25 μm in the proximal part of the stage to 0.3–0.4 mm at a diameter of 25 mm.

The outer prismatic layer and the nacreous layer are well developed from the very beginning of this stage (pl. 16). Also an incipient prismatic layer may be developed on the inner side of the earliest part of the ventral wall of this stage or it appears slightly later. A well developed inner prismatic layer, however, does not appear until half a whorl to about one whorl distal of the second change in growth (pl. 1, figs 5–8).

The relative thickness of the three shell layers varies widely with age. In the proximal part the outer and inner prismatic layers are of about equal thickness (the outer one slightly thicker than the inner one) and both attain a thickness of $^1/_2$–$^2/_3$ of that of the nacreous layer (pl. 1, fig. 5). In the distal part of the shell the thickness of the prismatic layers is only a fraction of that of the nacreous layer, which is the main contributor to the increasing thickness (pl. 1, fig. 6). The inner prismatic layer, which is relatively thin proximally, may gradually become thicker than the outer one. Locally in some cases the prisms of the inner prismatic layer may be obliquely deformed (pl. 1, figs 7–8).

At the umbilical edge the outer prismatic layer and the nacreous layer wedge out while the inner prismatic layer decreases in thickness, but continues on the dorsal side (pl. 2, fig. 3); in longitudinal ventro-dorsal sections it is seen as a thin prismatic layer, covering the outer prismatic layer of the previous whorl. Only in the early part of the third growth stage, where the inner prismatic layer is missing, the dorsal shell layer is not developed.

In the varices of this species (pl. 2, fig. 2) the nacreous layer shows a considerable increase in thickness. The shape of the swellings has much in common with the second change in growth, but there are no irregularities in the prismatic layers such as those at the second change in growth, thereby indicating that no interruption in growth occurred at the varices.

The true septa (Pl. 3, fig. 6; pl. 4, figs 2–6). In *Saghalinites* the second septum, here called the first true septum (the "primary septum" of Schindewolf (1954) and Erben, Flajs & Siehl (1968, 1969)), is of similar thickness and structure as the succeeding septa (pl. 4, figs 2, 6). It is therefore here considered along with the succeeding septa as a true septum.

All true septa are formed later than the adjacent shell wall and the junction is therefore always sharp. The first true septum is dorsally attached to the proseptum, where the latter wedges out on the protoconch, while all later septa are attached to the protoconch or to the shell wall of later whorls.

The septa increase in thickness from 2–3 μm in the first true septum to about 0.1 mm in septa at a shell diameter of 25 mm. The first true septum is about half as thick as the proseptum and similar to the second true septum in thickness.

All the true septa are constructed of nacre. The minute earliest septa are seldom well preserved. However, a few specimens show fairly well preserved nacreous structures, even in the first true septum (pl. 4, fig. 2). The nacre of well preserved septa is stacked as in the shell wall (pl. 3, fig. 6). Late septa may show an incipient prismatic layer on the distal side (pl. 3, fig. 6), but this layer is never as well developed as in *Hypophylloceras* (*Neophylloceras*) (pl. 10, figs 3–6).

The septal necks are also nacreous. No calcified auxiliary structures (false septal necks), so characteristically developed in *Hypophylloceras* (*Neophylloceras*), are seen.

The siphuncle (Pl. 3, figs 4–5, pl. 4, figs 3–7; pl. 5; text-figs 7 a–d). One specimen shows the caecum and early part of the siphuncle (pl. 4, fig. 6). The siphuncle is situated ventrally from the very beginning.

In some specimens the connecting rings seem to consist of two layers (pl. 4, figs 3–5): a thin inner layer and a considerably thicker outer layer. The inner layer is here interpreted as a conchiolin tube, similar to that of *Nautilus* (see Mutvei, 1972 b). The fibrous structure of the surface of the tube, shown in pl. 3, fig. 4, confirms the organic origin. The outer layer shows no recognizable structures in most specimens but in others it appears to be built up of calcareous prismatic sublayers (pl. 4, fig. 7; Birkelund & Hansen, 1968, pl. 4).

Birkelund & Hansen (1968) believed the outer calcareous layer to be of primary origin. However, Erben, Flajs & Siehl (1969) expressed doubts about the primary origin as none of the ammonites investigated by them showed any sign of a prismatic calcareous layer.

Reyment (1956) found parts of the siphuncle of *Speetoniceras versicolor* to consist of calcium carbonate. This he compared, with some doubt, to the outer layer of calcareous thornlets in the siphuncle of *Nautilus*. Except for this indication, and evidence of phosphatic siphuncles presented by Grandjean (1910), Trueman (1920), Reyment (1956) and Andalib (1972) (who argues in favour of a primary origin of carbonate fluor-apatite and calcite in siphuncular tubes), it seems to be generally accepted that

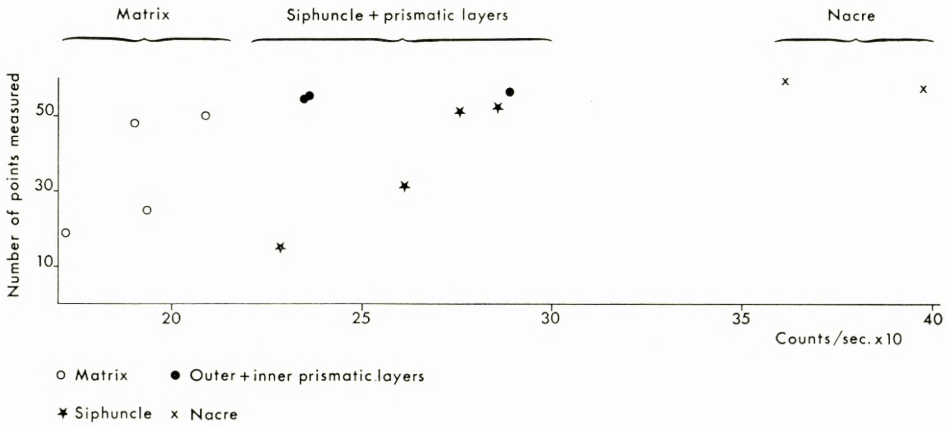

Fig. 3. Diagram illustrating the relative amounts of Sr in the different wall layers and matrix of *Saghalinites wrighti* BIRKELUND. All measurements have been made at identical sample current. MMH 12994.

the connecting rings of ammonites consist of an organic tube only (MUTVEI & REYMENT, 1973).

It is extremely difficult to prove the primary origin of the calcareous tube. An aragonitic composition of the tube would strongly support the theory of a primary origin, but because of the small thickness of the tube, it has not been technically possible to prove the crystallographic composition. Instead we have determined the relative strontium content of the tube wall, the calcite matrix of the adjacent chambers, and the shell wall by electron microprobe. This showed that the strontium content of the tube is distinctly higher than that of the calcite matrix of the chambers, but very similar to that of the prismatic layers of the shell wall, while the content in the nacreous layer is still higher (text-fig. 3). The measured series show extremely low standard deviations. In only one example (the matrix series at an $\bar{x}$ of 19.0) is the s-value at 1.58 while the remaining series are all less than 1. When averaging the measurements of the different wall structure layers here analysed the prismatic layers have Sr counts that are 25 $^0/_0$ higher than the matrix; the connecting ring is 27 $^0/_0$ higher while the measurements of the nacre is 95 $^0/_0$ higher in Sr counts than is the matrix. The analysis thus strongly suggests an aragonitic composition of the connecting rings of the tube pointing to a primary origin. The layer can be compared to the so-called spherulitic-prismatic layer of the connecting rings of *Nautilus* (MUTVEI, 1964, 1972b).

Each connecting ring comes into contact with the next at the septal necks. The contacts are situated at the distal end of the septal neck, where the proximal connecting ring wedges out after a slight swelling and the distal connecting ring appears on the inner side of the swelling (pl. 5, figs 2, 3, 5). The connecting rings are also slightly thickened at the proximal region of the septal necks, but here the rings seem to continue beyond the thickening (pl. 5, fig. 5). The swellings may be compared to the so-called annular calcareous deposit in *Promicroceras* sp., described by Mutvei (1967), and the swelling of the siphuncular tube in *Salfeldiella quettardi,* indicated by Drushits & Khiami (1970, fig. 5). The term annular ridges is preferred for the swellings of the connecting rings of *Saghalinites* as no special calcifications have been recognized. These structures are further discussed on p. 25.

Scaphites (Discoscaphites) sp.

Plates 6–7; text-figs 4, 5b.

Material.

4 specimens prepared for electron microscopical studies.

The first ontogenetic stage (Pl. 6, figs 1–2).

The thickness and shape of the protoconch is similar to that of *Saghalinites.* The thickness is thus 4–5 μm until the most distal part where it increases rapidly to about 13 μm. The structure of the protoconch is not well preserved. Only one layer of irregular structure has been recognized, except for the most distal part where a slight differentiation of an inner, more regularly prismatic sublayer may be distinguished (pl. 6, fig. 2).

The flange has an irregular prismatic structure, and seems to be connected with the protoconch proper.

The second ontogenetic stage (Pl. 6, fig. 1).

The new shell layer belonging to the second stage of growth appears less abruptly than in *Saghalinites* (pl. 6, fig. 1). The thickness and structure are similar to the second stage of *Saghalinites.* Thus there is a similar differentiation of an inner sublayer constructed of coarse, rather regular prismatic crystals and an outer sublayer consisting of smaller and more irregular crystals. The proseptum is poorly preserved in the specimens investigated.

The second change in growth (Text-fig. 5b).

The second change in growth is situated at about 260° from the protoconch. It is similar to that of *Saghalinites* with regard to both shape and shell structure. In the figured specimen the distal part of the irregular prismatic layer of the second ontogenetic stage of growth is dominated by the inner prismatic sublayer. The nacre is distinctly stacked from the very beginning.

The third ontogenetic stage.

The shell wall (Pl. 6, figs 3–8; pl. 7, figs 1–3). The thickness of the ventral wall increases from about 12 μm immediately after the second change in growth to 0.2–0.3 mm at a shell diameter of 20 mm.

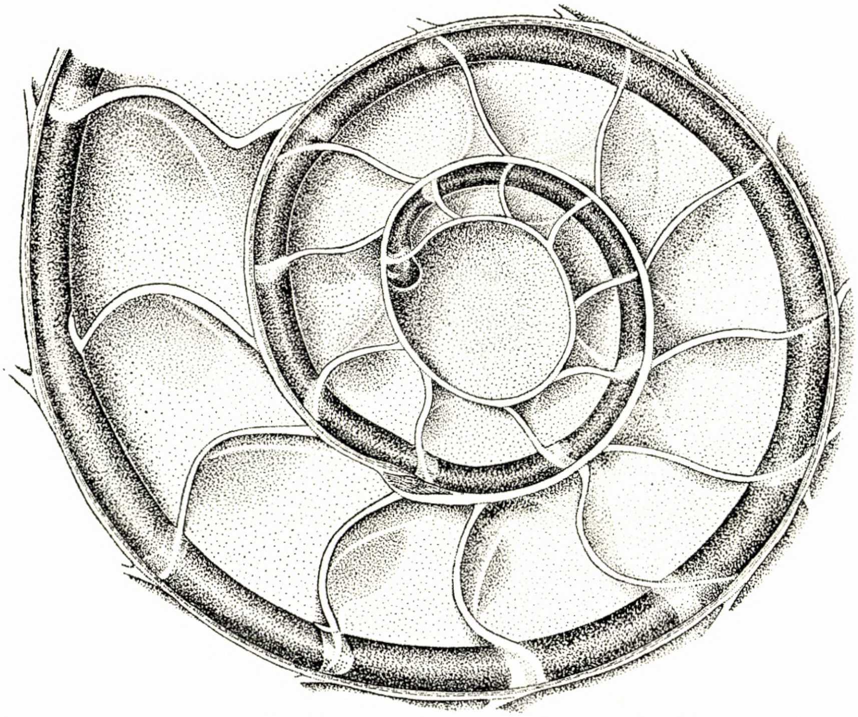

Fig. 4. Early growth stages of *Scaphites* (*Discoscaphites*) sp. Polished section. The caecum and the siphuncle are visible through the transparent calcite filling. ×60. MMH 12997.

An incipient prismatic layer is distinguishable one whorl distal of the second change in growth and slightly later it becomes well differentiated (pl. 6, figs 3–4). Two whorls distal of the second change in growth the inner prismatic layer is thicker than the outer prismatic one and maintains a slightly greater thickness in younger whorls. In this part of the whorls the prismatic layers make up only a minor part of the shell wall, while the nacreous dominates (pl. 6, fig. 6). In one specimen the prisms of the outer prismatic shell layer are locally obliquely oriented (pl. 6, figs 7–8). The shell structures are not influenced by the smooth ribbing pattern, which appears about three whorls distal of the second change in growth (pl. 7, fig. 3).

The relation between the stacked nacre and the prisms of the inner prismatic layer is seen in pl. 7, figs 1–2. The figures indicate that the prisms are formed in continuation of the stacks of nacre. The irregular polygonal cross section of the prisms is also seen.

Dorsally the outer prismatic layer and the nacreous layer wedge out and the inner prismatic layer forms a cover of variable thickness (pl. 6, figs 4–5), except for the first whorl distal of the second growth stage, where the inner prismatic layer is not yet developed.

The true septa (Pl. 7, figs 3–5). The septa increase in thickness from 3 μm in the first true septum to about 0.2 mm at a shell diameter of 25 mm. The first septum is extremely thin as in *Saghalinites* and likewise seems to be composed of nacre. All the younger septa are built up of stacked nacre and no prismatic layer appears to be present. The structure of the septa of this genus is in good accordance with that of the septa of other described ammonite genera (see Erben, Flajs & Siehl, 1969).

The siphuncle (Pl. 7, figs 6–7; text-fig. 4). Two specimens show the caecum. One of them seems to have two or three prosiphons (Birkelund & Hansen, 1968, text-fig. 1), attaching the caecum to the wall of the second growth stage.

The siphuncle is situated ventrally from the very beginning. It is narrowed at the septal necks by thickenings of the connecting rings (pl. 7, figs 6–7). The thickenings may have a texture differing from that of the adjacent connecting ring, but no calcification similar to the auxiliary structures (false septal necks) of *Hypophylloceras* (*Neophylloceras*) described below is seen. The thickenings are presumed to form the connection between succeeding connecting rings.

Hypophylloceras (Neophylloceras) groenlandicum Birkelund, 1965

Plates 8–12; text-figs 5 c, 6 a–d, 7 e.

Material.

5 specimens prepared for electron microscopical studies.

The first ontogenetic stage.

The wall of the protoconch is poorly preserved and apparently no primary structures have survived.

The second ontogenetic stage (Pl. 8, fig. 1).

The second stage is also rather poorly preserved. It appears from pl. 8, fig. 1 that the structure is more regularly prismatic than in *Saghalinites*.

The second change in growth (Text-fig. 5 c).

The prismatic layer of the second growth stage decreases in thickness in proportion to the increase of thickness of the nacre, but in a rather irregular way (text-fig. 5 c). The nacre is stacked from the very beginning. Where the nacre attains its greatest thickness a prismatic layer appears on the inner side and crosses obliquely through the nacre to the outer side, where it continues as the outer prismatic layer of the third ontogenetic stage.

The third ontogenetic stage.

The shell wall (Pl. 8, figs 2–8; pl. 9; pl. 11, figs 1–2; text-figs 6 a–d). The thickness of the wall is ventrally about 11 μm immediately distal of the second change in growth.

About $^3/_4$ whorl later it has increased to about 26 μm, one whorl later to 31 μm and two whorls later to 82 μm. At a shell diameter of 15 mm the shell is about 0.4 mm thick ventrally.

Immediately distal of the second change in growth the shell consists of a relatively thick outer prismatic layer, an extremely thin nacreous layer and, apparently, an incipient inner prismatic layer. $^3/_4$ whorl later the inner prismatic layer is distinctly developed.

From the beginning of the third ontogenetic stage a quasi-spherulitic arrangement of the prisms of the outer prismatic layer becomes visible. About one whorl distal of the second ontogenetic change in growth cavities appear between the nacreous layer and the outer prismatic layer (pl. 8, fig. 2). About $1^1/_2$ whorl later the nacreous layer starts to undulate and the cavities between this layer and the quasi-spherulitic outer prismatic layer become more distinct. The undulations of the nacreous layer and the intervening cavities are compensated for by the variable thickness of the inner and outer prismatic layers, so that the inner and outer surfaces of the shell are completely smooth (pl. 8, fig. 7; text-figs 6a–d).

In the second and third whorls the inner prismatic layer is $^1/_3$ to $^1/_5$ as thick as the quasi-spherulitic outer prismatic layer. The nacreous layer is extremely thin, and makes up a very small fraction of the shell wall. Further distally the quasi-spherulitic outer prismatic layer grows more in thickness relative to both the nacreous layer and the inner prismatic layer, and several sublayers of intermingling quasi-spherulitically arranged prisms can be distinguished (pl. 9, fig. 3). Thus the increase in shell thickness is largely accounted for by the quasi-spherulitic outer prismatic layer and not by the nacre as in the other ammonites here described.

The relations between the nacreous layer, the inner prismatic layer and the outer prismatic layer are shown in pl. 9, fig. 1. The nacre is distinctly stacked and the prisms of the inner prismatic layer are continuous with the stacks. No close connection between the nacre and the quasi-spherulitic outer prismatic layer can be seen.

The fine ribbing pattern of *Hypophylloceras* (*Neophylloceras*) shown in BIRKELUND (1965, pl. 1, figs 1–4) and in pl. 11, fig. 2 is due to the undulation of the nacre. Shells with the outer and inner prismatic layers preserved are completely smooth.

The full ventral thickness of the *Hypophylloceras* shell is slightly greater than that of shells of *Saghalinites* and *Scaphites* (*Discoscaphites*) of similar diameters. The reason why phylloceratids are often supposed to have an extraordinarily thin shell may well be that the thick quasi-spherulitic outer prismatic layer is often not preserved. Dorsally the quasi-spherulitic outer prismatic layer and the nacreous layer wedge out, while the inner prismatic layer either forms a thin investment (pl. 8, fig. 5) or wedges completely out with the other shell layers (e.g. pl. 8, fig. 6; pl. 11, fig. 4).

A dark pigmentation was found in the cavities between the undulating nacreous layer and the outer quasi-spherulitic prismatic layer (pl. 11, fig. 2). S. O. ANDERSEN, Copenhagen, made a chemical analysis of this material. It was removed from the shell by manuel preparation. In the residue after removal of the carbonate no reaction

Fig. 5. Slightly schematic drawings of second change in growth. a: *Saghalinites wrighti* Birkelund; ×500; MMH 12993. b: *Scaphites* (*Discoscaphites*) sp.; ×640; MMH 12996. c: *Hypophylloceras* (*Neophylloceras*) *groenlandicum* Birkelund; ×620; MMH 12998. P2: prismatic layer of second ontogenetic stage; OP: outer prismatic layer of third ontogenetic stage; NA: nacreous layer of third ontogenetic stage.

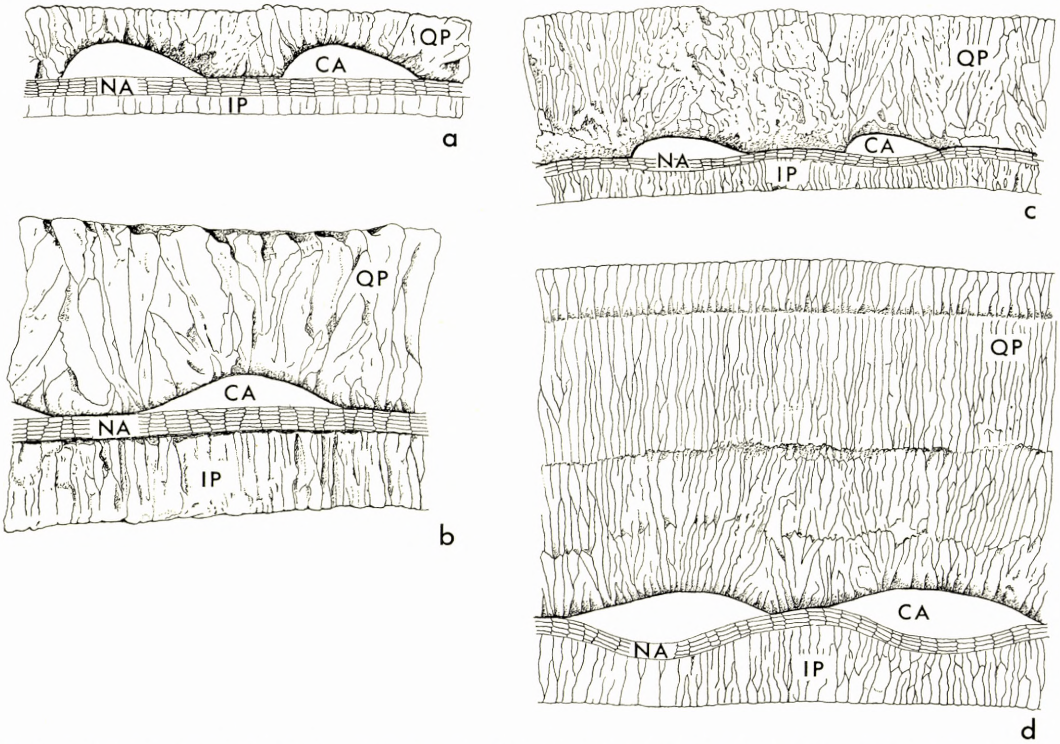

Fig. 6. Schematic drawings of the ventral wall of *Hypophylloceras* (*Neophylloceras*) *groenlandicum* Birkelund. a and b enlarged 2–3 times c and d. a: 1st whorl distal of the second change in growth. b: 2 whorls distal of the second change in growth. c: $2^1/_2$ whorls distal of the second change in growth. d: late whorl. QP: quasi-spherulitic outer prismatic layer; NA: nacreous layer; IP: inner prismatic layer; CA: cavities.

indicative of any animal pigment was obtained. The dark material is most probably pyrite. However, after dissolution of the supposed pyrite a small quantity of dark material was still left over. It is likely that this material is also of inorganic nature since it has a density of more than 3.3 (determined by heavy liquids).

The true septa (Pl. 9, fig. 2; pl. 10; pl. 12). The earliest septa are poorly preserved. In the first and second whorls they consist exclusively of stacked nacre (pl. 10, fig. 1). About $2^1/_2$ whorls distal of the second change in growth an incipient prismatic layer appears on the distal side of the septa (pl. 10, fig. 2) and between $2^1/_2$ and 3 whorls distal of the second change in growth this prismatic layer becomes more distinctly developed (pl. 10, fig. 3). The prisms are formed in direct continuation of the stacks of nacre as in the shell wall, but the boundary is not distinct. The prismatic layer comprises only $^1/_3$ to $^1/_7$ of the thickness of the septum. Pl. 9, fig. 2 demonstrates the connection between a septum with a well developed prismatic layer and the ventral shell wall.

Birkelund & Hansen (1968) considered the prismatic layer to be of primary origin, while Erben, Flajs & Siehl (1969) and Erben & Reid (1971) believed that

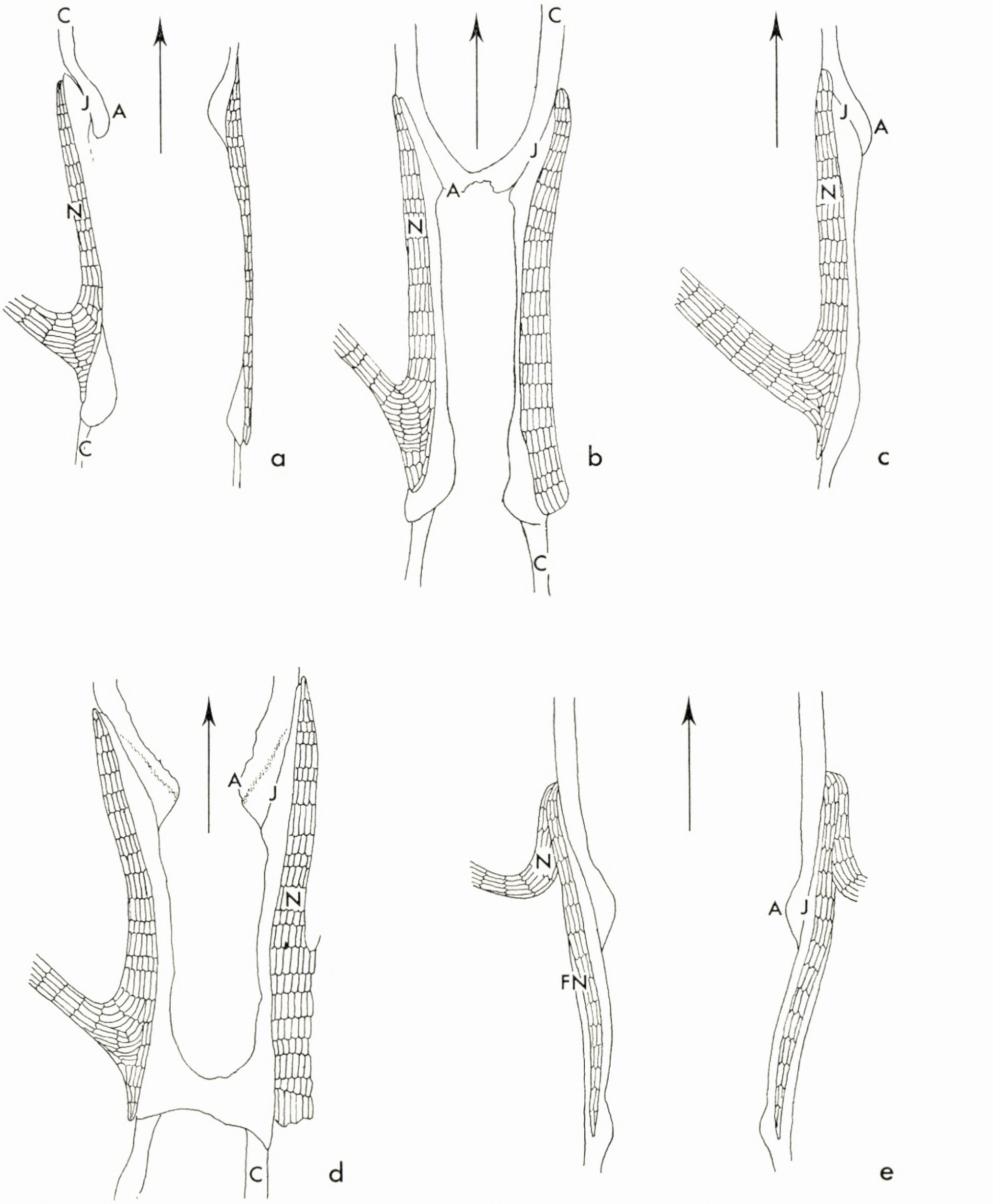

Fig. 7. Schematic drawings of septal neck and siphuncle of *Saghalinites wrighti* Birkelund (a–d) and *Hypophylloceras* (*Neophylloceras*) *groenlandicum* Birkelund (e). The specimens are sectioned at slightly different levels. N: neck; C: connecting ring; J: junction between two connecting rings; A: annular ridge. Arrows indicate adoral direction.

the prismatic layer was a result of recrystallisation of the nacreous layer, partly because all the septa studied by them were exclusively nacreous. The primary origin is indicated by the gradual appearance of the prismatic layer in successive septa, and by the complete absence of the prismatic layer on the proximal side, which was not to be expected if it was due to diagenesis.

False septal necks (Pl. 11, figs 3–5; pl. 12; text-fig. 7e). The term "false septal necks" is introduced here for calcified collars developed in *Hypophylloceras* (*Neophylloceras*) in close connection with the true septal necks. Similar collars in other phylloceratids were called "prolongement posterior" by GRANDJEAN (1910) and "connective rings" by DRUSHITS & KHIAMI (1970). In 1968 the present authors called them auxiliary deposits. The new name is introduced in order to avoid confusion with other auxiliary structures (e.g. the annular ridges of the connecting rings) and with the term connecting rings.

The false septal necks are built up of nacre (BIRKELUND & HANSEN, 1968, pl. 3; here pl. 12, fig. 4). They form collars which are in close connection with the true septal necks in the proximal part, while the distal part is free. A distinct boundary between the septal neck and the false septal neck is seen in pl. 12, fig. 4.

The siphuncle (Pl. 11, figs 3–5; pl. 12; text-fig. 7e). Our material does not show the caecum. In one well preserved specimen the earliest part of the siphuncle is more centrally placed than in *Saghalinites* and *Scaphites* (*Discoscaphites*) (pl. 12, fig. 2).

None of the connecting rings investigated shows prismatic structure. In one specimen the wall seems to be filled up with secondary calcite.

The siphuncle is slightly narrowed where it passes through the false septal necks. The proximal and distal connecting rings seem to be connected at an annular ridge (pl. 11, fig. 4) as in *Saghalinites*. The interpretation of the relationship between the false septal neck and the connecting rings with annular ridges shown in text-fig. 7e is similar to the interpretation given by DRUSHITS & KHIAMI (1970) of the siphuncle in *Salfeldiella*. DRUSHITS & KHIAMI stressed that the false septal necks (their "connective rings") are surrounded by an organic mantle. An organic mantle covering the outer side of the false septal necks is usually not preserved in the Greenland material. However, in the specimen figured in pl. 12, fig. 1 an outer mantle may be distinguished, and also the organic tube shown in pl. 12, figs 2–3 may be an outer mantle, apparently with impression of blood vessels preserved.

Discussion and Concluding Remarks

First and second ontogenetic stages.

The early growth stages are best preserved in *Saghalinites*. Both first and second growth stages (protoconch and first whorl) are characterized by a rather regular prismatic structure of the inner sublayer and a more irregular structure of the outer sublayer. In *Scaphites* (*Discoscaphites*) a similar differentiation of the shell structure of the two early growth stages can be distinguished. In our material of *Hypophylloceras* (*Neophylloceras*) the structure of the first growth stage is poorly preserved. The structure of the second growth stage is more regularly prismatic than in *Saghalinites* and *Scaphites* (*Discoscaphites*).

The growth of the protoconch cannot yet be fully explained. Composite micrographs of several complete protoconchs of *Saghalinites* show that the protoconch is thinnest close to the flange and that the sublayers of the protoconch gradually differentiate in the direction of the first change of growth. We are therefore most inclined to interpret the flange as the first beginning of the protoconch as we did in 1969, a view supported by Drushits & Khiami (1970). However, the material does not fully show whether the flange is continous with the protoconch or separated, as interpreted by Erben, Flajs & Siehl (1969).

As indicated by Birkelund (1967) and by Erben, Flajs & Siehl (1968, 1969) the proseptum belongs to the second stage of growth, being continous with the shell wall of that stage. The first true septum of *Saghalinites* and possibly also of *Scaphites* (*Discoscaphites*) is similar to the succeeding septa both in structure and thickness. Because of its nacreous structure it is considered to have formed at the beginning of the third growth stage, since the nacreous layer of the shell wall does not appear until that stage. In *Hypophylloceras* the structure of the first true septum is not well preserved. In many other ammonites the first true septum (the "primary septum" of Schindewolf (1954), the second septum of Drushits & Khiami (1970)) is considerably thicker than the following septa and differs further from these in having prismatic structure (Erben, Flajs & Siehl, 1969, 1970). Because of its structure, Erben, Flajs & Siehl suggest that it was formed during the second growth stage. The difference in morphology of the first true septum in genera investigated by Erben, Flajs & Siehl (most convincingly in the Jurassic genera *Xipheroceras, Androgynoceras, Eleganticeras, Quenstedtoceras* and *Pavlovia*) and those investigated here may be due to a difference in ontogeny.

The second change in growth is constructed in a very similar way in the three genera here investigated, only differing slightly in shape and in distance from the protoconch. This confirms investigations by Erben, Flajs & Siehl (1969) and shows that this characteristic change in growth is remarkably constant in all ammonites.

The first and second changes in growth were extensively discussed by Erben (1964), who also reviewed earlier observations by e.g. Hyatt (1889), Grandjean (1910), Böhmers (1936) and Currie (1944).

The early growth stages have been interpreted in many different ways. Branco (1879) supposed that the embryonic shell probably consisted of only a part of the protoconch. Schindewolf (1929) included the protoconch as well as the proseptum in the embryonic stage. Spath (1933) suggested a change in mode of life after the ammonite animal left the protoconch stage, i.e. when it ceased to drift as a planktic larva. Arkell (1957, p. L 101) suggested that the protoconch belonged to a larval stage and that the second change in growth represented the end of the first post-larval stage. Shimanskij (1954), Erben (1962, 1964, 1966) and Erben, Flajs & Siehl (1969) suggested that the protoconch was embryonic and that the first whorl (to the second change in growth) belonged to a larval stage. Grandjean (1910), Bodylevsky (1926), Böhmers (1936), Currie (1944), Balashow (1953), Drushits (1956), Drushits & Khiami (1969, 1970) and Zakharov (1972) included the shell to the second change in growth in the embryonic stage. Only the most recent points of view expressed by Erben and Erben, Flajs & Siehl on the one side and by Drushits & Khiami on the other are further discussed here.

Erben (1964, 1966) based his interpretation of the early ontogeny on detailed studies on bactritid and early goniatitid cephalopods. His concept of an embryonic stage including the protoconch, and a larval stage including the first whorl to the second change in growth was based partly on the two characteristic changes of growth, and partly on the absence of a ventral modification of the aperture in the first growth stage, while in the second growth stage a wide ventral apertural sinous bend is developed. He supposed that "hier dürfte begrenze Eigenbeweglichkeit bereits bestanden haben, höchst wahrscheinlich mit Hilfe eines ventral herausragenden Velums" (Erben, 1966, p. 651). This stage was compared to the veliger stage of gastropods and bivalves. The presence of an embryonic stage and a larval stage, according to Erben, Flajs & Siehl (1969) is further supported by the remarkable changes in shell structure at the first and second changes in growth. Further evidence of their point of view was found in the early appearance of the nacreous layer in the nautiloids studied, together with the lack of any metamorphosis in the shell morphology of nautiloids. This is in agreement with the lack of free-living larval stages in nautiloids (Erben, 1964; Eichler & Ristedt, 1966a, 1966b).

Drushits & Khiami (1969, 1970) suggested the presence of two principal ontogenetic stages in ammonites: an embryonic and a post-embryonic. The embryonic shell consists of the protoconch and the first whorl (to the second change in growth); this part of the shell is called the ammonitella. The ammonitella animal is supposed to have had a long vermiform body, separated from the protoconch by the proseptum. Drushits & Khiami supported their view by: (1) the small size of the ammonitella (0.6–1.1 mm in Cretaceous ammonites, up to 2.0 mm in Devonian ammonites); (2) the completely smooth protoconch and first whorl of forms investigated by them; (3) the growth lines observed by Erben on the first whorl could equally well have developed during embryonic growth, as there is evidence for this in the juvenile sculpture observed on the first whorl of the shell in coiled nautiloids; (4) the discovery of large numbers of embryos in the Lower Aptian of Ul'yanovsk, consisting of protoconch, first whorl, proseptum, prosiphon and caecum; and (5) it was considered more likely that ammonites developed directly without a larval stage as do all other cephalopods, than they passed through trochophor or veliger stages, characteristic of marine gastropods.

Drushits & Khiami mentioned that the second septum (the first true septum) could well have been constructed during the embryonic stage. After adapting to the new environment, the ammonites started growing rapidly after the second change in growth.

We follow the main points of Drushits & Khiami's view. It should be stressed, furthermore, that in recent coleoids the size of the eggs varies a great deal in different species. Forms with small eggs, after hatching pass through an inactive planktic stage (Mangold-Wirz, 1963), during which the animal is often slightly modified in comparison with later stages. The "ammonitella" corresponds very well in size with these small eggs (stressed also by Zakharov, 1972), and it is likely that the ammonites passed through a similar inactive planktic "larval" stage, which may correspond with the second change in growth. The close relation between ammonites and coleoids, suggested by Zeiss (1968) on the basis of the number of arms in goniatites, and by Lehmann (1971) on the basis of the type of radula, also supports this theory.

Third ontogenetic stage.

Remarkable differences exist in the structure of shell wall and septa between the lytoceratid and phylloceratid ammonites here described. The structure of the shell wall of *Saghalinites* and *Scaphites* (*Discoscaphites*) seems to be in good accordance with the structure of other ammonite walls described up to now involving relatively thin inner and outer prismatic layers sandwiching a thick nacreous layer. The prisms of both the inner and outer prismatic layer are oriented with the c-axis perpendicular to the shell surface and not parallel to the surface as in the inner prismatic layer of orthocerid cephalopods (according to Ristedt, 1971, p. 174). The c-axis of the crystallites of the inner prismatic layer may deviate as much as 5° from the perpendicular (H. Micheelsen, personal communication). In the forms here investigated the prismatic layers are unilayered, and the ribbing pattern of *Scaphites* (*Discoscaphites*) does not influence the shell structure. In other forms with more prominent sculpture the shell structure may be influenced by this, particularly so in forms which show a marked difference between the sculpture of the inner and outer surfaces of the shell wall. An example of this was shown by Erben (1972b), who demonstrated that the inner prismatic layer of *Eleganticeras elegantulum* is divided into two sublayers, the one forming the top, the other forming the bottom of the hollow keel.

The structure of the septa of *Saghalinites* and *Scaphites* (*Discoscaphites*) is also in good agreement with other ammonites described: they are nacreous throughout or, at most, have only an incipient distal prismatic layer. Only the first true septum differs significantly in being nacreous and not prismatic.

The structure of the shell wall of *Hypophylloceras* (*Neophylloceras*) differs from that of other ammonites so far described in having an extraordinarily thin nacrous layer and a thick outer prismatic layer built up of many sublayers in late ontogenetic stages. The prisms of the outer prismatic layer are quasi-spherulitic, giving the layer a remarkable similarity to the prismatic portion of the prismatic-spherulitic layer of living *Nautilus* (Erben, Flajs & Siehl, 1969, pl. 2, fig. 1; Wise, 1969, fig. 13). However, there is no layer similar to the outer spherulitic portion of the *Nautilus* shell. It also shows close resemblance to the inner prismatic layer of *Aturia aturia* (Erben, Flajs & Siehl, 1969, pl. 2, fig. 6). The pigmented intervals between the undulating nacreous layer and the outer prismatic layer are also characteristic of *Hypophylloceras* (*Neophylloceras*). The fine ribbing pattern of many phylloceratids suggests that the special structure of the shell wall of this form is also developed in other genera of the suborder Phylloceratina.

For comparison the pigment of amaltheids was studied. The pigment in the shell of *Amaltheus* was described as "Punkstreifen der äusseren Schale" by Quenstedt (1858, p. 166, pl. 20, fig. 1; see also Quenstedt, 1851, p. 204). In *Pleuroceras solaris* (Phillips), here investigated, the dark points are connected with the outer part of the nacreous layer, but do not appear to influence the structure. The yellowish pigment of the *Nautilus* shell is connected with the outer spherulitic portion and has likewise no influence on the structure.

A functional interpretation of the shell structure of the phylloceratids is hazardous but tempting. The strength of the shell is likely to have been less than that of lytoceratid shells because of the dominance of prismatic layers. The extremely complex phylloid sutures, supporting the shell, may have developed as compensation for this weakness. The pigmentation is considered to be of importance as camouflage pattern, like the pigment pattern of living *Nautilus* (Coven, Gertman & Wiggett, 1973). It may compensate for the missing shell sculpture, which is also thought to have provided camouflage in ammonites (Coven, Gertman & Wiggett, 1973). The camouflage pattern would have been especially functional in the early part of the third ontogenetic stage, where the cavities of the shell are relatively dominant and the outer quasi-spherulitic layer is still thin. The wall structure as seen in relation to the shell proper when exposed to incident light would evidently have functioned as a lens system, where the quasi-spherulitic layer would cause a concentration of the light predominantly in the pigmented fillings the inner side of which are equipped with a light reflecting thin nacreous layer. Many authors stress that phylloceratid ammonites (together with some lytoceratid ammonites) had a mode of life different from other ammonites, being connected to deep-water facies (especially in the Tethyan realm). Ziegler (1967, p. 452) points out that they might be nektic, but connected to deep-water areas.

It is not known if the prismatic layer of the septa of *Hypophylloceras* (*Neophylloceras*) is developed in other phylloceratids.

The siphuncle of *Saghalinites* and *Scaphites* (*Discoscaphites*) is simple, being constructed of connecting rings, joined together at the septal necks in the annular ridges. The connecting rings are possibly calcified, but it must still be assumed that secretion of gas and liquid through the walls was possible as in living *Nautilus,* the connecting rings of which are also calcified (see Mutvei, 1972b). There seems to be no special calcification of the annular ridges.

Contrary to *Saghalinites* and *Scaphites* (*Discoscaphites*), *Hypophylloceras* (*Neophylloceras*) has developed long, calcified nacreous collars (here called false septal necks) in connection with the septal necks. Also in this genus the connecting rings are joined together at the annular ridges.

Böhmers (1936) and Miller & Unklesbay (1943) described the siphuncle of many Palaeozoic ammonites in detail, but only scattered information has been published on the character of the siphuncle of Mesozoic ammonites, e.g. by Grandjean (1910), Trueman (1920), Mutvei (1967), Drushits & Khiami (1970), Westermann (1971) and Mutvei & Reyment (1973).

It appears from Miller & Unklesbay's work that the characteristics of the siphuncle are highly variable in Palaeozoic ammonites. Most of the prochoanitic forms seem to develop auxiliary deposits on the inside of the septal necks. In a few forms these auxiliary deposits seem to consist of simple rings, but in others they are relatively complex and are composed of several parts. The connecting rings are attached to the auxiliary deposits where they are preserved. In some cases the connecting rings are continuous through the septal necks, but in other cases they are shown to be interrupted. In some forms, for example *Neodimorphoceras texanum* it is especially indicated that the long auxiliary collar is calcified, and the structure of this deposit seems to be very similar to the false septal neck of *Hypophylloceras* (*Neophylloceras*) here described. In some cases the connecting rings are thickened at the necks, for example in *Medlicottia burckhardti* (Miller & Unklesbay, 1943, fig. 6 E), *Stacheoceras toumanskyae* (figs 9 H–L) and in *Perrinites hilli* (fig. 9 N). These thickenings may be compared to the annular ridges of the connecting rings of our forms.

In Mesozoic ammonites Mutvei (1967) described annular calcareous deposits at the septal necks in *Promicroceras* sp. at the junction of the connecting rings, and Drushits & Khiami (1970) figured the siphuncle of a *Zurcherella* species, also showing an auxiliary calcification at the septal necks. Mutvei & Reyment (1973) discussed the growth and function of the siphuncle of prochoanitic ammonites and compared the construction to the very different organization of the siphuncle of living Nautilus, but add no new data on the morphology of the ammonite siphuncle.

Descriptions of Mesozoic phylloceratid ammonites by Grandjean (1910), Böhmers (1936), and by Drushits & Khiami (1970) (*Salfeldiella, Ptychophylloceras, Phyllopachyceras*) show that all these forms have long calcified collars similar to the false septal necks of *Hypophylloceras* (*Neophylloceras*) here described. The distal extension of the prochoanitic septa formed by the false septal necks must have strengthened the proximal part of the connecting rings considerably.

Both the morphology of the siphuncle and the structure of the shell wall and septa of phylloceratid ammonites accentuate the difference to the lytoceratid stock and may prove to be useful characters in addition to the suture line, in phylogenetic studies.

Genus ***Groenlandibelus*** Jeletzky, 1965

The genus *Groenlandibelus* Jeletzky is known only from the Maastrichtian of West Greenland. The genus is characterized by an unique combination of morphological features, which has caused much discussion about its taxonomic position.

Birkelund (1956) placed it in the genus *Belemnoteuthis* because of the great similarity of the guard to representatives of that genus. Jeletzky (1965) placed it in a new genus, *Groenlandibelus,* within a new suborder, Diplobelina, with the single family Diplobelidae Naef, 1926. According to Jeletzky, Diplobelina differ from Belemnitina and Belemnopsina in their extremely narrow, anteriorly sharpened proostracum, more deeply incised suture line with a dorsal saddle and ventral lobe, and a ventralward incurved axis of the phragmocone. Finally, in 1966, Jeletzky referred the genus *Groenlandibelus,* together with the poorly known genus *Naefia,* to the new family Groenlandibelidae on the basis of the morphology of the phragmocone. The family was referred to the order Sepiida and the genus was thus removed from Belemnitida.

The morphology of the genus is extensively discussed by Birkelund (1956, pp. 17–26) and by Jeletzky (1966, pp. 92–103). A short description will therefore suffice here, with, in addition, a review of the controversial questions concerning its taxonomic position illustrated by new information on the ultrastructures of the phragmocone and guard.

Groenlandibelus rosenkrantzi (Birkelund, 1956)

Pl. 13, figs 1–5; pl. 14, figs 1–5.

1956 *Belemnoteuthis rosenkrantzi* Birkelund, p. 17, pl. 1, figs 9a–g.
1965 *Groenlandibelus rosenkrantzi* (Birkelund): Jeletzky, p. 76.
1966 *Groenlandibelus rosenkrantzi* (Birkelund): Jeletzky, p. 92, pl. 18, figs 3A–D; pl. 20, figs 1A–D; pl. 21, figs 1A–D; pl. 22, figs 1A–F; pl. 23, figs 1A–E.

Material.

4 specimens, 2 of which have been prepared for electron microscopical studies.

Description.

The small guard of the longitudinally split type specimen (Birkelund, 1956, pl. 1, figs 9a–b) consists of prismatic crystals of light-brown calcite, radiating from the apical line. In juvenile specimens the guard covers the phragmocone as a thin investment and no apical line can be seen (Jeletzky, 1966, pl. 18, figs 3 A–D; pl. 20, fig. 1 A).

The ultrastructures are shown in pl. 13, figs 1–5. The primordial guard has a very fine prismatic structure with distinct growth-lamellae. The guard proper consists of more regular coarse prisms. The thin investment covering the phragmocone has a similar coarse prismatic structure.

The phragmocone of *G. rosenkrantzi* has an apical angle of 12°–15° and the chambers a length of 0.24–0.47 of the width. The sutures are slightly oblique in relation to the longitudinal axes of the phragmocone, the dorsal part being situated more adorally than the ventral part. On the ventral side the sutures form a small narrow lobe and on the dorsal side a wide, low saddle. The inner side of the phragmocone wall is slightly constricted at the sutures and swollen in between. The outer side of the phragmocone wall is not or only slightly reflected by these undulations, because of corresponding variation in thickness of the wall. The siphuncle has a marginal position in all chambers (pl. 14, fig. 3). It is wide, 20–28 $^0/_0$ of the width of the chambers in ventro-dorsal view and a little less in lateral view. It is asymmetrical in lateral view (JELETZKY, 1966, pl. 20, fig. 1 A), the connecting rings being ventrally expanded between the septa. Dorsally the connecting rings are proximally connected to the distal end of the septal necks and distally the next connecting ring surrounds the short neck (JELETZKY, 1966, pl. 20, fig. 1 A; pl. 21, figs 1 A, 1 D). Ventrally the first connecting ring is proximally attached to the tip of the neck, while the next one lines up with the distal surface of the septum, only becoming free at the mural end of the septum (JELETZKY, 1966, pl. 21, fig. 1 D). Early connecting rings, to the 5th septum, are constructed in a similar way. In younger septa, however, the connecting ring adheres not only to the distal surface of the septum, but also to the inner surface of the phragmocone (JELETZKY, 1966, pl. 21, fig. 1 A; pl. 22, fig. 1 A; pl. 23, figs 1 D–F) (pl. 14, figs 3–4). The septa are characteristic in having achoanitic or slightly retrochoanitic club-shaped necks (JELETZKY, 1966, pl. 20, figs 1 A, 1 C; pl. 21, figs 1 A, 1 B, 1 D; pl. 22, figs 1 A, 1 E, 1 F; pl. 23, fig. 1 E) (pl. 14, fig. 3).

Orally directed, short, blunt protuberances may be developed on the distal ends of some later septa (JELETZKY, 1966, pl. 20, fig. 1 A; pl. 22, fig. 1 D; pl. 23, fig. 1 D). The mural parts of the septa are strongly thickened (pl. 14, figs 1–2). They form a long forward flange ($^1/_4$–$^1/_5$ the length of the corresponding chamber) and a considerably shorter backward flange. A flap of the phragmocone wall covers the ventral side of the forward flange (JELETZKY, 1966, pl. 22, fig. 1 C; pl. 23, fig. 1 A) (pl. 14, fig. 1).

The ultrastructure of the phragmocone wall is coarsely prismatic and very similar to the guard (pl. 13, fig. 5). It is distinctly unilayered, as pointed out by JELETZKY (1966).

Although the structure of the septa is always slightly altered, the best preserved specimens bear a clear resemblance to nacreous structure with stacked crystals (pl. 14, fig. 5). The calcified septa have the same structure throughout. The septal necks are always structureless, probably because the nacreous structure was secondarily altered. The forward flange of the septum is formed as a direct continuation of the nacreous septum, while the backward flange is an auxiliary deposit built up of more irregular, possibly still nacreous, material (pl. 14, fig. 2). The boundary between the septa and the phragmocone wall is sharp.

The siphuncular tube is poorly preserved in the specimens investigated except in the juvenile specimen described by JELETZKY (1966), which shows the presence of a caecum and a prosiphon (JELETZKY, 1966, pl. 20, figs 1 A, 1 B; pl. 21, fig. 1 C).

According to Jeletzky's investigations the connecting rings appear to consist of two layers, a relatively thick inner layer and a thin outer layer. The two layers are sharply delimited and both are believed to be largely or entirely organic.

The proostracum consists of a very narrow median field limited by somewhat wider hyperbolar zones (Birkelund, 1956, pl. 1, figs 9a–c, g).

Groenlandibelus sp.

Pl. 13, fig. 6; pl. 15, figs 1–3, 6.

1956 *Belemnoteuthis*? sp. Birkelund, p. 23, pl. 1, figs 10a–d, 11, 12a–b, 13a–b.

Material.

9 specimens, 4 of which have been prepared for electron microscopical studies.

Description.

Birkelund (1956) described some phragmocones, found together with *Groenlandibelus rosenkrantzi,* under the name *Belemnoteuthis?* sp., because they differed from *G. rosenkrantzi* in having, e.g. a larger alveolar angle (20°–24° in dorsal view) and generally a smaller ratio of length to width of the chambers (0.21–0.28). Additional material shows that the siphuncular tube has a less marginal position and that distinct retrochoanitic septal necks are developed in younger parts of the phragmocone (Birkelund, 1956, pl. 1, fig. 11) (pl. 15, fig. 3). The less marginal position of the siphuncle probably also implies that the ventral part of the connecting rings could hardly have been attached to the phragmocone wall, as it is in *G. rosenkrantzi.* In other characters the phragmocones are similar to the phragmocone of *Groenlandibelus*: a slightly ventrally curved shape; an undulating phragmocone wall being slightly constricted at the sutures and swollen in between; oblique suture-lines, with a ventral lobe and a dorsal saddle; an apparently similar proostracum; and similar structures of both the phragmocone wall and the septa (pl. 13, fig. 6; pl. 15, figs 1–2, 6).

The similarity in a number of characters which are rather unique for *Groenlandibelus* implies that these phragmocones belong to the same genus. It may be interpreted as a new species or as a sexual dimorph of *G. rosenkrantzi.*

Evaluation of the taxonomic position of Groenlandibelus

Jeletzky (1966, p. 103) emphasized the presence of a number of diagnostic characters in *Groenlandibelus rosenkrantzi* which were absent in all specimens of Belemnitida and Aulacocerida examined by him. These were the presence of a caecum and prosiphon; marked contraction and expansion of early portions of the phragmocone wall; an unusually wide siphuncle; unilayered appearance of the phragmocone wall and septa; extreme marginal position of the siphuncle already in early segments; and marked asymmetry. A number of other characters are unique for *Groenlandibelus rosenkrantzi,* such as: strong thickening of distal and mural ends of the dorsal septa;

strong thickening of the ventral septa; inclusion of adorally directed flanges of the septa in the phragmocone wall (implying that the septa were formed simultaneously with the phragmocone wall); general achoanitic appearance of septal necks; adherence of oral ends of connecting rings to apical surfaces of the septa rather than to tips of their necks; and lining of adoral surfaces of ventral septa by thickened connecting rings which results in strong reduction of ventral parts of the chambers. The great similarity of the guard of *Groenlandibelus rosenkrantzi* to that of *Belemnoteuthis* and the great similarity of the proostracum to that of diplobelid belemnites are considered to be due to homoemorphy.

A closer comparison of the ultrastructures of the guard of *Groenlandibelus* with guards of *Belemnitida* accentuates the similarity. For comparison, the ultrastructures of a *Belemnitella* is shown in pl. 15, fig. 4. The structure of the primordial guard is also similar to that of Belemnitida (compare for example *Somalibelus somaliensis* JELETZKY, 1972, pl. 36, fig. 1 d with pl. 13, fig. 3 in this work). The lamellar ultrastructures of Sepiida (*Sepia* and *Spirulirostra*), on the other hand, are distinctly different.

JELETZKY stressed that the unilayered appearance of the phragmocone wall and septa are diagnostic sepiid characters. The phragmocone wall is certainly more similar to the internal "semi-prismatic" layer of the *Spirula* wall (MUTVEI, 1964 a) than to the phragmocone wall of Belemnitida, which always seems to consist of more than one layer. However, there are many different opinions as to the exact number of layers in the phragmocone wall of Belemnitida and the structure of these layers (summarized by BARSKOV, 1972). In more recent works MUTVEI (1964 b) recognized two calcified layers (an inner prismatic layer and an outer nacreous layer) and two non-calcified layers in the phragmocone wall of *Megateuthis*. JELETZKY (1966) distinguished three layers in the same genus: relatively thick, well-calcified inner and outer layers and a much thinner, more or less "clouded" intermediate layer, which was sometimes not clearly discernible. On the basis of scanning electron microscopy SPAETH (1971) and BARSKOV (1972) distinguished two layers in the phragmocone wall of *Neohibolites, Mesohibolites, Pachyteuthis* and *Conobelus*: an inner prsimatic layer and an outer nacreous layer.

We have investigated a phragmocone of *Belemnitella* and have found it also to consist of two layers. However, in this case the outer layer unexpectedly seems to be prismatic, while there is no discernible structure preserved in the inner layer (pl. 15, fig. 4). While this appears to contradict the findings of SPAETH (1971) and BARSKOV (1972), it should be emphasized that our observations are based on a single specimen.

A comparison of the septa of *Groenlandibelus* with septa of Sepiida and Belemnitida does not confirm the sepiid character of the *Groenlandibelus* septa.

The shiny lustre of the septa of *Spirula* is due to a fine lamellar structure (pl. 14, fig. 6) very different from real nacre, as the tabular, polygonal, aragonite crystals are entirely absent in the horizontal mineral lamellae. MUTVEI (1970, p. 49) referred this structure to nacre "type 2" and ERBEN (1972 a, p. 28) named it lamello-fibrilar structure.

The structure of the septa of Belemnitida is poorly known. Grandjean (1910), Christensen (1925) and Müller-Stoll (1936) separated five to seven different layers, some of them doubled, as they occur on the distal, as well as on the proximal side of each septum. Jeletzky (1966) recognized only two principal layers of the belemnitid septa: an inner, well-calcified layer and an outer one, which surrounds the inner layer and is thus divided into a distal and a proximal division, except at mural ends and in early septal necks. Mutvei (1971, pl. 1, fig. 3) figured a septum of *Megateuthis gigantea*, which seems to show a nacreous structure throughout. Mutvei referred the nacre to the same structural type as that of recent *Spirula* (type 2).

We investigated septa of *Belemnitella bulbosa* (pl. 15, fig. 5). Neither the *Megateuthis* septum nor the *Belemnitella* septum show well preserved structures. The *Megateuthis* septum shows a striation perpendicular to the surface and the *Belemnitella* septum shows irregular crystals arranged in stacks. The structure of the *Belemnitella* septum may be similar to that of *Groenlandibelus* septa, which are better preserved and is clearly reminiscent of stacked nacre with tabular polygonal crystals.

The calcified septum of *Megateuthis, Belemnitella* and *Groenlandibelus* shows the same structure throughout. The outer septal layer described by Jeletzky (1966) is most likely present in our material of *Belemnitella* and *Groenlandibelus* (pl. 15, figs 6–7). Its structure is uncertain but it may be organic.

In conclusion it should be stressed that first and foremost the unilayered phragmocone wall and the presence of a caecum and a prosiphon are strong evidence for referring *Groenlandibelus* to Sepiida, but that the structure of the rostrum and septa of this genus, together with the morpholgy of its proostracum, are unknown in Sepiida. The taxonomic position of this apparently aberrant off-shoot is thus still uncertain.

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Indleveret til Selskabet den 1. november 1973.
Færdig fra trykkeriet den 22. juni 1974.

PLATES

Abbreviations.

Ammonoidea

A	Annular ridge
C	Connecting ring
CA	Cavities in rib-intervals (*Hypophylloceras*)
CAE	Caecum
CAL	Calcareous connecting ring
F	Flange
FN	False septal neck (*Hypophylloceras*)
IP	Inner prismatic layer of third ontogenetic stage
J	Junction between two connecting rings
N	Septal neck
NA	Nacreous layer of shell wall
O	Organic tube of connecting ring
OP	Outer prismatic layer of third ontogenetic stage
P1	Prismatic layer of first ontogenetic stage
P2	Prismatic layer of second ontogenetic stage
PS	Proseptum
PSE	Prismatic layer of septum (*Hypophylloceras*)
QP	Quasi-spherulitic outer prismatic layer of third ontogenetic stage (*Hypophylloceras*)
SE	Septum

Arrows indicate adoral direction

Coleoidea

C	Connecting ring
G	Guard
PG	Primordial guard
PH	Phragmocone wall
S	Septum

The numbers prefixed by the letters "MMH" refer to the type collection of the Mineralogical Museum of the University of Copenhagen.

All figures are SEM micrographs unless otherwise indicated.

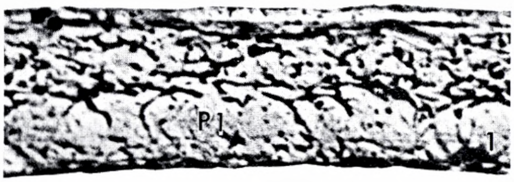
PLATE 1

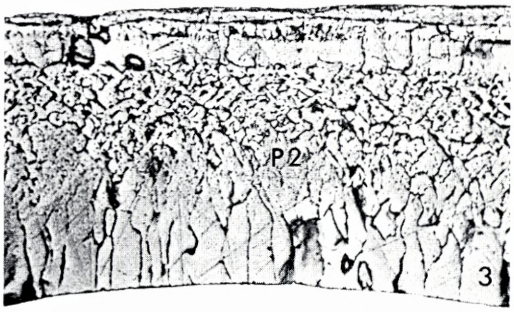
Saghalinites wrighti BIRKELUND. Longitudinal dorso-ventral sections.

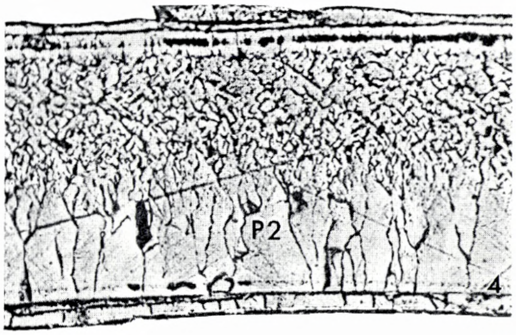
1. Early part of protoconch. × 4310. MMH 12989.
2. Late part of protoconch. × 2760. MMH 12989.
3. Early part of 1st whorl. × 1725. MMH 12989.
4. $^1/_2$ whorl distal of proseptum. × 1725. MMH 12989.
5. 1 whorl distal of second change in growth. × 985. MMH 12990.
6. 2 whorls distal of second change in growth. × 860. MMH 12989.

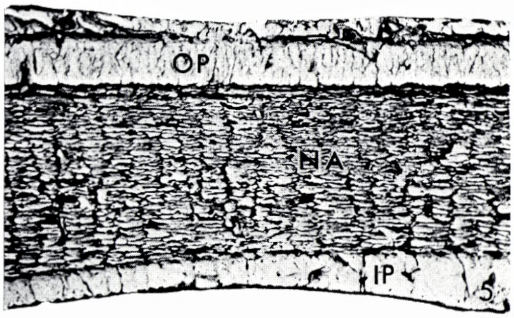
7–8. Shell wall with obliquely deformed prisms in the inner prismatic layer. 7: × 430; 8: × 1740. MMH 12989.

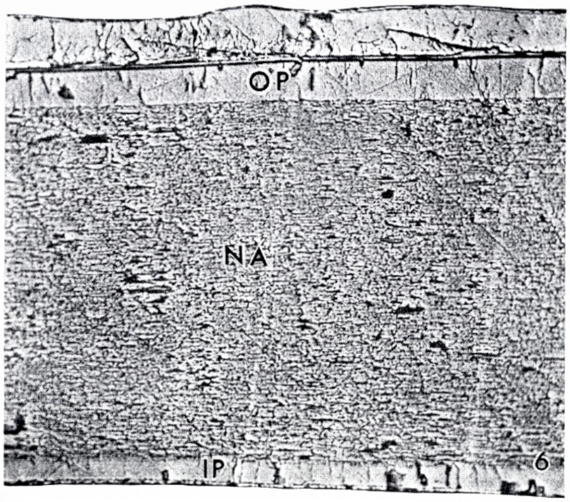
PLATE 1











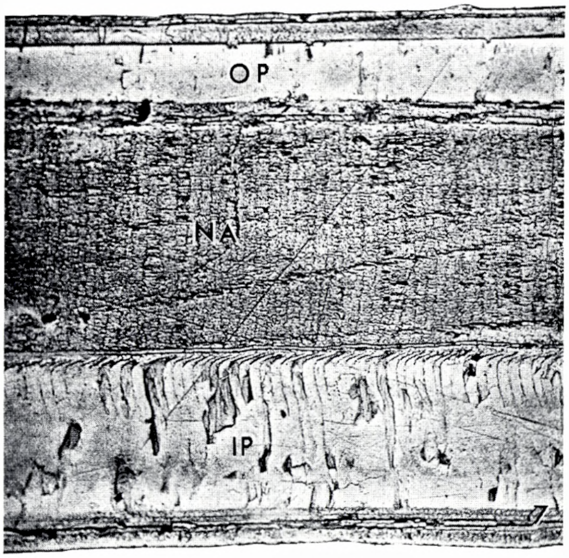


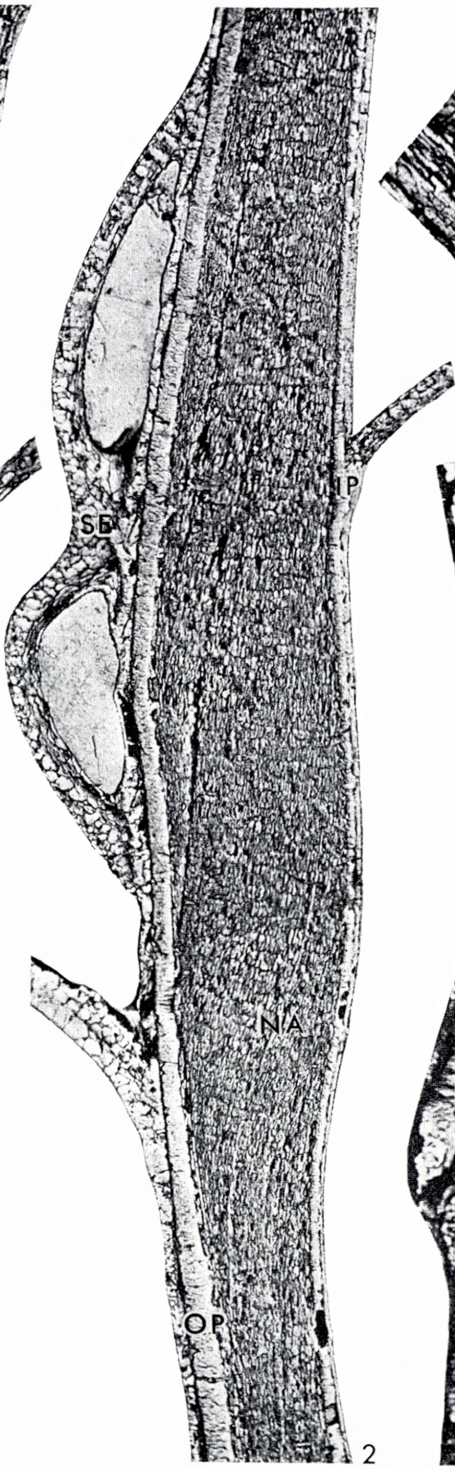
PLATE 2

Saghalinites wrighti BIRKELUND.

1. Second change in growth. Longitudinal dorso-ventral section. × 650. MMH 12990.
2. Third varix. Longitudinal dorso-ventral section. × 500. MMH 12990.
3. Umbilical edge. The outer prismatic layer and the nacreous layer wedge out dorsally. Transversal dorso-ventral section. × 490. MMH 12991.

4–5. Flange, proseptum and early part of protoconch (P1). Longitudinal dorso-ventral sections. 4: × 1315. MMH 12990. 5: × 1430. MMH 12989.

1



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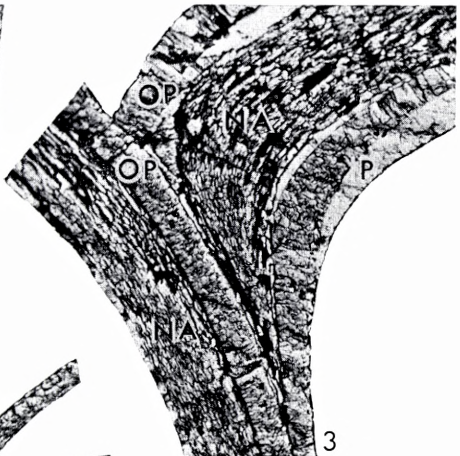

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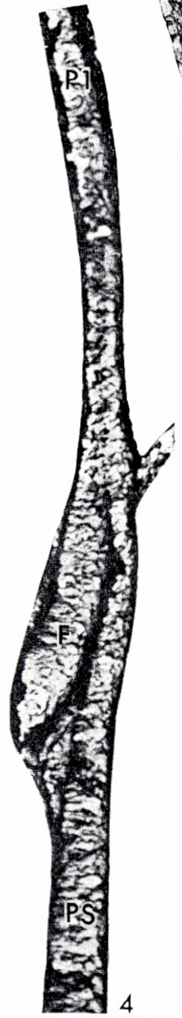


4

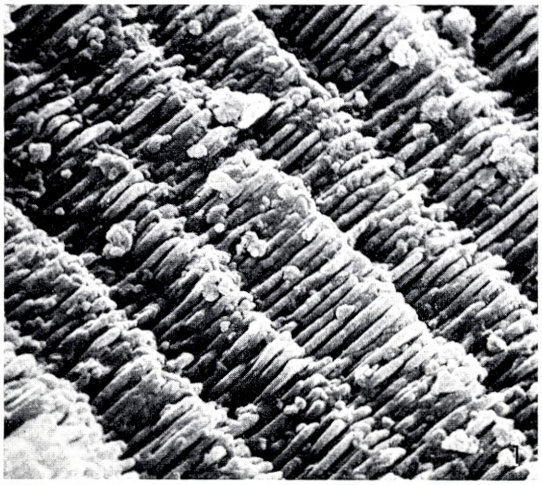
5

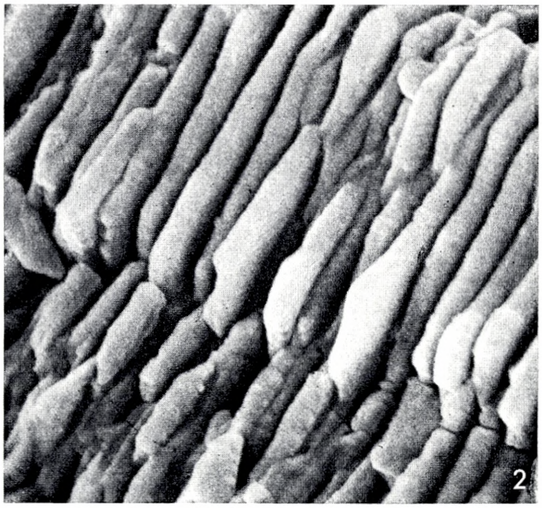
PLATE 3

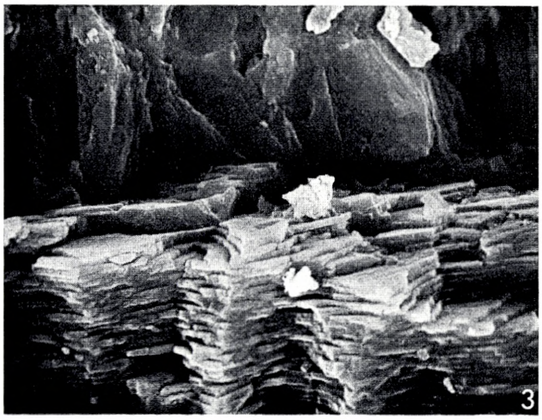
Saghalinites wrighti BIRKELUND.

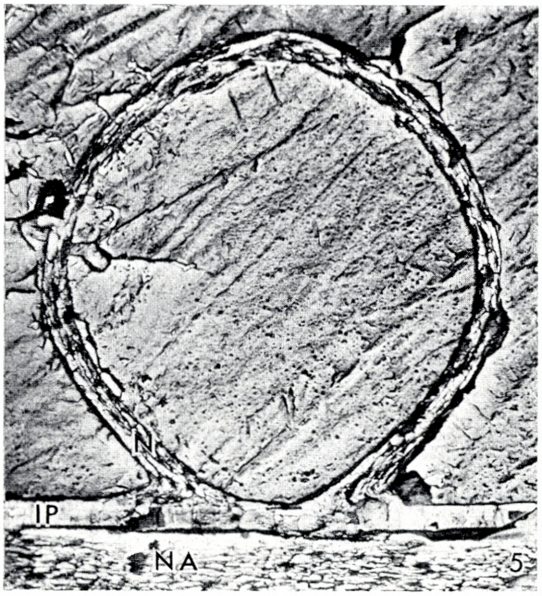
1–2. Fracture surfaces of stacked nacre of the shell wall. 1: × 3750. 2: × 10830. MMH 12992.
3. Fracture surface of the inner prismatic layer and the nacreous layer of the shell wall. × 2300. MMH 12992.
4. Inner surface of the organic tube of a connecting ring. × 4640. MMH 12993.
5. Transversal dorso-ventral section of septal neck in close connection with the inner prismatic layer of the shell wall. × 1480. MMH 12991.
6. Late septum showing incipient prismatic layer on distal side. Longitudinal dorso-ventral section. × 985. MMH 12990.

PLATE 3









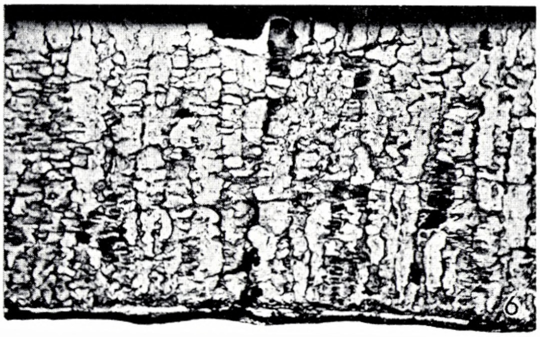


PLATE 4

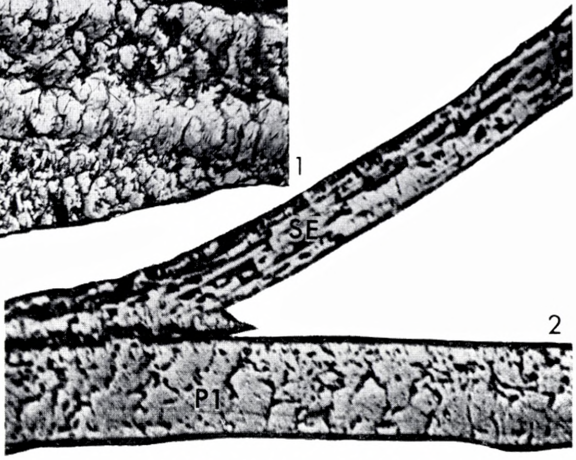
Saghalinites wrighti BIRKELUND. Longitudinal dorso-ventral sections.

1. Ventral part of proseptum and its connection with the prismatic layer of the second ontogenetic stage. × 1275. MMH 12990.
2. First true septum, showing nacreous structure, and its contact with the prismatic shell wall of first ontogenetic stage. × 3255. MMH 12989.

3–5. Connecting ring consisting of an inner organic tube and an outer calcareous tube. In 4 the organic tube has been slightly removed from the calcareous one. 3–4: × 820; 5: × 1630. MMH 12993.

6. Caecum and siphuncle of the earliest whorl. × 190. MMH 12989.
7. Connecting ring showing primary (?) calcareous tube with prismatic structure. × 785. MMH 12993.


P1
P2
PS
1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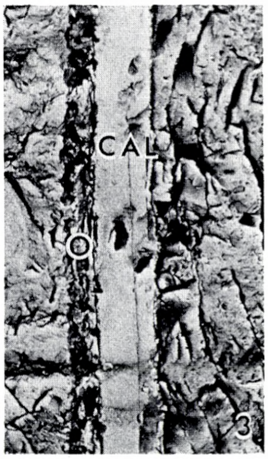
P1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O
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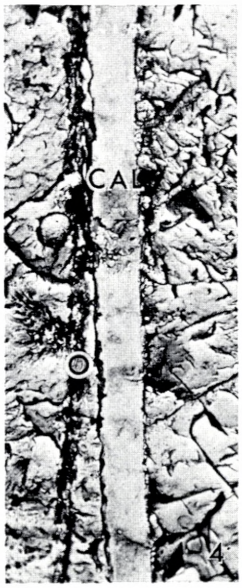
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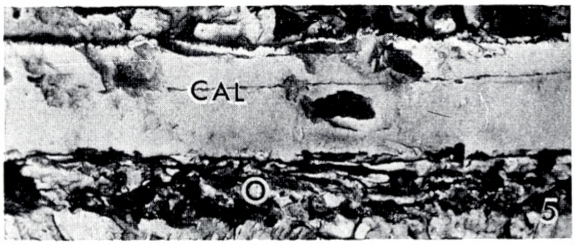

CAL
O
5


CAE
6


CAL
7

PLATE 5

Saghalinites wrighti BIRKELUND.

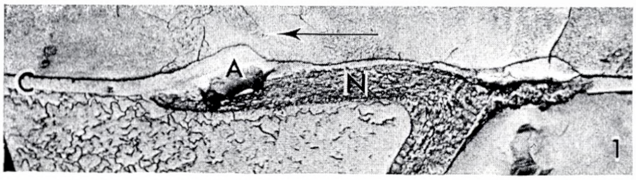
1. Septal neck and connecting rings. Longitudinal dorso-ventral section. × 335. MMH 12989.

2–3. Septal neck and junction between two connecting rings. Longitudinal dorso-ventral sections. 2: × 365; 3: × 335. MMH 12989.

4. Connection between septal neck and inner prismatic layer of shell wall. Transversal dorso-ventral section. × 5920. MMH 12991.

5. Septal neck and junction between two connecting rings. Longitudinal dorso-ventral section. × 495. MMH 12990.

PLATE 5



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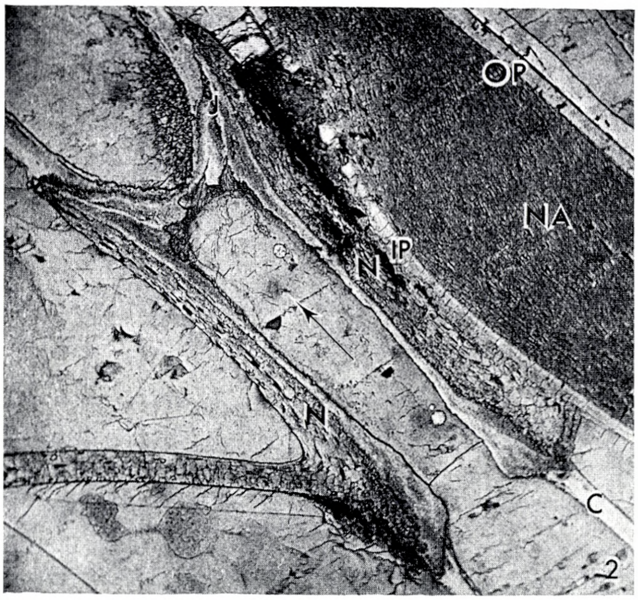

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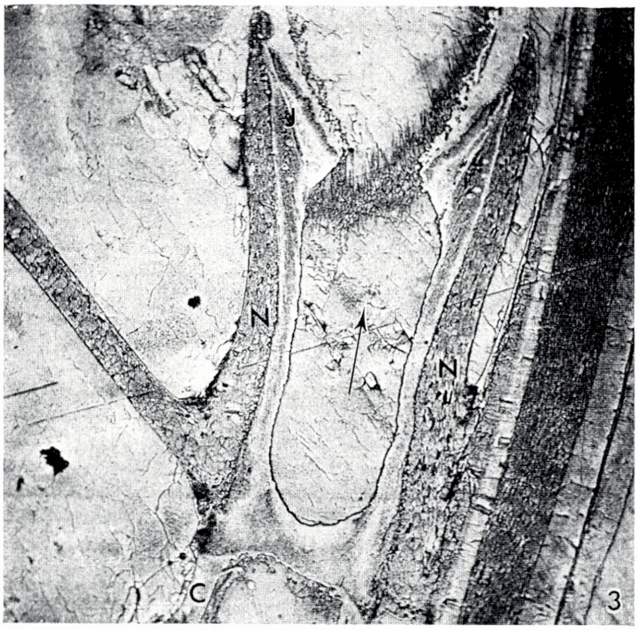

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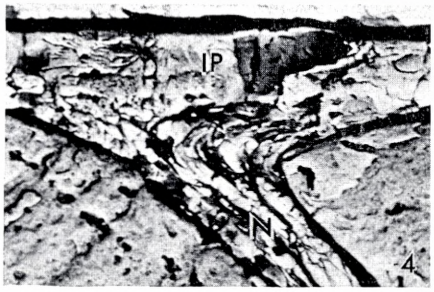


4

5

PLATE 6

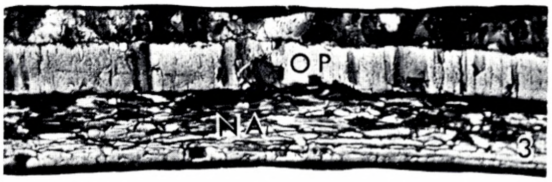
Scaphites (*Discoscaphites*) sp. Longitudinal dorso-ventral sections.

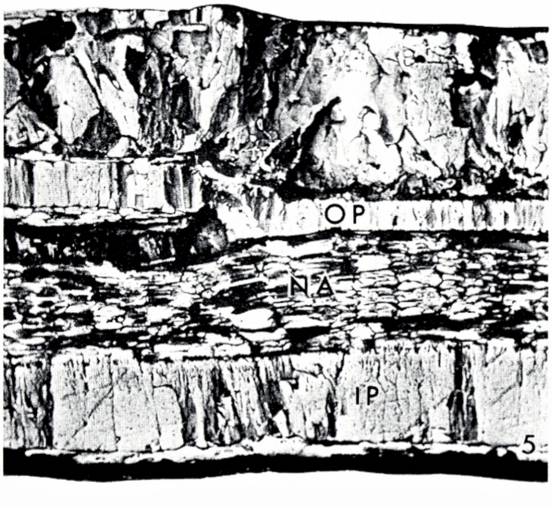
1. Boundary between first and second ontogenetic stages. × 1400. MMH 12995.
2. Early part of first whorl. × 1560. MMH 12996.
3. One whorl distal of the second change in growth. × 1235. MMH 12996.
4. $1^1/_3$ whorl distal of the second change in growth. × 1250. MMH 12996.
5. 2 whorls distal of the second change in growth. × 1250. MMH 12996.
6. Late part of third growth stage. × 1340. MMH 12996.

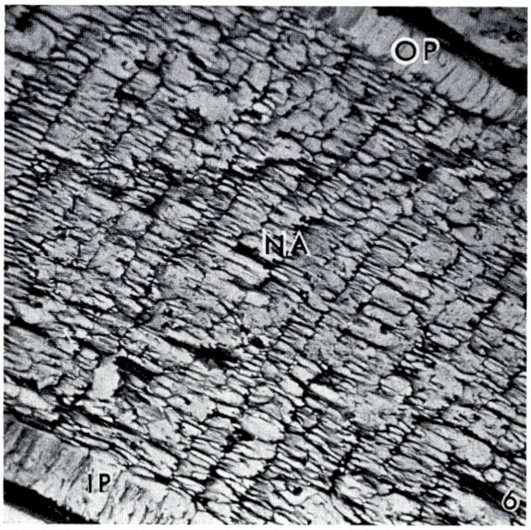
7–8. Late part of third growth stage. Notice the obliquely oriented prisms in the outer prismatic layer. 7: × 385; 8: × 1540. MMH 12996.

PLATE 6

1







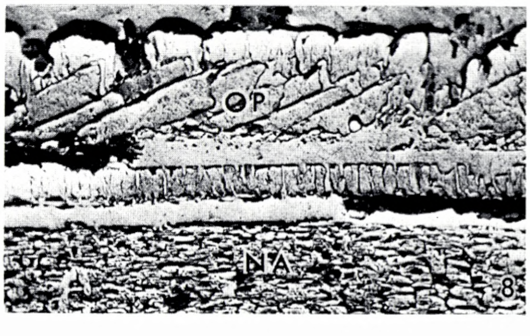
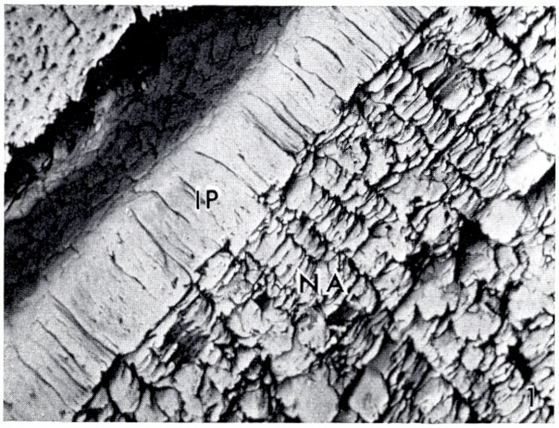


PLATE 7

Scaphites (*Discoscaphites*) sp. Longitudinal dorso-ventral sections.

1–2. Late whorl showing the nacreous layer and the inner prismatic layer. Note the polygonal cross section of the prisms. 1: × 1480; 2: × 3695. MMH 12995.
3. Ribbed ventral wall and septa. × 78. MMH 12996.
4. Septum in first whorl distal of the second change in growth. × 2780. MMH 12996.
5. Late septum. × 905. MMH 12995.
6–7. Septal neck and siphuncle showing the annular ridge. × 180. MMH 12995.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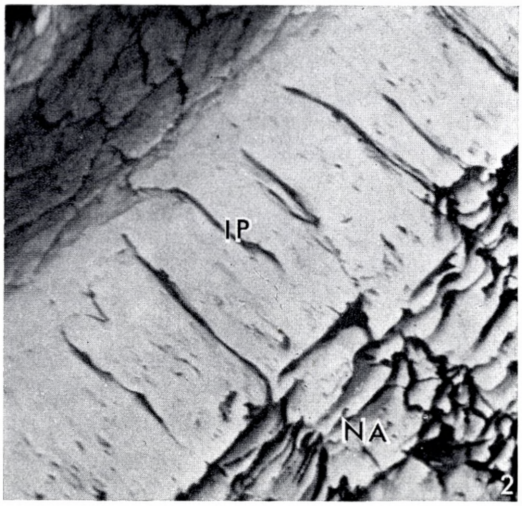
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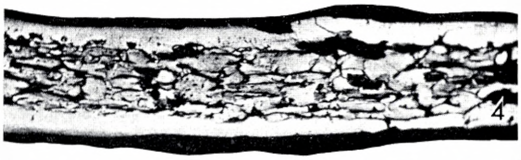
SE
SE
3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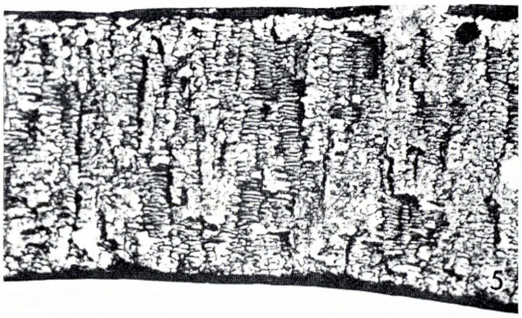
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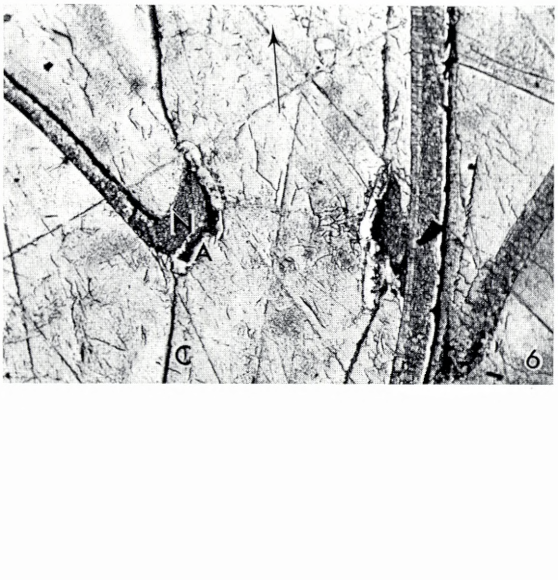

N
A
C
6

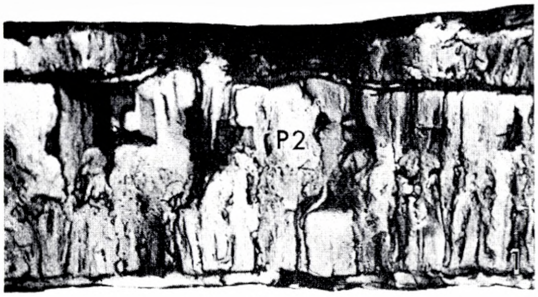

C
N
A
7

PLATE 8

Hypophylloceras (*Neophylloceras*) *groenlandicum* BIRKELUND. Longitudinal dorso-ventral sections.

1. 1st whorl. × 1985. MMH 12998.
2. 1st whorl distal of the second change in growth. × 500. MMH 12999.
3–4. 2 whorls distal of the second change in growth. 3: × 190; 4: × 475. MMH 12999.
5. $2^1/_2$ whorl distal of the second change in growth. × 195. MMH 12999.
6. Late whorl. × 195. MMH 12999.
7–8. Inner part of shell wall of late whorl. Note the secondary fillings in the cavities. 7: × 215; 8: × 490. MMH 12998.

PLATE 8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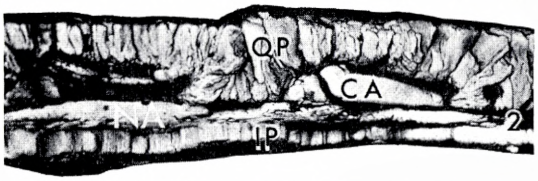
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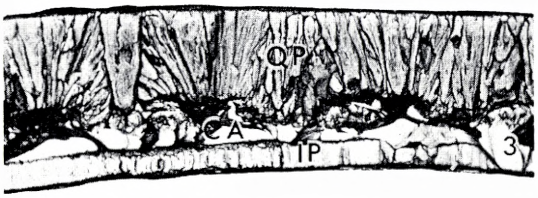
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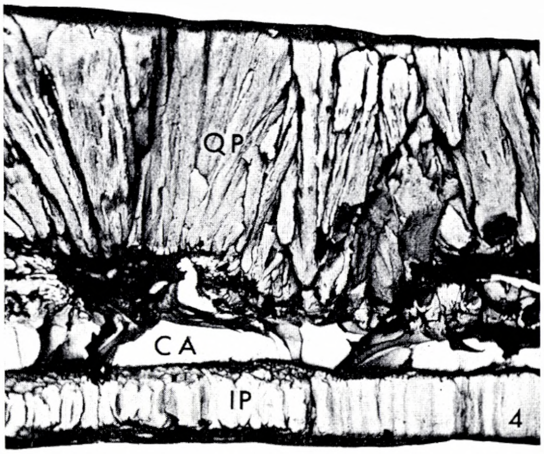
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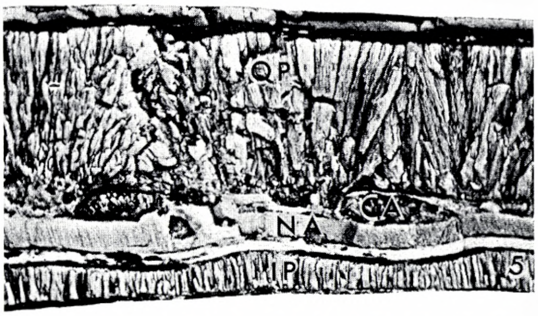
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QP
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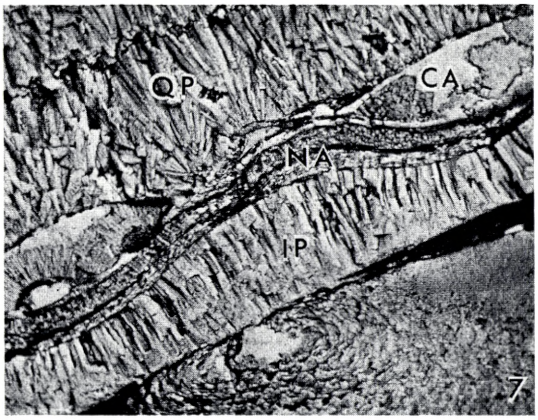
CA
IP
6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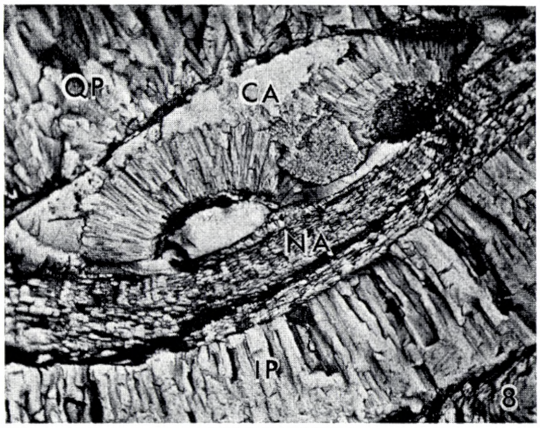
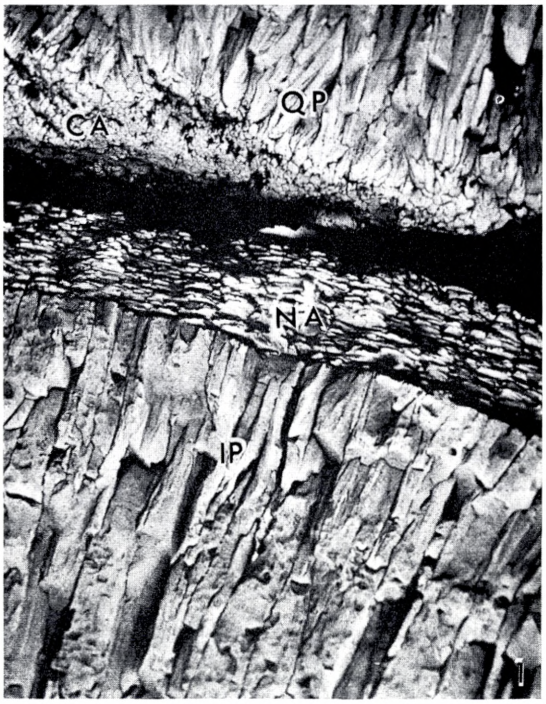

QP
CA
NA
IP
8

PLATE 9

Hypophylloceras (*Neophylloceras*) *groenlandicum* BIRKELUND. Longitudinal dorso-ventral sections.

1. Detail of shell wall showing part of inner prismatic layer, nacreous layer and part of quasi-spherulitic outer prismatic layer at the edge of a secondarily filled cavity. × 1125. MMH 12998.
2. Inner part of shell wall and adjacent septum. Note the prismatic layer on the distal side of the septum. × 555. MMH 12998.
3. Shell wall of late whorl, showing inner part, only, of the quasi-spherulitic outer prismatic layer. × 555. MMH 12998.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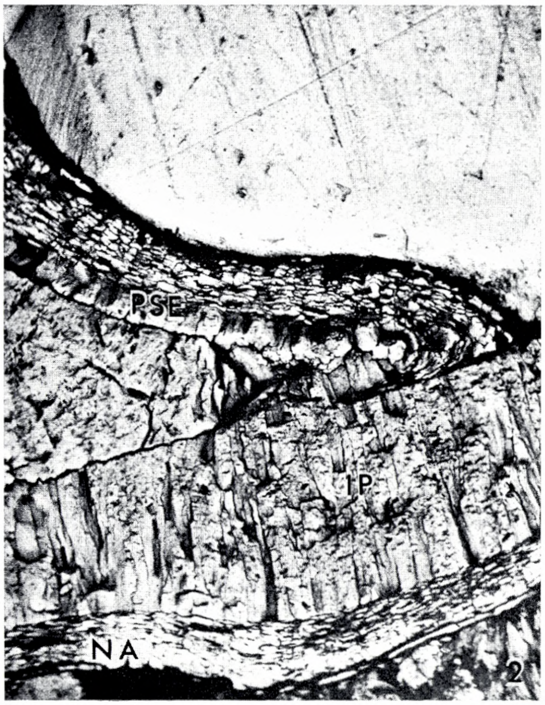

PSE
IP
NA
2


QP
NA
CA
IP
3

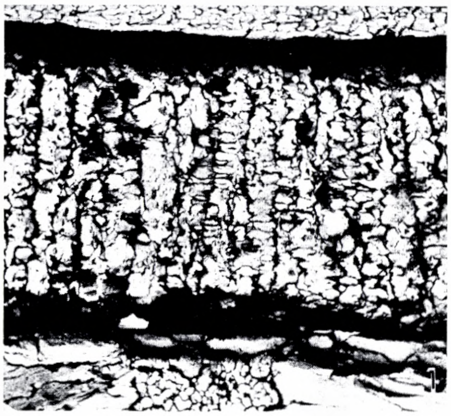
Plate 10

Hypophylloceras (*Neophylloceras*) *groenlandicum* Birkelund. Longitudinal dorso-ventral sections of septa.

1. Septum $2^1/_4$ whorl distal of second change in growth. × 960. MMH 12999.
2. Septum $2^1/_2$ whorl distal of second change in growth. Note the incipient prismatic layer. × 1010. MMH 12999.
3. Septum $2^3/_4$ whorl distal of second change in growth. × 1020. MMH 12999.
4. Late septum. × 100. MMH 12999.

5–6. Details of the prismatic layer of the septum shown in fig. 4. 5: × 510; 6: × 985. MMH 12999.

PLATE 10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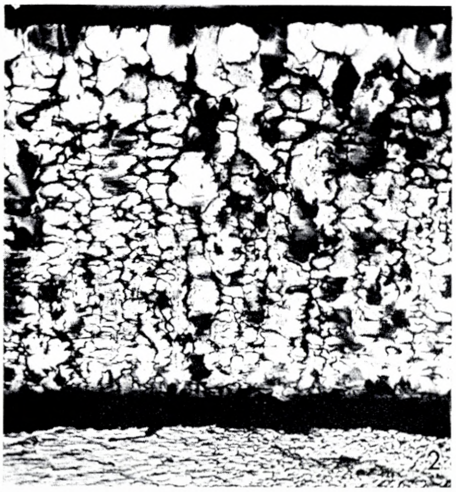
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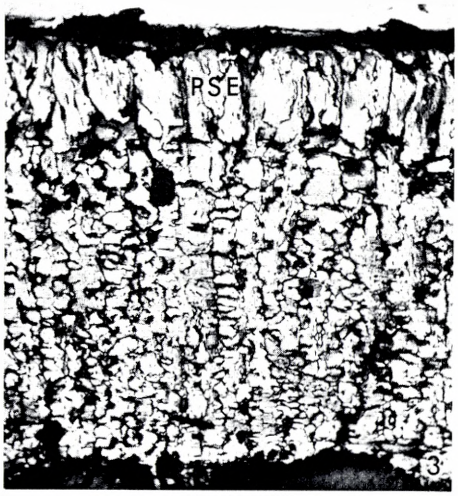

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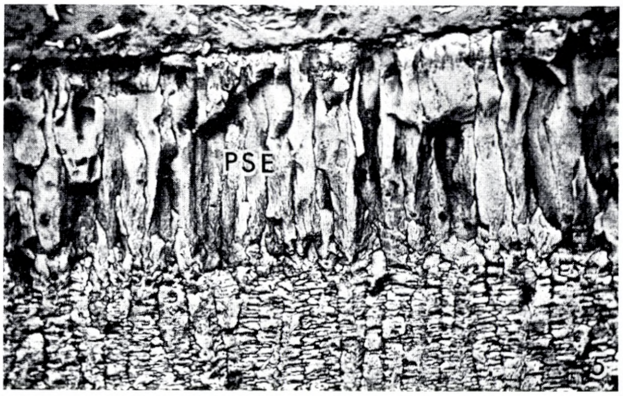

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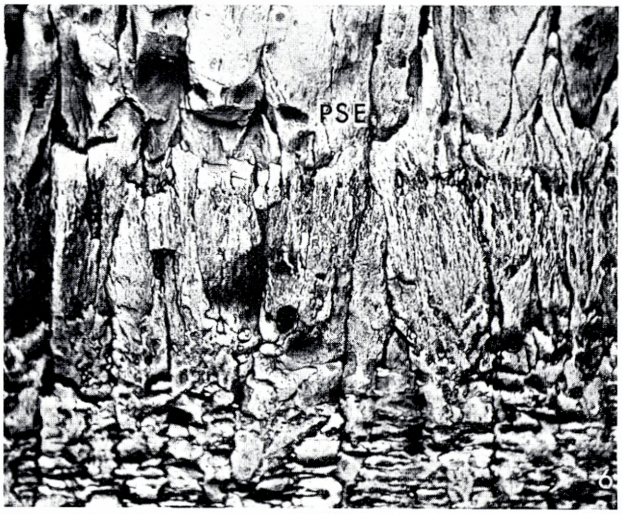

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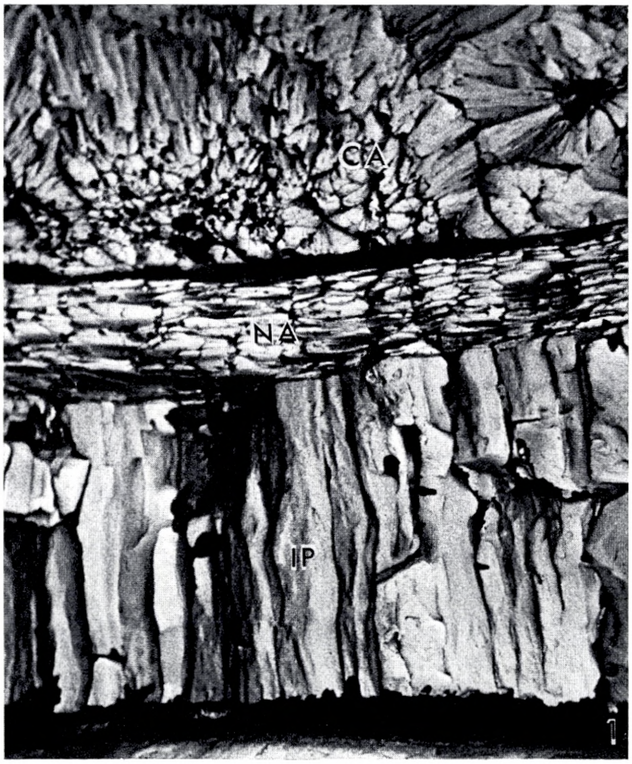
PLATE 11

Hypophylloceras (*Neophylloceras*) *groenlandicum* BIRKELUND.

1. Detail of shell wall showing relations between inner prismatic layer, nacreous layer and secondary filling of a cavity. Longitudinal dorso-ventral section. × 1560. MMH 12998.
2. Internal ribbing pattern of shell wall exposed on surface by removing the inner prismatic layer. Note the dark pigment in the rib-cavities. Light-microscope photography. × 13. MMH 12998.
3. Septal neck and false septal neck. 2 whorls distal of second change in growth. Longitudinal dorso-ventral section. × 190. MMH 12999.
4. Septal neck, false septal neck and connecting rings. 2 whorls distal of second change in growth. Longitudinal dorso-ventral section. × 100. MMH 12999.
5. Septal neck and false septal neck (diagenetically altered?). Longitudinal dorso-ventral section. × 100. MMH 12999.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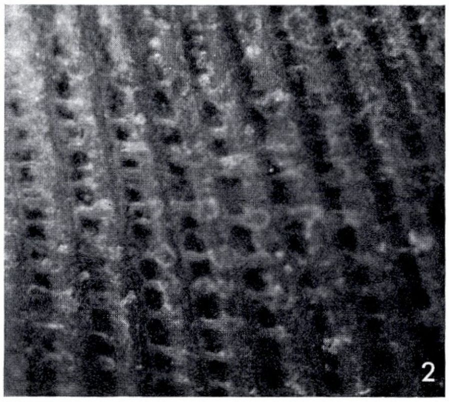
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PLATE 12

Hypophylloceras (*Neophylloceras*) *groenlandicum* BIRKELUND. Longitudinal dorso-ventral sections.

1. Septal neck, false septal neck and part of connecting ring. × 105. MMH 12999.
2. Siphuncle of 1st whorl showing a long false septal neck. × 390. MMH 12998.
3. Organic tube covering the false septal neck shown in fig. 2. Note the imprints possibly attributable to blood-vessels. × 157. MMH 12998.
4. Detail of fig. 1. × 510. MMH 12999.

PLATE 12

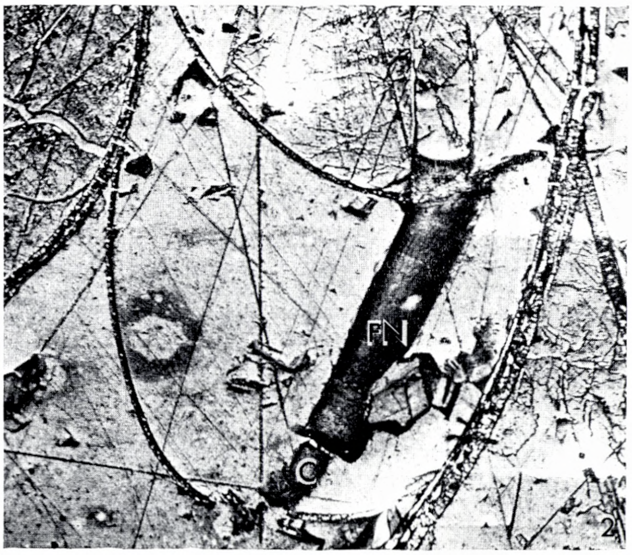


PLATE 13

Groenlandibelus rosenkrantzi (BIRKELUND). Longitudinal sections.

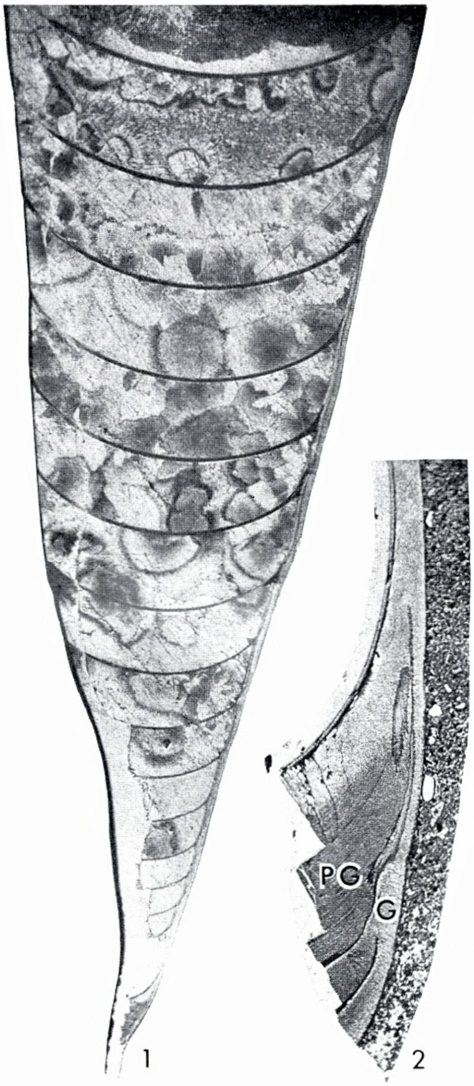
1. Phragmocone and guard. × 18. MMH 13000.

2–4. Guard of specimen shown in fig. 1. Note the difference in structure between the primordial guard and the guard proper. 2: × 125; 3: × 1215; 4: × 2455. MMH 13000.

5. Guard and phragmocone wall. × 905. MMH 13001.

Groenlandibelus sp.

6. Longitudinal section of phragmocone wall showing forward flange of septum (S). × 615. MMH 13002.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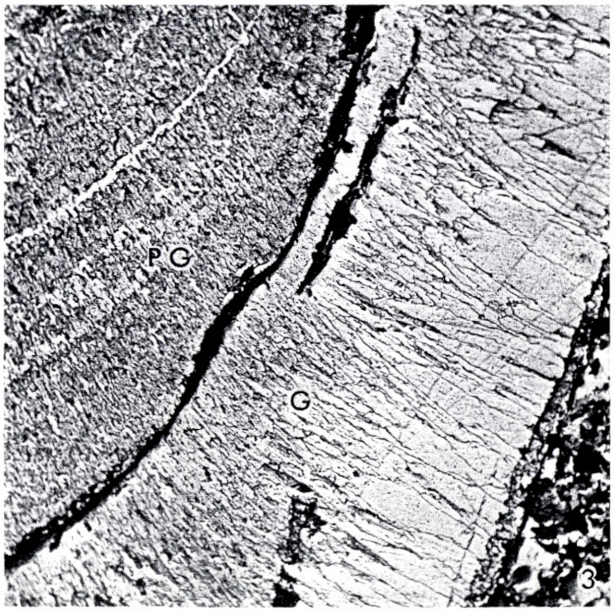
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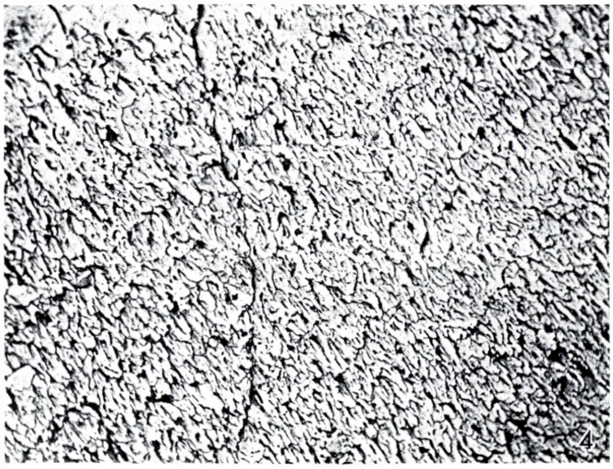
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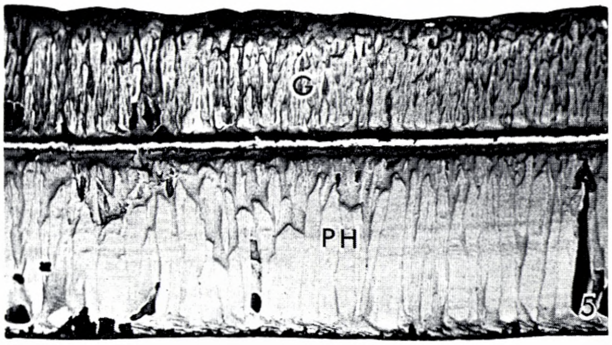
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PLATE 14

Groenlandibelus rosenkrantzi (BIRKELUND).

1–2. Contact between septum and phragmocone wall. Note inclusion of adoral flange of the septum in the wall. Longitudinal section. 1: × 140; 2: × 450. MMH 13000.

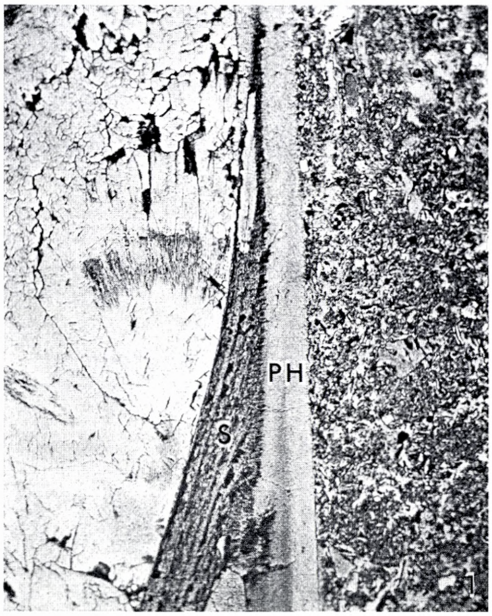
3. Adoral part of siphuncle with parts of connecting rings preserved. Longitudinal dorso-ventral section. × 18. MMH 13001.

4. Connecting ring and septum in adoral part of phragmocone. Note the lining of the ventral septum by the connecting ring. Longitudinal dorso-ventral section. × 82. MMH 13001.

5. Fracture surface of youngest septum, showing reminiscense of nacreous structure. × 510. MMH 13001.

Spirula spirula (LINNÉ).

6. Septum in 1st whorl. Longitudinal dorso-ventral section. × 935. MMH 13004.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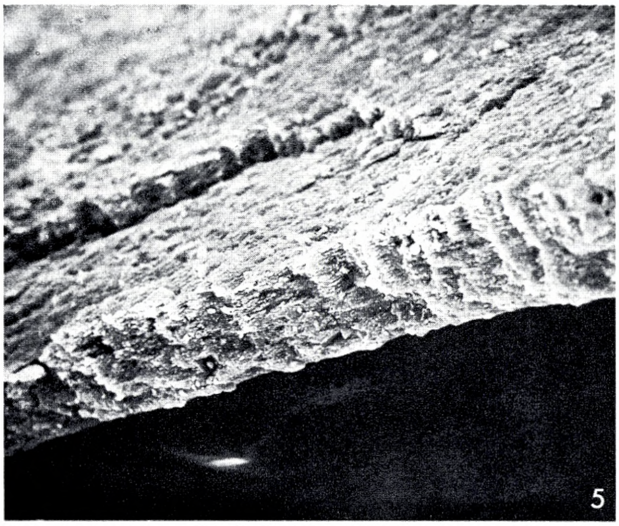
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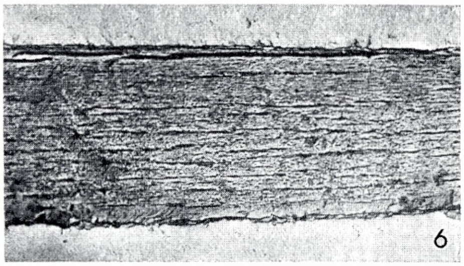
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PLATE 15

Groenlandibelus sp. Longitudinal sections.

1–2. Dorsal side of phragmocone, showing septum, phragmocone wall and guard. 1: × 430; 2: × 860. MMH 13002.
3. Phragmocone with retrochoanitic septal necks. × 26. MMH 13002.

Belemnitella bulbosa MEEK & HAYDEN. Longitudinal sections.

4. Two-layered phragmocone wall and guard. × 1820. MMH 13003.
5. Septum showing weak reminiscense of nacreous structure. × 1845. MMH 13003.

Groenlandibelus sp. Longitudinal section.

6. Late septum, showing reminiscense of nacreous structure. × 840. MMH 13002.


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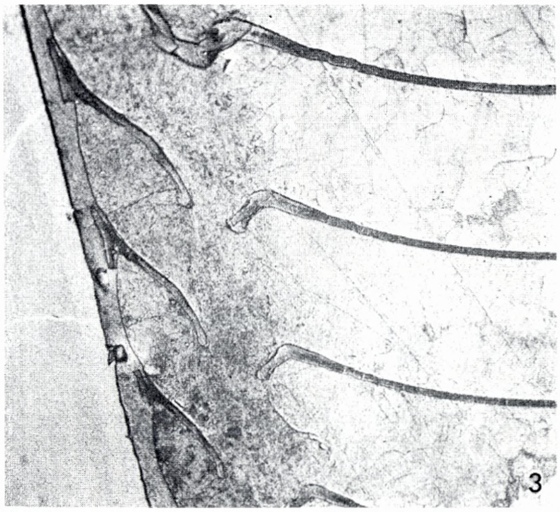
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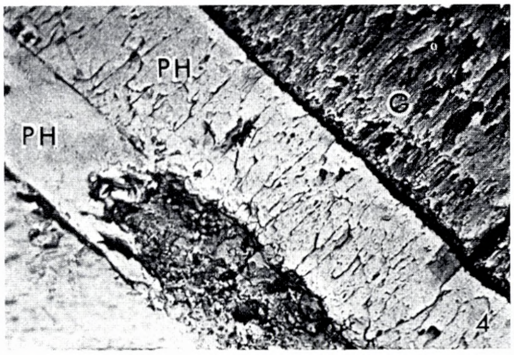
PH
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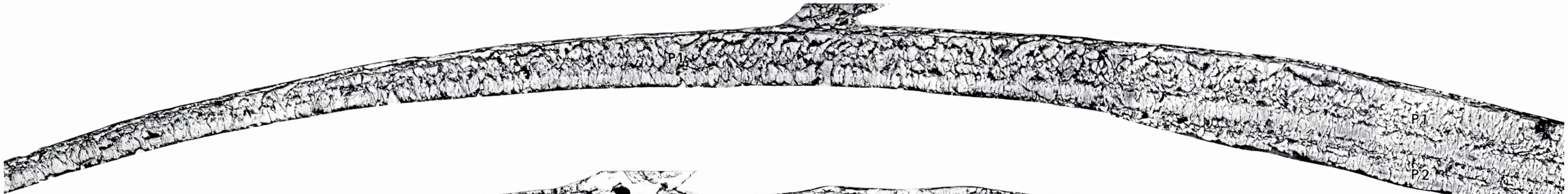
PLATE 16

Saghalinites wrighti BIRKELUND. Longitudinal dorso-ventral section. × 1500. MMH 12994. TEM.

1. Late part of protoconch showing first change in growth.
2. 1st whorl showing a gradual differentiation of the two sublayers of second ontogenetic stage.
3. Early part of second change in growth.
4. Late part of second change in growth and early part of third ontogenetic stage.
Adoral direction to the right.



1

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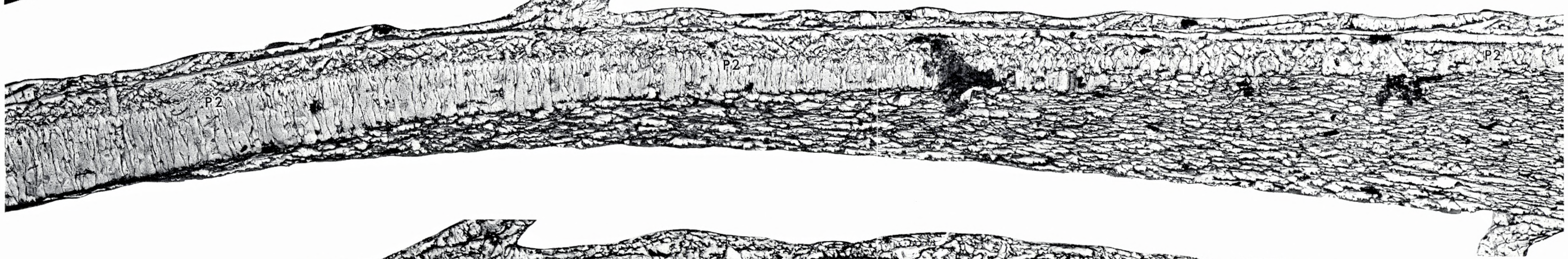

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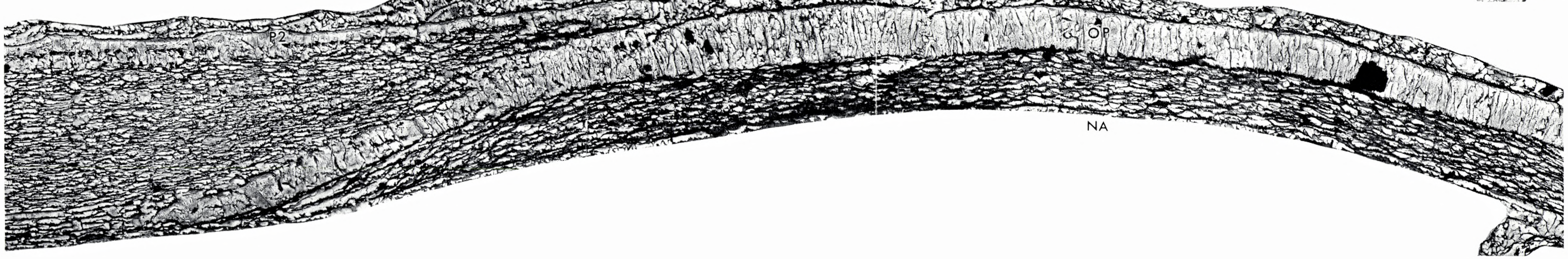

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