EARLY SHELL GROWTH AND STRUCTURES OF THE SEPTA AND THE SIPHUNCULAR TUBE IN SOME MAASTRICHTIAN AMMONITES

By

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Abstract

Submicroscopic shell structures of *Saghalinites, Scaphites* and *Hypophylloceras* show that the proseptum and the adjacent shell wall are continuous, as opposed to the relationship found in younger septa. The second ontogenetic stage in these forms thus includes the proseptum and the first whorl, the nepionic constriction marking the end of this stage.

The structure of the proseptum is similar to the structure of the first whorl. Younger septa show a gradual differentiation into a proximal prismatic layer and a distal nacreous layer.

In the third ontogenetic stage an inner prismatic layer can be recognized in the shell wall. This is the only layer forming the dorsal part of the whorls.

The siphuncular tube has a prismatic structure and is attached to the septal necks by auxiliary annular deposits.

MATERIAL

All the specimens investigated here are from the Maastrichtian of West Greenland. The material was collected by ROSENKRANTZ and his collaborators and described by BIRKELUND (1965). The specimens are enclosed in calcareous concretions and the chambers usually filled with brownish, transparent calcite. The shell material is excellently preserved.

PREPARATION

Median dorso-ventral sections and cross-sections were prepared. The sections were partly studied using an optical microscope (polished surfaces and replicas of polished and etched surfaces), partly using a transmission electron microscope. A technique developed by one of the authors (HANSEN, 1967) was used to prepare composite electron micrographs.

DESCRIPTION

In 1967 BIRKELUND described the shell structures of early growth stages of *Saghalinites* and *Scaphites (Discoscaphites)*. Distinct successive changes

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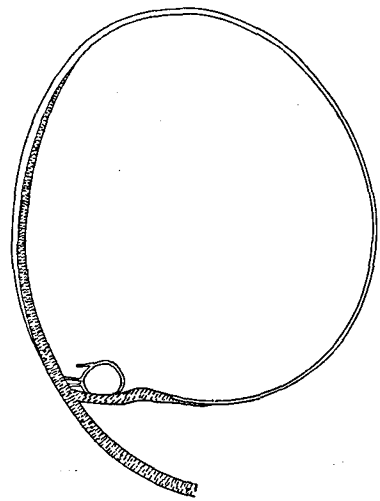

Fig. 1. *Scaphites (Discoscaphites)* sp. Section close to the median plane. The protoconch, the proseptum, the caecum, and the early part of the first whorl is shown. The caecum is attached to the shell wall of the second ontogenetic stage. × 120.

of the shell structure in the early ontogenetic stages were found. It was shown that the protoconch is composed of a thin layer, partly consisting of elongated crystals set at right angles to the shell surfaces, partly of crystals without any apparent preferred orientation.

At the beginning of the first whorl a new layer appears ventrally on the inner side of the protoconch and the protoconch shell gradually wedges out. The shell wall of the first whorl is thicker than the shell wall of the protoconch. It is composed of an inner prismatic part and an outer part with crystals showing no preferred orientation.

At the nepionic constriction a nacreous layer gradually appears and the layer of the first whorl wedges out. Finally the prismatic and the nacreous layers of the later part of the shell wall appear.

These changes in shell structures were thought to mark ontogenetic stages in the development of ammonites and were supposed to confirm the ontogenetic phases suggested by ERBEN (1964, 1966).

Since the work of BIRKELUND (1967) was published, extensive investigations of the structures of other parts of the shell of *Saghalinites* and *Scaphites* have been carried out as well as studies of the shell structures of *Hypophylloceras (Neophylloceras)*. A detailed description of the shell structures of these genera is in preparation. The present paper only deals with structures, which might throw further light on problems recently discussed by PALFRAMAN (1967) and MUTVEI (1967).

PALFRAMAN (1967) described the mode of early shell growth in *Promicroceras marstonense* SPATH. Of especial interest the growth lines of the early stages were described and the nature of the proseptum discussed.

PALFRAMAN reviewed the controversial theories on the nature of the proseptum. Some authors have suggested that the nature of the transition between the proseptum and the shell wall indicates that they are continuous, and resulted from contemporaneous formation (for example

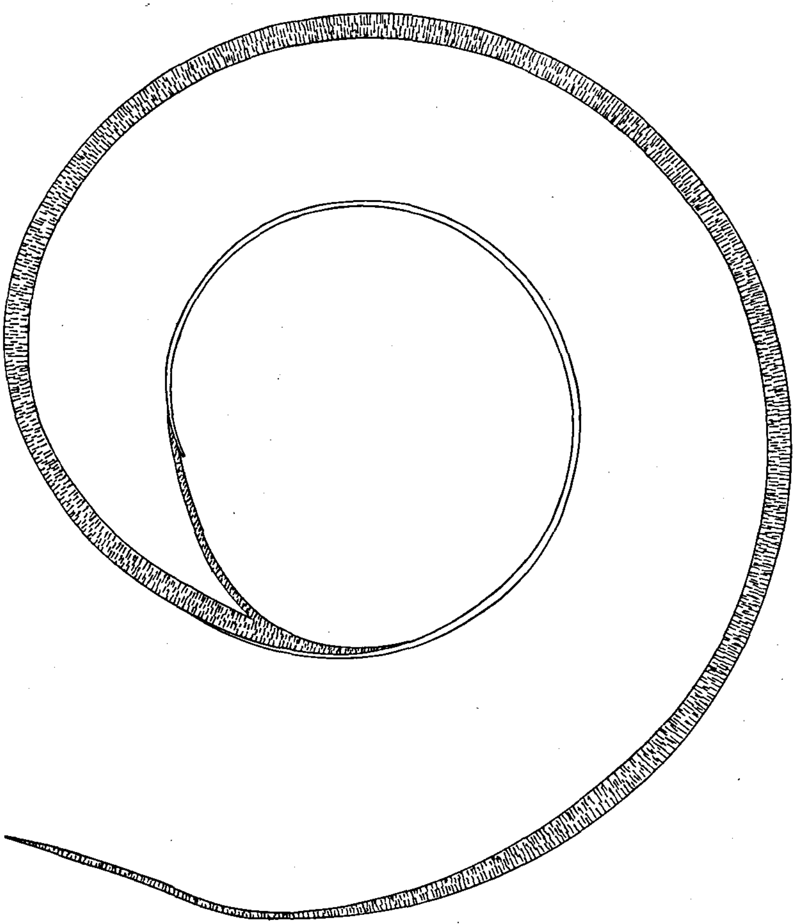

Fig. 2. *Saghalinites wrighti* BIRKELUND. Section parallel to the median plane between the median plane and the outer flank. Second ontogenetic stage. Besides the proseptum a few of the successive septa may belong to this stage. × 120.

GRANDJEAN, 1910, MILLER & UNKLESBAY, 1943, and ARKELL, 1957). Other authors (for example HYATT, 1900, HOUSE, 1965, and ERBEN, 1962 and 1966) have suggested that the proseptum was inserted in a manner identical to normal septa. ERBEN suggested that the formation of the proseptum and the nepionic constriction were contemporaneous. PALFRAMAN studied the junction between the proseptum and the ventral wall on polished sections and considered the junction to be identical to the junction between successive septa and the shell wall. He suggested that the formation of the nepionic constriction and the secretion of the proseptum were contemporaneous.

Electron micrographs of the proseptum and the ventral shell wall of the

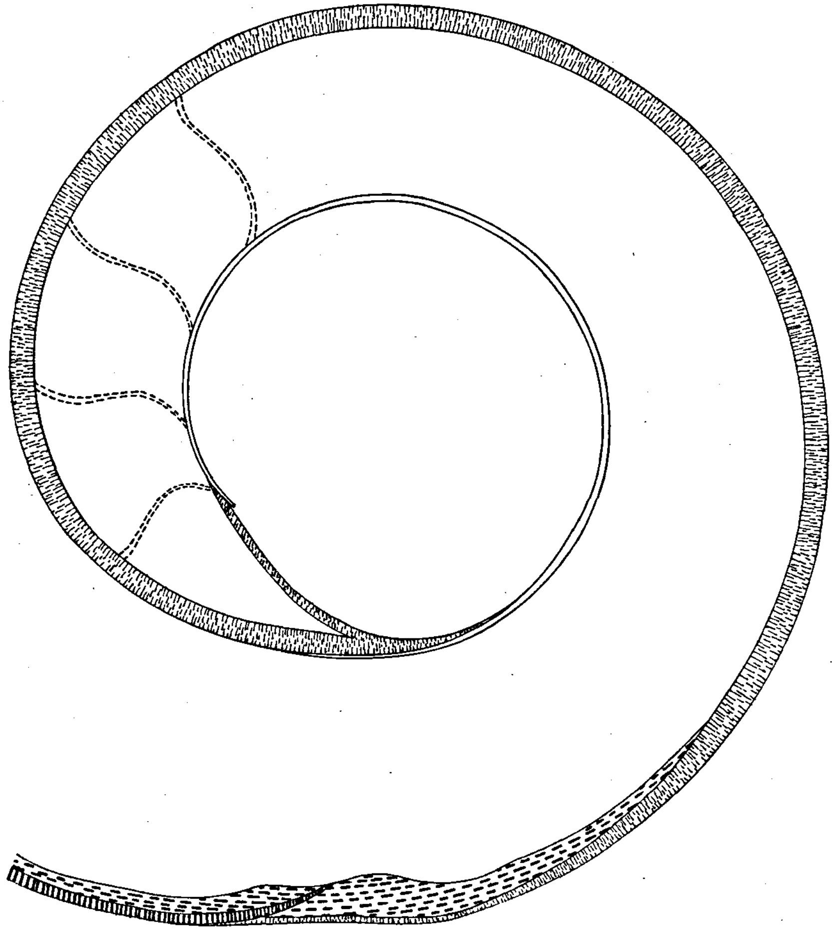

Fig. 3. *Saghalinites wrighti* BIRKELUND. Same specimen as shown in Fig. 2. Early phase of the third ontogenetic stage. The number of septa is hypothetical. × 120.

specimens investigated here show that the proseptum and the ventral shell wall are continuous. The proseptum is also considerably thicker than the successive septa and has an irregular prismatic structure similar to that of the first whorl. It thus seems as if it was formed simultaneously with the early part of the second ontogenetic stage. Pl. 1 shows an electron micrograph of the transition from the ventral shell wall to the proseptum in *Saghalinites* and Pl. 2 shows the shell wall and the very beginning of the proseptum in the same genus.

Fig. 2 shows the parts of the shell of *Saghalinites* supposed to belong to the first and the second ontogenetic stage. Fig. 3 shows an early phase of the third stage. On the basis of the juvenile specimens figured by TRUEMAN

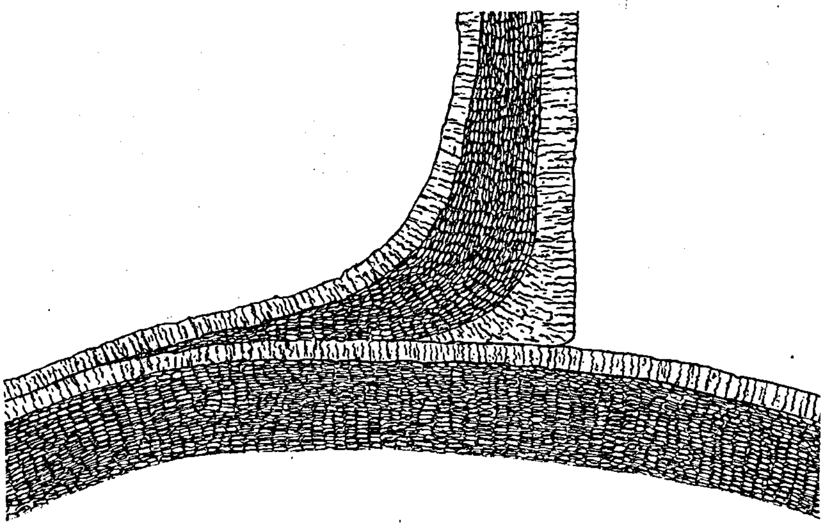

Fig. 4. *Saghalinites wrighti* BIRKELUND. Diagrammatical cross section of part of the 6th whorl and the 7th whorl, showing the wedging out of two of the shell layers (the outer prismatic layer and the nacreous layer) at the umbilical seam. × 150.

(1941), it is suggested that the living chamber is very long at this stage (the number of septa shown is hypothetical). It is possible that some of the early septa were formed before the second stage was finished.

Fig. 1 demonstrates the continous nature of contiguity of the proseptum and the shell wall in *Scaphites (Discoscaphites)*. This section cuts through the lateral part of the caecum.

PALFRAMAN points out that in general, planispirally coiled ammonites do not secrete a dorsal wall, unlike the nautiloids.

Electron micrographs confirm that both the outer prismatic shell layer and the nacreous layer of the lateral shell wall wedge out at the umbilical seam. However, the inner prismatic layer, which gradually becomes visible within the second whorl, is also secreted dorsally as shown in Fig. 4.

Septa of *Promicroceras* were described by MUTVEI (1967). In these septa MUTVEI found nacreous material throughout, but no prismatic material.

In *Hypophylloceras* the early septa have an irregular structure without any apparent preferred orientation of the crystals. Gradually the structures become more differentiated to form a proximal prismatic layer and a distal nacreous layer. The boundary between the two different structures is irregular. Pl. 3 and Figs. 5–6 illustrate successive stages in the development. In the septa of *Saghalinites* and *Scaphites* the prismatic layer is less prominent.

MUTVEI (1967) also described the siphuncular tube of *Promicroceras*. He stated that the tube is composed of conchiolin. Only a small part of this conchiolin tube is calcified and attached to the septal necks, where it forms an annular, ridgelike deposit ("auxiliary deposit").

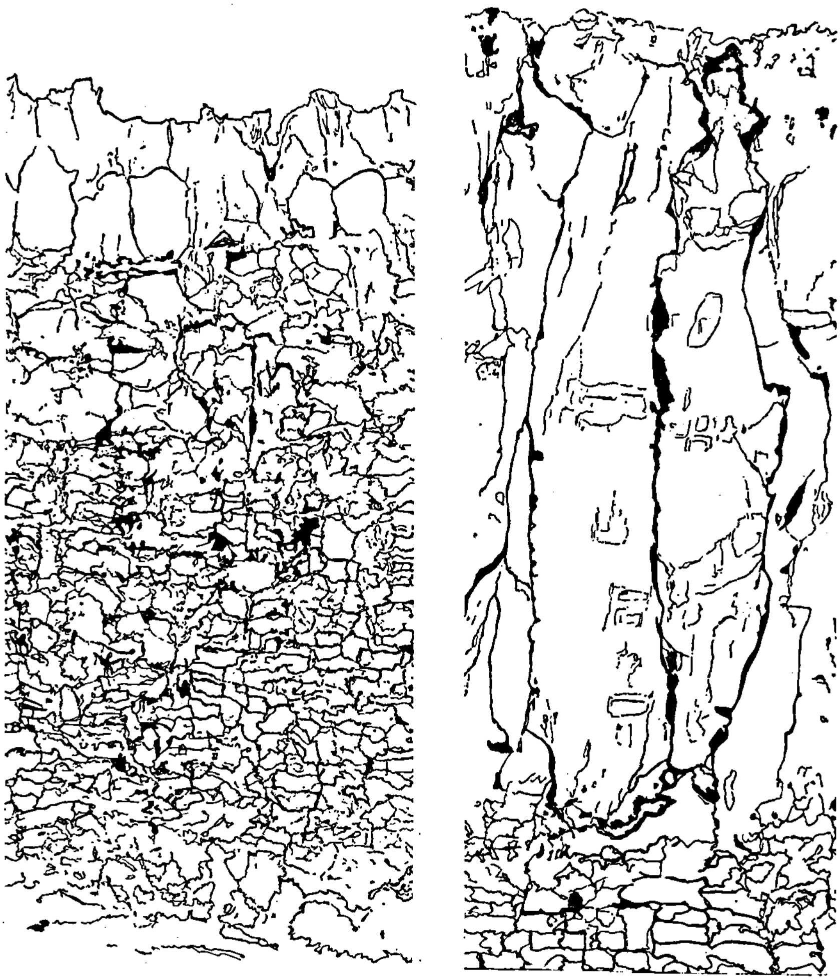

Fig. 5, 6. *Hypophylloceras (Neophylloceras) groenlandicum* BIRKELUND. Median sections of septa, showing the prismatic and nacreous layers. × 1650. 5: the 36th septum. 6: the 45th septum; only a small part of the nacreous layer is shown in this figure.

In most specimens investigated here the siphuncular tube is dissolved and only an empty tube is preserved which shows the course of the siphuncle. Some specimens, however, are so well preserved that the structures of the siphuncular tube can be studied. Pl. 4 shows part of the siphuncular tube in the early part of a *Saghalinites* shell. The structure of the calcareous material of this siphuncular tube is prismatic.

The auxiliary deposits are also well preserved. Pl. 3 shows an auxiliary deposit at an septal neck of one of the early septa of *Hypophylloceras,* while Fig. 7 shows the junction between an "empty" siphuncular tube and an

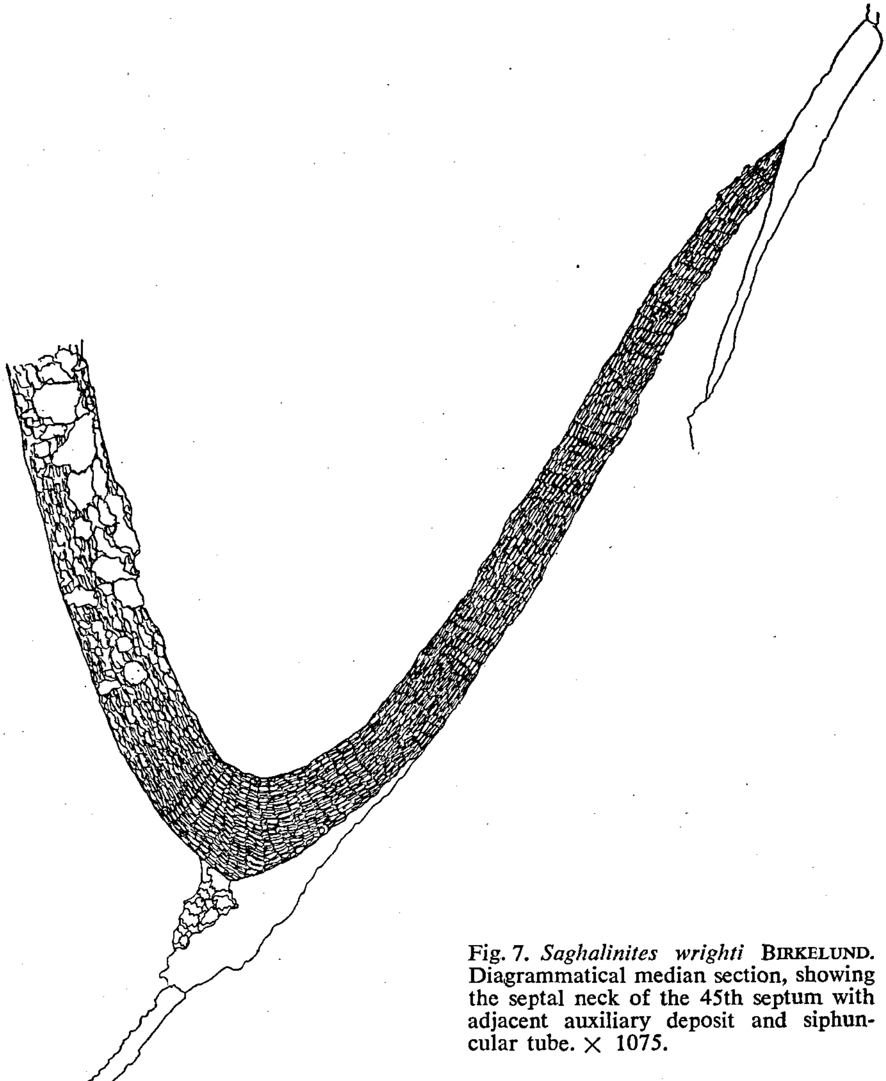

Fig. 7. *Saghalinites wrighti* BIRKELUND. Diagrammatical median section, showing the septal neck of the 45th septum with adjacent auxiliary deposit and siphuncular tube. × 1075.

auxiliary deposit in *Saghalinites*. The variation in shape and structure of the auxiliary deposits is considerable.

The structures of the septa and the siphuncular tube described here seem to indicate that the hydrostatic apparatus of nautiloids and ammonoids resemble each other more than suggested by MUTVEI.

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Pl. 1. *Saghalinites wrighti* BIRKELUND. Electron micrograph of a section parallel to the median plane of the same specimen as shown in Figs. 2–3. Part of the proseptum and the adjacent shell wall to show the gradational transition between the two. × 2500.

Pl. 2. *Saghalinites wrighti* BIRKELUND. Electron micrograph of a median section of the shell wall showing from the left to the right: the shell layer of the protoconch (wedging out) and the shell layer of the first whorl at the beginning of the proseptum. The arrow at the outer shell wall indicates the adoral direction. Same specimen as shown in BIRKELUND (1967, text-fig. 1, pl. 1–4). × 3750.

Pl. 3. *Hypophylloceras (Neophylloceras) groenlandicum* BIRKELUND. Electron micrograph of the 26th septum with the septal neck and auxiliary deposit. The septum shows the beginning differentiation in prismatic and nacreous structures. × 1100.

Pl. 4. *Saghalinites wrighti* BIRKELUND. Electron micrograph of a median section, showing from below: a part of the nacreous layer of the ventral shell wall, the inner prismatic layer of the ventral shell wall, and the siphuncular tube with prismatic structure. × 3330.

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