A C T A P A L A E O N T O L O G I C A P O L O N I C A

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STRUCTURE AND MODE OF ORIGIN OF THE AMMONITE PROSEPTUM

Abstract. — Results of studies of the structure and the relation of proseptum to the shell walls are presented. Proseptum develops in a deepening furrow extending around the posterior body part, simultaneously with the internal prismatic lamina of the initial chamber and the first whorl. Prosiphon and caecum appear later than proseptum. The proseptum is an extraordinary element dissimilar to subsequent septa.

INTRODUCTION

This paper is a preliminary presentation of results of the author's studies of the early phases of ammonoid shell morphogenesis.

The first septum called proseptum is developed in a different way from the others hence particular attention is being paid to it by many paleontologists. So far two interpretations exist about the relation of the proseptum to the shell walls. Erben, Flajs and Siehl (1968, 1969) based on excellently preserved material, studied by means of SEM. Birkelund and Hansen (1968, 1974) and Drushtchits and Khiami (1970) differ considerably from Erben *et al.*

The relation of proseptum to the shell is easy to apprehend after the reconstruction of the secretion zones in early phases of shell development is done. Such a reconstruction allows to understand why the second septum shows the same relation to the shell walls like all the subsequent ones, but possibly built up of prismatic tissue (Erben *et al.*, 1969) or of nacreous one (Birkelund & Hansen, 1974 and the author's own observations).

Specimens of *Quenstedtoceras* Hyatt and *Kosmoceras* Waagen have been used in the study. These forms occur in great abundance in calcareous concretions of the Upper Callovian at Łuków (Central Poland).

The polished surfaces have been obtained from specimens either filled with calcite or totally empty; the latter being infilled with Canada balsam prior to polishing. Cut and polished specimens were then treated with 2 per cent EDTA solution during 3—10 minutes. They were then covered with gold. Broken specimens were covered with carbon and gold. Electron microscope JSM-1 has been used in the research. The terminology concerning septa is that of Drushtchits and Khiami (1970) i.e. the first septum is called proseptum, the subsequent ones — second, third etc. The collections and scanning negatives are stored in the Palaeozoological Institute of the Polish Academy of Sciences (Polska Akademia Nauk, Zakład Paleozoologii) in Warsaw, abbreviated as ZPAL.

Thanks are due to Miss L. A. Doguzhaeva and Mr. I. S. Barskov both of the Geological Department of the Moscow University for discussions.

OBSERVATIONS

Relation of proseptum to the shell walls in the dorsal part. The most typical relations between the flange, proseptum and the wall of initial chamber in median section are illustrated in pl. XXXVIII, fig. 1. A distinct secretion discontinuity is observable between the flange and the wall of initial chamber (text-fig. 1, *1*). It separates both these elements. Another such discontinuity is to be found between the proseptum and the wall of initial chamber. It gradually disappears toward the aperture. Both discontinuities but in different configuration are illustrated in (pl. XXXVIII, fig. 2, text-fig. 1, *2*). Sections parallel to median one are illustrated in pl. XXXVIII, figs 3, 4. Both sections show some deviation from average relations: in both cases there is no protruding element toward the initial chamber, and there is no boundary separating the flange from the wall of the initial chamber. The boundary between the proseptum and the wall of initial chamber is distinct (text-figs 1, *3*—*4*). From the observations of the polished surfaces and broken preparations it comes that the flange is of variable width: it is broadest as a rule within the middle saddle, outside it is narrow or does not occur at all.

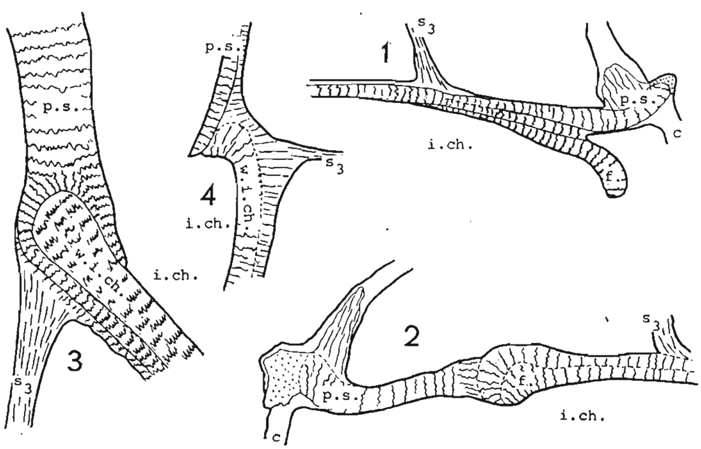

Fig. 1. Relations of proseptum, wall of initial chamber and flange. (Sketches of structures illustrated on Plate XXXVIII). *c* caecum; *d w n w* dorsal wall of next whorl; *f* flange; *i ch* initial chamber; *ps* proseptum; *siph* siphuncle; s_2, s_3 subsequent septa; *s t* soft tissues; *w i ch* wall of initial chamber.

Relation of proseptum to the shell walls in ventral part. In median plane the proseptum is very short and relatively thick (pl. XXXIX, fig. 1). The bend of internal lamina of prismatic layer inwards and its disruption are well observable. Space inbetween the disrupted margins of the internal lamina of prismatic layer, and partly between the laminae is filled by mineral tissue, the mineral component of which makes neither distinct crystals nor crystallites (text-fig. 2, *1*). On the

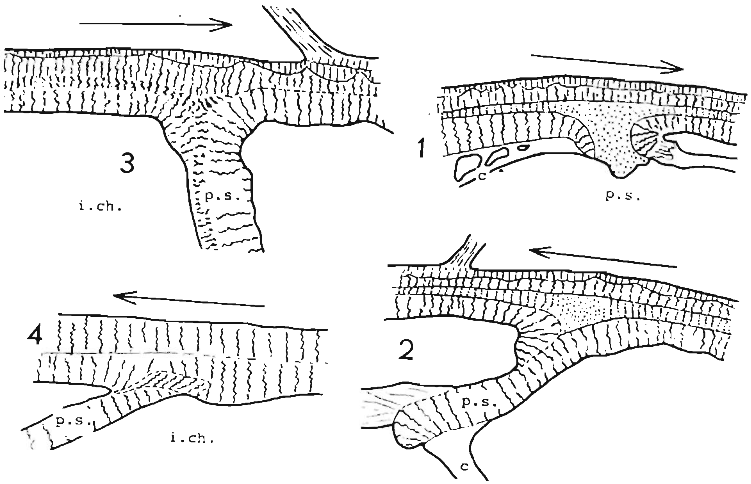

Fig. 2. Relation of proseptum to the shell walls in ventral part. (Sketch of structures illustrated on Plate XXXIX). Explanations — see Text-Fig. 1.

section slightly displaced in relation to the median plane (pl. XXXIX, fig. 2) the proseptum part is much longer than in the latter case. The prismatic tissue of the proseptum passes gradually into the wall of initial chamber. The prismatic tissue of the first whorl is incorporated within the proseptum base. For the sections much deviating from median plane the characteristic relations are presented on pl. XXXIX, figs 3, 4 and text-figs 2, *3—4*.

DISCUSSION AND INTERPRETATION

From the above results the following:

1. *The flange is of variable width, broadest within the external saddle and is usually separated from the wall of initial chamber by a secretion discontinuity.* These relations have been shown by Erben, Flajs and Siehl (1969), (text-fig. 5) in similar way but all the specimens illustrated by those authors have been polished in median plane. Birkelund and Hansen (1968, 1974) illustrate the flange as a termination of the wall of initial chamber without any discontinuity surface. Their interpretation has been illustrated only on sections parallel to median one. Drushtchits and Khiami (1970) and Drushtchits and Dogushaeva (1974) confirm the interpretation of Birkelund and Hansen (1968) but do not present convincing photographs.

2. *The proseptum is separated from the wall of initial chamber by a secretion discontinuity in dorsal part* which resembles the relations between the shell wall and the subsequent septa in which mural part is particularly well developed. Interpretation by Birkelund and Hansen (1968, 1974) and by Drushtchits and Khiami (1970) as well as by Drushtchits and Dogushaeva (1974) agree with the above one but Erben *et al.* (1969) do not mention that discontinuity.

3. *In ventral part* the proseptum is somewhat variable toward the shell walls depending on the position of the section: a) *basal part of the proseptum is built of two laminae of prismatic layer which pass gradually into the shell wall,* b) *the prismatic tissue of the proseptum forms a continuation of the internal prismatic lamina of the initial chamber* as pointed out by Erben *et al.* (1968, 1969), c) *the prismatic tissue of the proseptum is a continuation of the prismatic lamina of the first whorl,* d) *the prismatic tissue of the proseptum lies discordantly toward the prismatic layer of the shell wall.* Birkelund and Hansen (*l.c.*) have never described the relation of proseptum to the shell walls in ventral part in detail. Drushtchits and Dogushaeva (1974, p. 54) maintain that the relation of the proseptum to the shell walls is similar as that of the subsequent septa and the only difference is that in the case of proseptum a shift of the crystal position takes place at the base of septum and in the shell wall what makes an impression of passage of the proseptum into the shell

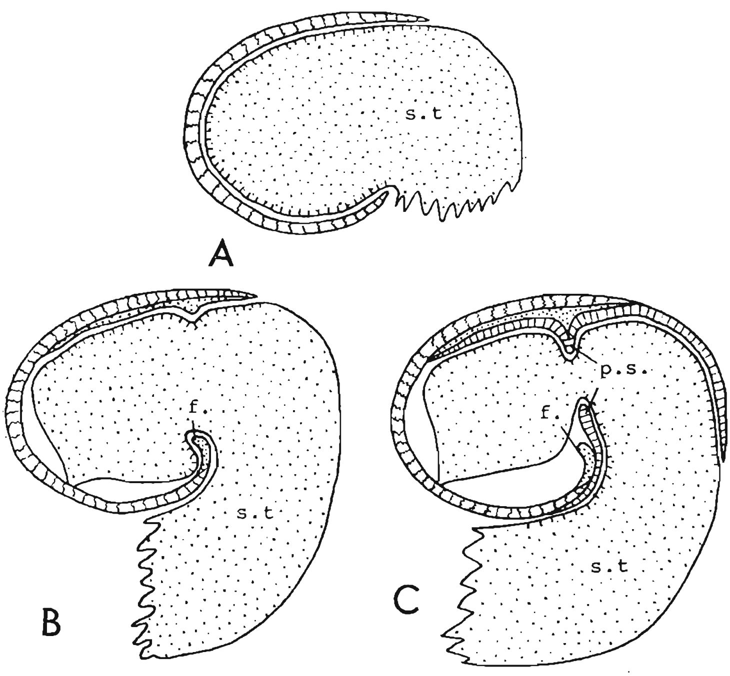

Fig. 3. Development of the initial chamber, proseptum and flange with the secretion zones marked. Explanations — see Text-Fig. 1.

wall. They do not explain, however, why such a situation does not pertain to the second septum.

Erben *et al.* (1969, text-fig. 5) show subsequent growth phases of the initial chamber expressed as the subsequent sublayers (a_1, a_2, b). Birkelund and Hansen (1974) suggest simultaneous secretion of the initial chamber as a whole. Study of numerous, well preserved specimens of *Quenstedtoceras* and *Kosmoceras* from Łuków did not reveal the existence of the sublayers in the sense of Erben *et al.* (1969). Simultaneous secretion as assumed by Birkelund and Hansen (*l.c.*) is unacceptable mainly because the subprismatic layer of which the initial chamber is built, gradually thins out toward the front of shell and disappears altogether which suggest a rapidly broadening and broad secretion zone.

It seems probable that the initial chamber has been formed by a continuous, dome-like secretion zone that quickly gained in width (text--fig. 3B). It is also possible that during the final stage of the formation of the initial chamber the apical part of the epithelium surface loses its secretion possibilities hence the whole secretion zone becomes tube like. The development of the flange may have taken place during additional secretion frequently on the dorsal side which did not embrace the whole width of shell. A very thin layer that separates on ventral side the subprismatic layer of the initial chamber from the prismatic layer of the first whorl and proseptum (text-fig. 3b) has been probably formed during the same phase of secretion. This layer has become much thicker at the base of proseptum on ventral side of median zone. It disappears towards the sides of shell. A swell of the layer in place where a proseptum will appear later points to an initial phase of the development of a perpendicular furrow on the embroyon body (text-fig. 3*B*).

The next stage is the secretion of the internal prismatic lamina of the initial chamber, proseptum (dorsal and ventral parts) and the first whorl. The secreting layer rapidly expanded to form tube-like physiologically undiferentiated zone of soft tissue. This phase is also characterized by the formation of a deep furrow around the posterior body part in which the secretion of prismatic tissue of the proseptum takes place (text-fig. 3*C*).

The character of mineral tissue of the second septum (prismatic or nacreous one) depends on the phase during which the physiological differentiation of initially uniform secretion zone had taken place in relation to the development of the second septum. In both cases (second septum either prismatic or nacreous) the relation of the second septum to the shell walls is the same i.e. the former is separated from the wall of the first whorl by a distinct boundary. The above interpretation requires another developmental sequence of the caecum and prosiphon in relation to the proseptum than that put forth by Zakharov (1972, p. 68). In the opinion of the present author the development of prosiphon and caecum followed that of the proseptum during and after the process of withdrawal of solt tissues from the initial chamber.

In most cases described here the proseptum is attached on the dorsal side behind the flange, and only in the case of *Tornoceras simplex* illustrated by Bogoslovsky (1969, text-fig. 3b) it is placed in front of the flange termination, thus, protrudes inside the second chamber of the phragmocone. Some resemblances can be noted in the structures on the internal wall of protoconch (initial chamber) of a belemnite *Cenobelus conicus* described by Barskov (1971). They have been interpreted by him as muscle scars because of the similarity to metameric pattern of muscle scars in *Monoplacophora* and some nautiloids.

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BUDOWA I SPOSÓB POWSTAWANIA PROSEPTUM AMONITÓW

Streszczenie

W pracy przedstawiono wyniki badań nad budową i stosunkiem proseptum do ścianek muszli. Ustalono, że proseptum tworzy się w głębokiej bruździe, biegnącej w tylnej części ciała poprzecznie, równocześnie z wewnętrzną laminą pryzmatyczną komory początkowej i pierwszego skrętu. Prosyfon i cekum pojawiało się po uformowaniu proseptum.

Zgodnie z przedłożoną interpretacją proseptum stanowi element swoisty nie porównywalny z kolejnymi septami.

ЦЫПРИАН КУЛИЦКИ

СТРОЕНИЕ И СПОСОБ ОБРАЗОВАНИЯ ПРОСЕПТА АММОНИТОВ

Резюме

В статье автор представляет результаты исследования строения и взаимоотношения просепты и стенки раковины. Установлено, что просепта образуется одновременно с внутренним призматическим слоем первоначальной камеры и первого оборота, в глубокой складке, окружающей заднюю часть тела. Просифон и цекум возникают позже чем просепта.

Согласно с представленной интерпретацией просепта является своеобразным элементом септального аппарата, отличающимся по способу образования от других септ.

EXPLANATIONS OF PLATES

Plate XXXVIII

Fig. 1. *Quenstedtoceras henrici* R. Douv, juv., Łuków, Callovian, ZPAL Am. I/21, relations between flange, wall of initial chamber and proseptum in median section. ×1400.

Fig. 2. *Quenstedtoceras henrici* R. Douv., Łuków, Callovian, ZPAL Am. I/27, Relations between the flange, wall of initial chamber and proseptum in median section. ×1800.

Fig. 3. *Kosmoceras* sp. juv., Łuków, Callovian, ZPAL Am. I/28, Relations of wall of initial chamber and proseptum in section parallel to median. (Flange does not occur as a protruding element). ×1400.

Fig. 4. *Quenstedtoceras* sp., Łuków, Callovian, ZPAL Am. I/29, Relations between proseptum and wall of initial chamber in section parallel to median. (Flange does not occur as a protruding element, but the proseptum stretches toward interior of the initial chamber). ×2100.

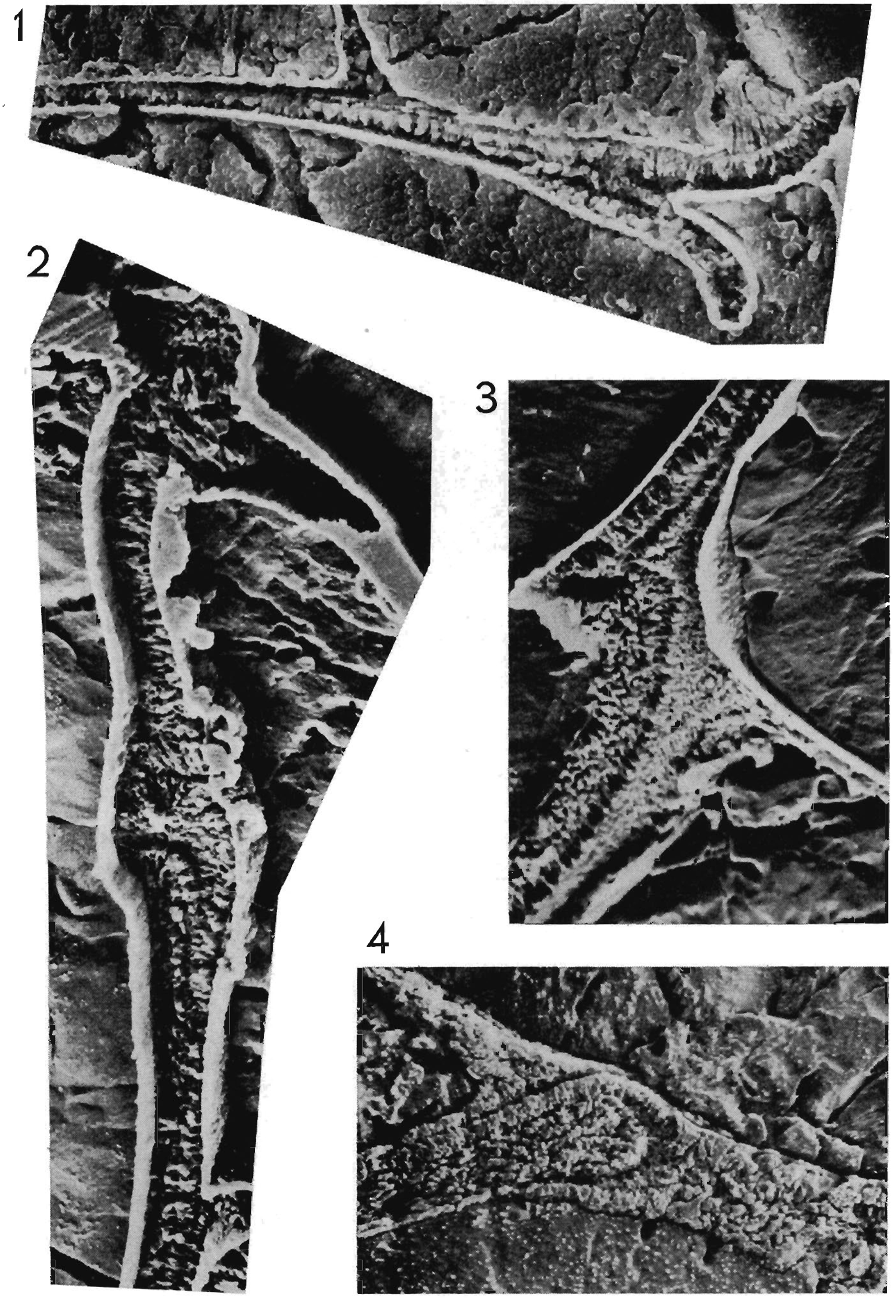
Plate XXXIX

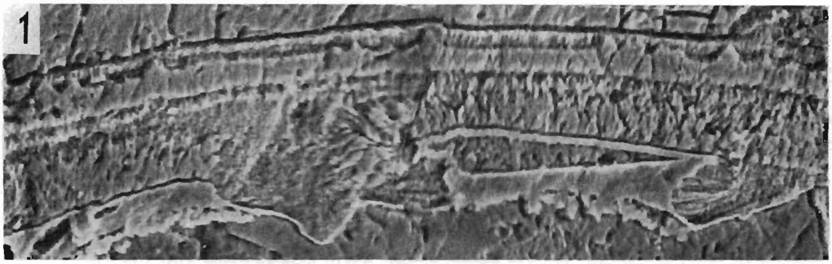
Fig. 1. *Quenstedtoceras* sp. juv., Łuków, Callovian, ZPAL Am. I/30, Relation of proseptum to the wall of shell in ventral part in median section. ×1200.

Fig. 2. *Quenstedtoceras* sp. juv., Łuków, Callovian, ZPAL Am. I/29, Relation of proseptum to the shell wall in a section close to median. ×1000.

Fig. 3. *Quenstedtoceras* sp. juv., Łuków, Callovian, ZPAL Am. I/31, Relation of proseptum to the shell wall in ventral part, section parallel to median. ×1100.

Fig. 4. *Kosmoceras* sp. juv., Łuków, Callovian, ZPAL Am. I/28, Relation of proseptum to the shell wall in ventral part, section parallel to median. ×1400.

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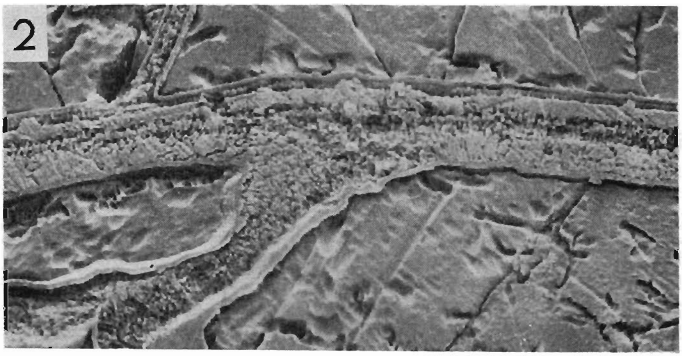
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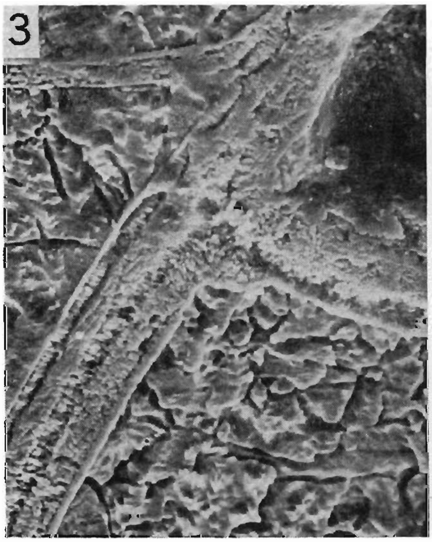
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