Development and calcification of the ammonitella shell

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Aconeceras trautscholdi ammonitellae mass occurring in the Aptian of Symbirsk, central Russia represent consecutive calcification stages of the primary organic shell wall. Already after the formation of the organic shell with proseptum, the first whorl and umbilical walls of the initial chamber were calcified, then the remaining part of the initial chamber, and finally the nacreous primary constriction was formed and the proseptum was calcified. The original mineral participating in calcification was aragonite, which formed primary prismatic layers. The ammonite embryonic shell was thus formed similarly to the archaeogastropod larval shell. This explains the microstructural distinction of the ammonitella and proseptum walls with respect to the rest of the ammonite shell.

Key words: ammonites, ontogeny, biomineralization, Cretaceous, Jurassic.

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Introduction

Since 1967 several papers on the structure of ammonitellae have been published, based on studies under the transmission electron microscope TEM (Birkelund 1967) or, more frequently, the SEM (Erben, Flajs & Siehl 1969).

These, and numerous subsequent, more or less detailed works on the structure of the ammonitella shell provided a picture of ammonitella structures differing only in details among various taxonomic groups.

In interpretative parts of all these elaborations simultaneous secretion of organic and mineral phases was assumed as observed in the postembryonic shell of molluscs.

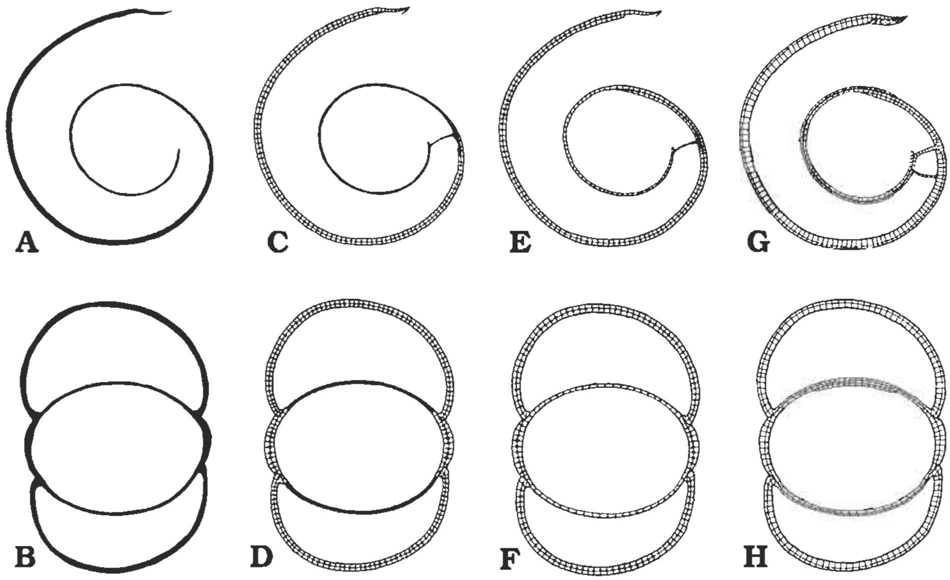

Fig. 1. Consecutive developmental stages of ammonitella shell. ❑A–B. Completed organic stage. ❑C–D. End of the first calcification stage. ❑E–F. End of the second calcification stage. ❑G–H. End of the third calcification stage (immediately before hatching).

Bandel (1982) suggested that in the case of ammonitella the shell may have been originally produced only from organic matter that became later mineralized as is the case in Archaeogastropoda. According to Bandel (1982), calcification does not repeat the secretion stages, but generally has an opposite direction, i.e., the first whorl becomes calcified first and only then the process reaches the initial chamber. However, Bandel (1982) did not provide any direct empirical evidence supporting his interpretation.

Extraordinary preservation of ammonitellae from the Aptian gray and black clays of Symbirsk (Uljanovsk) enable a new approach to the problem of secretion and mineralization of the embryonic shell of ammonites. The ammonitellae occur in sideritic concretions. They are sometimes very abundant – over a hundred specimens in a cubic centimeter (Fig. 2A). Their occurrence has been mentioned first by Kabanov (1958). Adults of two ammonite species, *Aconeceras trautscholdi* Sinzow 1870 and *Deshayesites deshayesi* (Leymerie 1941), are associated with ammonitellae in concretions. Both species differ in the diameter of the initial chamber (cf. Druzchits & Doguzhaeva 1981). The abundantly occurring ammonitellae belong mostly to *Aconeceras.*

Aptian deposits near Simbirsk, where the studied material was collected, crop out along the high right coast of the middle reaches of the Volga River and abound in stratigraphic gaps. They are represented by clays about 50 m in thickness with numerous sandstone intercalations and sideritic nodules. The latter contain exellently preserved ammonites, sometimes even showing muscle-scars and with the buccal apparatus still within the body chamber.

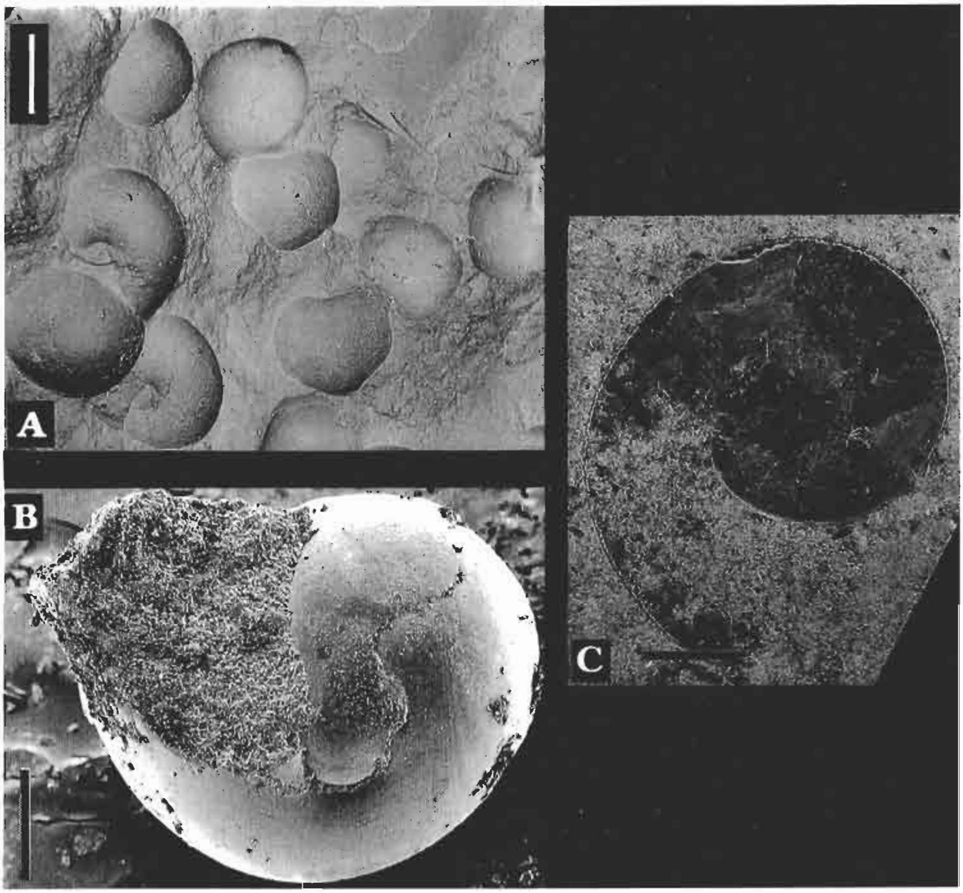

Fig. 2. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. ❑A. Split limestone concretion with ammonitellae. Scale bar 250 µm. ❑B. Single ammonitella – view from aperture. Distinct proseptum outline, before which inner mould is covered by an original shell, behind the shell is exfoliated. Scale bar 100 µm. ❑C. Longitudinal section of ammonitella in the second stage. Primary varix is lacking and the wall of initial chamber is partly calcified; treated in EDTA. Scale bar 100 µm.

Aragonite was protected inside the sideritic concretions from the Aptian clays (65–79% iron carbonate, 9–15% calcite, 11–15% $MgCO$, 1–8% $MnCO$). The ammonoid shells from the Aptian clays are composed of 95–99% aragonite (unpublished data by I.V. Pochtareva, Paleontological Institute, Moscow). The concretions contain also small gastropods, bivalves, rare remains of teuthids, fishes, ichthyosaurs, insects, and woody plants.

The discussed strata represent mainly the *Deshayesites deshayesi* Zone of the early Aptian. In the lower part of the formation species of *Aconeceras* and *Deshayesites* predominate with their shell diameters up to 60 mm. Among them very rare and small heteromorphs *Toxoceratoides* occur.

Above the clay more sandy strata follow. From this part of the Early Aptian *Deshayesites* and heteromorphs *Ancyloceras*, *Australiceras*, *Pseu-*

doaustraliceras, Hamites, and *Tropaeum* are known. Shells of *Deshayesites* are of larger size than in the lower part of the section and the heteromorphs are abundant and large-sized (Doguzhaeva & Mikhailova 1991).

Also an ammonitella of *Quenstedtoceras* from the Callovian of Łuków, Poland, has been studied. The characteristics of the outcrop, concretion, and species taxonomy have been given by Makowski (1952, 1962) and Dzik (1990).

The studies were conducted using SEM on broken, serially ground and polished specimens. After polishing they were treated in 1% HCl, 2% EDTA or boiled for 10–15 minutes in 3% H_2O_2.

As a result of boiling of the polished specimens in H_2O_2 some of the shell matrix was removed leaving components of walls or laminae with a distinct structure of polyhedral crystallites (Fig. 13 A–D; vertical angular plates of Mutvei 1979). Mutvei (1979) has obtained similar results when examining the nacreous layer of the Recent bivalves *Mytilus* and gastropods *Gibbula* treated in sodium hypochlorite and afterwards in 25% glutaraldehyde.

The *Quenstedtoceras* specimen used in investigations and photographic documentation are kept in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw. The materials from the Volga region and SEM negatives are stored at the Paleontological Institute of the Russian Academy of Sciences in Moscow.

Observations

Cretaceous ammonitellae from Simbirsk

With respect to the calcification degree, the ammonitellae examined can be divided into several groups corresponding to successive stages of calcification of shells. These are as follows:

(1) Specimens retaining only the first whorl with a characteristic nepionic constriction, and lateral walls of the initial chamber (Fig. 1C–D).

(2) Specimens also having a mineralized wall of the initial chamber in the part separating its interior from the first whorl (Fig. 1E–F).

(3) Specimens with calcified first whorl and initial chamber, with proseptum and a nacreous primary varix. In this stage the wall of the first whorl is slightly thicker from the inside, whereas in *Quenstedtoceras* from Łuków the second septum occurs (Fig. 1G–H).

(4) The fourth final stage of mineralization and development of ammonitellae is observed in larger specimens with a postembryonic shell. This stage is characterized by a final thickening from the inside of the inner prismatic layer and sometimes by an addition from the inside of a second prismatic layer.

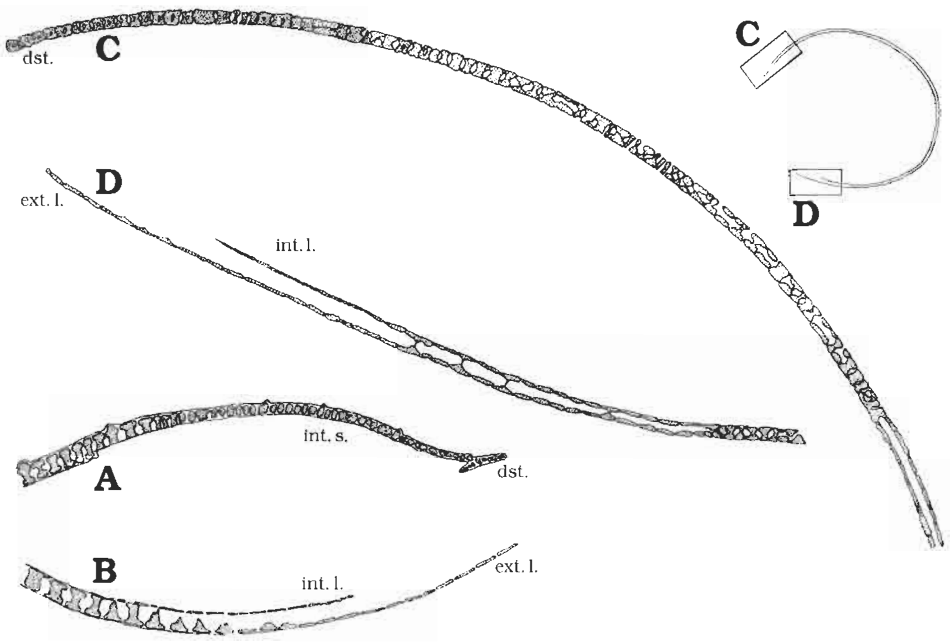

Fig. 3. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. ❑A–B. Longitudinal section of calcified part of shell; advanced first stage; A – section of shell near aperture; B – section of calcification front from initial chamber side. ❑C–D. Earlier stages of calcification; C – shell section in vicinity of aperture; D – section through the calcification front. Abbreviations: dst – distal part of aperture of ammonitella with a short return section of prismatic layer (A) and with straight end (C); ext. l. – layer of external plates; int. l. – layer of internal plates; int. s. – attachment for soft tissues at the inner surface of aperture, in next phases epithelial cells lining this zone secreted the nacreous layer.

First stage of calcification. — In polished sections treated with HCl or EDTA, the wall of the first whorl of ammonitella has a characteristic structure (Fig. 6). Near the proseptum it is about 5 µm thick and before the primary constriction – 7 µm. Both the external and internal wall surfaces are covered with closely packed plate elements. In the middle part of the section particular plates are connected, but between the junctions there are quite distinct gaps, broader or narrower, filled with a carbonate material of different microstructure.

As regards the microstructural aspect, both external and internal plates and the junction elements after being treated with HCl and EDTA display an acicular microstructure. The needles are parallel towards one another and perpendicular to the external and internal wall surface (Figs 6A, E–G, 13C).

At this stage the nacreous layer is always missing in the shell aperture (Fig. 3A, C). The shape of the apertural edge is characteristic, frequently flanged outside, which indicates the primary constriction (Figs 7B, F, 8C).

On the inner apertural edge surface there is frequently a section of a short return segment of the prismatic layer (Figs 7B, 8C). The proximal part of the constriction is frequently indicated by a step dividing the shell part of normal thickness from that with gradually decreasing thickness to apertural edge. In the area of the primary constriction there is no layer of so-called inner plates, the median layer decreases relatively fast towards the aperture, and a considerable part of the constriction is made of external plates (Fig. 3A).

In longitudinal sections of the stage discussed the wall of the first whorl of the ammonitella on the side of the initial chamber is characteristically terminated (Fig. 3B, D). The external layer of plates extends the most towards the initial chamber, whereas the layer of internal plates is the most restricted. Going in the distal direction the thickening of external plates in the central part towards the inside of the wall can be observed and next their junction with internal plates, at first only by apices of conical thickenings and later forming column-like junctions (Figs 3B, D; 4A). Each external and internal plate consists of thin (ca 0.2 µm thick) aragonite needles closely adjoining and perpendicular to the surface of plates (Fig. 6G). The plates in outline are pseudohexagonal and are divided into 6 sectors, thus making them similar to the so-called pseudohexagonal trilling (Fig. 4B–C). External and internal plates are placed consistently in pairs, one above another, as indicated in Fig. 11F. In the median part, not so densely packed, there are the same aragonite trillings consistent with those overlaying and underlaying, but not so closely packed, showing gaps among pseudohexagonal plates and also between sectors (Figs 11A–B, 12A–C, 13B). The growth of needle-like crystallites is especially strong in central part of plates or sectors. Thus the section shows triangular thickenings, their sharp apices towards the internal surface of the organic shell wall (Figs 3B, D, 4A).

Before the growing apices of external plates attain the inner surface of the organic wall, the internal plates appear on this surface from the inside (Figs 3B, D, 4A). When the ingrowing apices of external plates penetrate the whole thickness of the organic wall and attain the surface of internal plates, the two elements become integrated into one. Some specimens of ammonitellae from Symbirsk sporadically show junctions between two layers of plates (Fig. 6B), and they should be considered as representing the earliest calcification stage of the wall of first whorl. In specimens representing later calcification stages, the wall of the first whorl and lateral walls of the initial chamber have a tri-layer structure. Plate-like elements in external and internal layers closely adjoin, whereas in the median layer they are not densely packed (Figs 6C–G, 11B, 12C).

Such a structure suggests that we are dealing with a calcification front of an originally organic wall of ammonitella, shifting from the first whorl towards the initial chamber, i.e., in opposite direction as the secretion of organic shell.

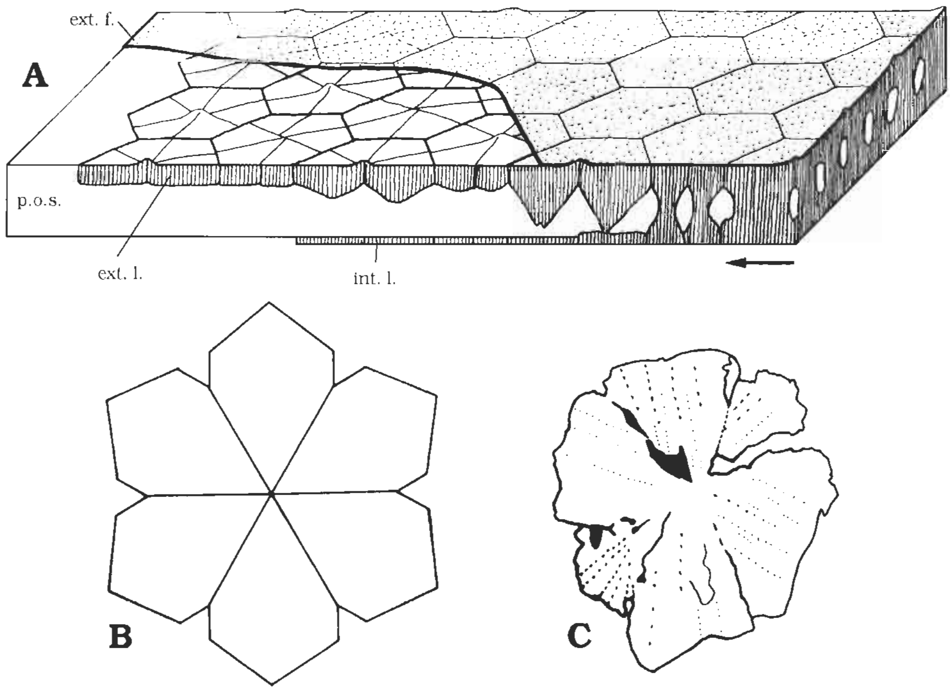

Fig. 4. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. ❑A. Schematic diagram presenting the *Aconeceras* ammonitella shell structure at the calcification front of the first whorl wall.❑B–C. Pseudohexagonal trilling from the *Aconeceras* ammonitella shell wall (C) compared with an idealized pseudohexagonal trilling (B). Abbreviations: ext. f. – external organic membrane do not undergoing calcification; ext. l. – external layer of plates; int. l. – layer of internal plates; p.o.s. – primary organic shell. The arrow points toward the initial chamber.

In specimens with a sufficiently long mineralized segment, in place where the proseptum base should be found (attachment zone of proseptum to external wall) there is a gap in plating of the internal layer, or sometimes within the initial chamber in front of the proseptum base there is a very thin additional internal layer (Figs 5A–B, 7C). The umbilical wall of the initial chamber even at this stage is calcified in its whole thickness. Its structure is the same as that of the first whorl, i.e., tri-fold: external plates, internal plates and median layer (Fig. 7D). Thickness of the umbilical wall is ca 8 μm. The layer of external plates covers the whole umbilical part of the initial chamber and ends under the umbilical by seam of the first whorl as shown in cross-sections, whereas internal plates go further under the umbilical seam and at this stage only very short segments of the wall of the initial chamber, which were calcified, are visible in cross-sections (Fig. 7E).

Second stage of calcification. — At this stage microstructures of the above discussed elements do not undergo visible changes, but calcification of the whole wall of initial chamber, separating the interior of the initial chamber from the first whorl is observed. This wall is not very thick, some 1–1.8 μm (Fig. 8B).

The umbilical walls of the initial chamber are quite thick, almost such as the wall of the first whorl. In the material examined we have found only specimens where it was calcified in the entire thickness, i.e., consisted of external, internal, and middle plates. The external and median layers get wedged out under the umbilical seam, similarly as in cross-sections of the wall of first whorl (Figs 7D–E, 8B, 14E). A similar situation has been presented by Bandel (1982: Fig. 41). In specimens representing the first calcification stage, the layer of internal plates ends immediately after going under the umbilical seam. Only in specimens representing the second stage is the whole wall of the first chamber calcified, and in the part separating the interior of initial chamber from the first whorl it is very thin and is a continuation of the internal layer of umbilical wall plates (Figs 8B, 14E).

In the surroundings of the proseptum base there is a layer of internal plates or a thin internal lamina (cf Fig. 5A–B) more developed and partly covering the broad base of not mineralized proseptum (Figs 5C, 8D). The space of the proseptum base itself is filled with the same sparite as the whole interior of ammonitella, proving thus that the entire base and the proseptum itself was not calcified yet.

Third calcification stage. — This stage is not well represented in our material. Only in longitudinal sections the presence of nacreous primary varix corresponds to the occurrence of calcified proseptum. The material from Symbirsk shows no traces of further septa (Fig. 8A). The caecum is not preserved.

Fourth calcification stage. — This developmental stage corresponds to the postembryonic phase. Changes concern the first whorl i.e., thickening of the inner walls. These changes are seen the best near the primary varix in its proximal part and in these surroundings are expressed by an inner prismatic layer running under the nepionic thickening (Fig. 14A–C).

Jurassic ammonitella from Łuków

In the case of the Jurassic ammonitella of *Quenstedtoceras* from Łuków in Poland, the fully developed nacreous primary varix is accompanied in the posterior part by two septa, i.e., proseptum and first nacroseptum (Fig. 9A–B). Thus, it represents final phases of the third calcification stage. In ammonitellae from both localities the caecum is not preserved at this stage, although in the specimen from Łuków the proseptum and the first septum have visible anterior and posterior auxilliary deposits (Fig. 9B, E), proving thus the occurrence of formed caecum.

In the specimen from Łuków, on the external surface near the proseptum base the section shows symetric tubercles being a result of lengthening of the axis of crystallites (Fig. 9B–C), and also the main ornamentation element of the outer surface of the ammonitella. On the outer surface of the initial chamber inside the aperture of the ammonitella, structures

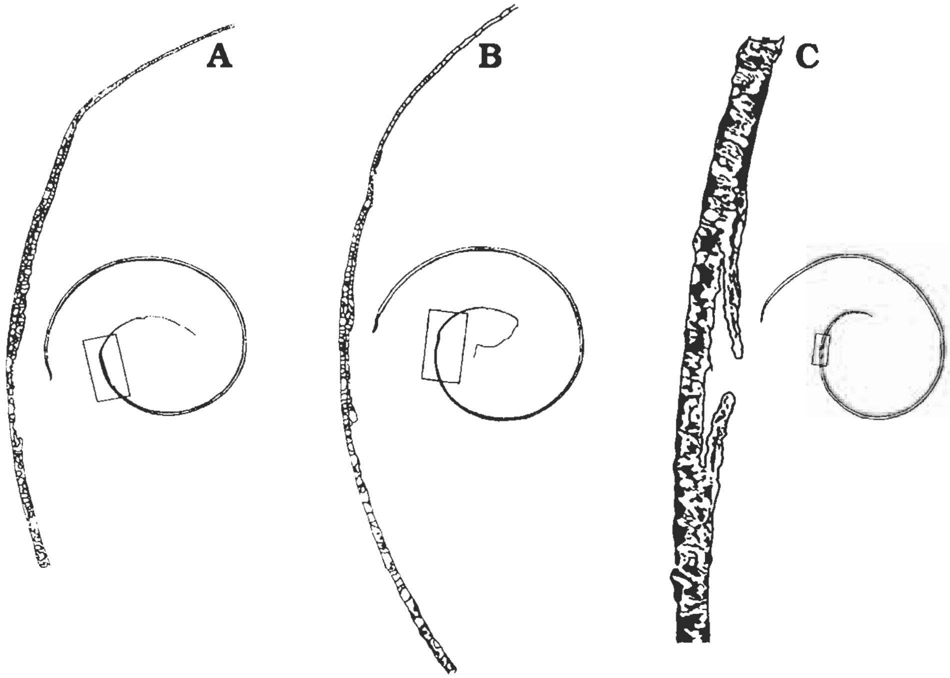

Fig. 5. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. ❑A–B. Two ammonitellae in similar calcification phases of the initial chamber; in both cases the internal prismatic layer before the base of proseptum is developed; A – at non-calcified proseptum the wall thickness distinctly decreases, with no internal plates; B – wall of the initial chamber partly calcified, its remaining part smoothly bent, indicating lack of calcification. ❑C. Longitudinal section of *Aconeceras* ammonitella in the second calcification stage. Enlarged section of the wall with a base of non-calcified proseptum.

resembling wrinkle-layers are visible in the section. The wrinkles have a mild adapical slope, but a steep adapertural one (Figs 9C–D, F, 13F). These elements belong to the dorsal wall and reach up to 90° into the living chamber of the ammonitella. In the specimen described by Kulicki (1979: Pl. 44: 3) and reproduced here (Fig. 13F), the same wrinkle-like elements are seen for some distance in front of the caecum and prosipho, but are embedded in a subprismatic layer of dorsal wall. Such state indicates a complex multi-layered structure of dorsal wall. As already mentioned by Kulicki (1979, p. 120) and further evidenced by the illustrated material (Figs 9C–D, F, 13F), there is no sharp border between the external wall of the initial chamber and the dorsal one of the first whorl, although they differ in their microstructure. Instead a sharp border occurs between the dorsal wall and the ventral one of the subordinate whorl, with the appearance of tuberculous ornamentation on the subordinate wall.

The ammonitella from Łuków, similarly as ammonitellae of *Aconeceras*, has a tri-layered structure of the wall of the first whorl, but the median layer is much thicker there, and also the external and internal layers do not indicate such an aggregation of aragonite needles as in *Aconeceras* (Fig. 10).

Ornamentation of ammonitella walls

On the outer surfaces of Mesozoic ammonitellae there is a characteristic tuberculous ornamentation (Fig. 11D). In *Aconeceras* the tubercles are connected with the central part of external plates (Fig. 11F). Sections of *Quenstedtoceras* and *Aconeceras* show that the tubercles are simply outside extensions of aragonite needles of the external layer (Fig. 9B–C).

On the basis of several longitudinal sections of ammonitellae from Łuków it could be determined that the tuberculous sculpture covering the whole outer surface of the first whorl and umbilical walls of the initial chamber, does not cover the wall of the initial chamber under the first whorl, similarly as determined by Bandel (1982) and Landman (1987).

Interpretations

The problem of diagenetic alteration

In the preceding chapter the series of ammonitellae with incomplete and complete wall layering has been interpreted as a result of progressive calcification of the primary organic shell. However, an alternative interpretation could be offered that this is actually a series leading from ammonitella with complete walls to incomplete ones as a result of early diagenetic decalcification processes.

The following observations support our thesis:

(1) The complete nacreous primary varix is always accompanied by a completely calcified very thin and delicate wall of the initial chamber. There are no specimens with a nacreous thickening without that wall.

(2) Non-calcified and broad proseptum base at the first and second stage is covered frequently by fine internal plates on a considerable, well preserved surface (Figs 5C, 8D). During fossilization the organic matter of the proseptum was decomposed and the remaining free space was filled with the same kind of cement as the remaining part of the initial chamber and the first whorl.

It seems hardly possible to maintain such high correlation in occurrence of nacreous thickening with an entirely calcified wall of the first chamber in the process of dissolution of entire ammonitic shells. Also

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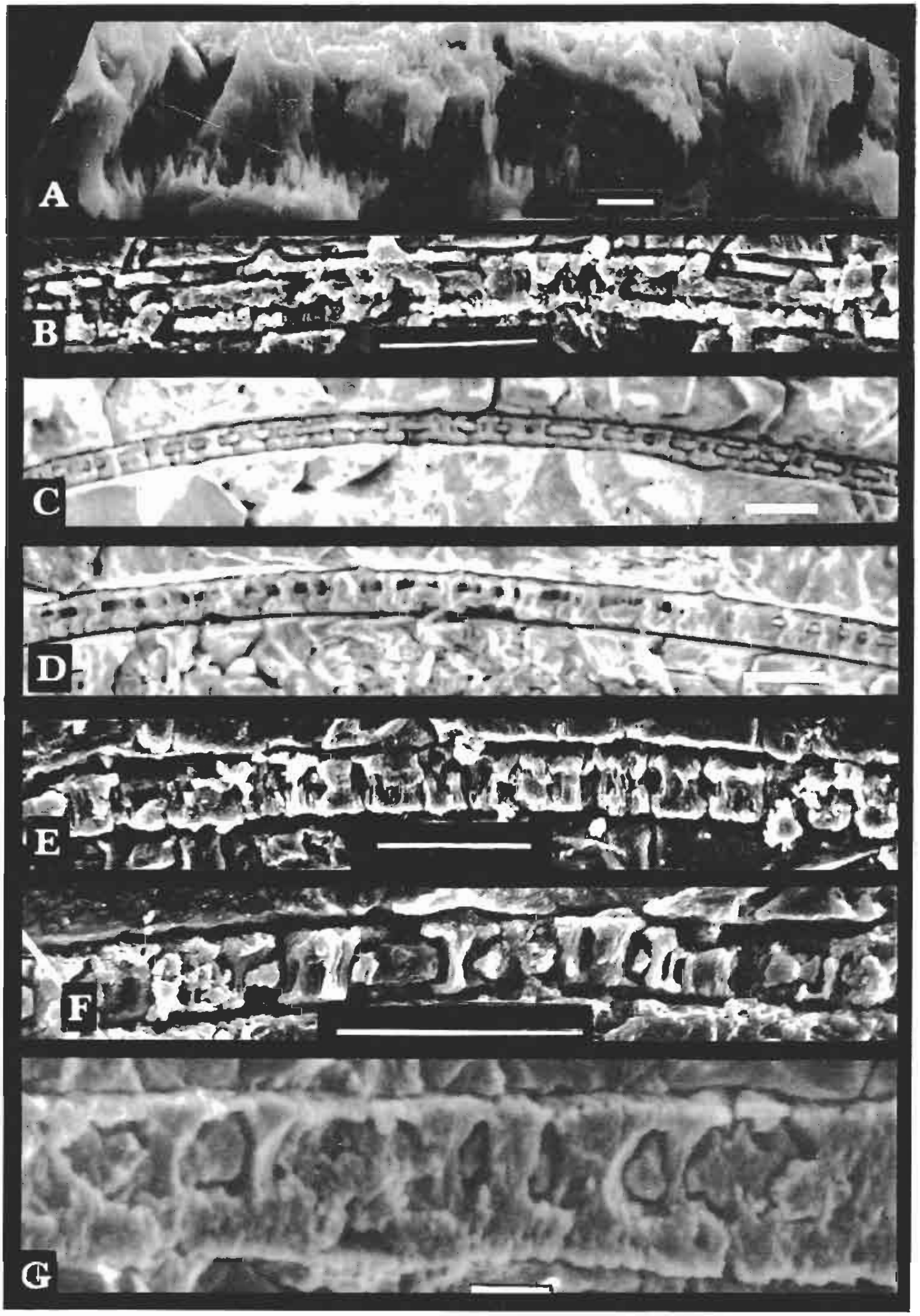
Fig. 6. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. Sections of wall of first whorl of ammonitella. ❑A. Thin needle-like elements of primary structure prepared in H_2O_2. Scale bar 1 µm. ❑B–G. Section of poorly calcified wall, layer of extrenal plates at the top, and of internal plates, junctions between layers of plates sporadic and barely developed; C – more numerous junctions between



layers of plates; D – wall stronger calcified; layer of internal plates (at the bottom) is much thicker; E – sporadic primary needle-like elements; G – layer of internal plates slightly thicker, visible needle-like primary elements: all treated in EDTA. Scale bars 10 μm except for G, which is 2 μm.

selective dissolution of the whole proseptum with the broad base (when at the same time fine inner laminae covering the proseptum base remain untouched) seems unlikely.

Inferred calcification model

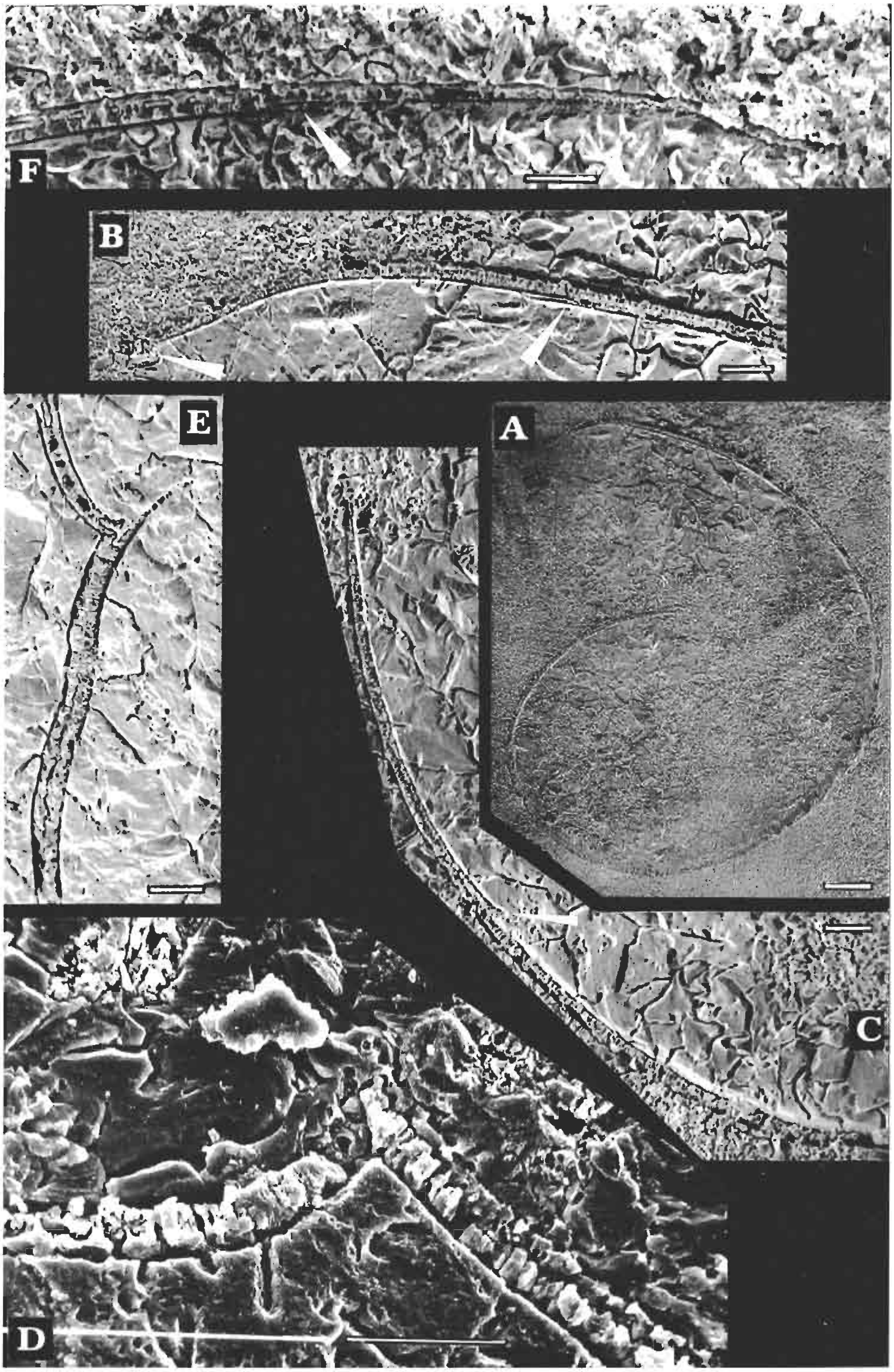
Wall of the first whorl of ammonitella. — The characteristic termination of the calcified part of the shell on the side of the initial chamber in the first stage (Figs 3A–B, 4A), and the observed increase of mineral elements and junctions among plate layers at that termination, suggest that it was the front of calcification of the organic primary shell moving from the end of the first whorl towards the initial chamber, and so in opposite direction than the secretion of the primary shell.

Bandel (1982) proposed that calcification of the primarily organic shell wall of ammonitella was secondary, as in the Archaeogastropoda, although he was not able to prove this with evidence on actual specimens.

Judging from longitudinal sections of calcification front in *Aconeceras* the first mineral elements that have been formed were more or less the hexagonal plates on the outer surface of the organic primary shell. Then a lamina of internal plates was formed having a similar structure as the external one and identically packed. The growth of external plates to the inside and thus junction of two layers, external and internal, produced a median layer calcified to a various extent.

According to this model (Fig. 4A), the source of calcium carbonate were soft tissues lining the shell inside, and the first surface for the growth of aragonite crystals would be the external organic membrane on the outside of the organic shell. The second surface would be the inner surface of organic shell. In the further calcification process a median layer was formed, in result of mineralization of the internal layer of the organic primary shell, joining the layers of external and internal plates. A free space visible in the median layer and filled with calcite or kerogen is preserved, because this layer is not completely calcified or perhaps due to the inhibiting effect of organic matter on the growth of aragonite crystallites.

Fig. 7. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. Sections of ammonitellae. Scale bars 10 μm except for B–C, which is 50 μm. ❑A–C. Longitudinal section of ammonitella in final phase of the first stage; B – enlarged apertural margin; treated in EDTA, distal thickening and poorly developed step indicated by arrows; C – enlargement of the opposite edge of ammonitella shell illustrated in A (arrows indicate the end of inner prismatic layer of the initial chamber). ❑D. Cross-section of the surroundings of seam dividing the umbilical wall of the initial chamber from the first whorl. Treated in HCl. ❑E. Section as in D, but with the wall separating the interior of the initial chamber from the inside lumen of the first whorl incipiently calcified. ❑F. Section of the apertural margin of ammonitella at the same stage as in B but without a distinct return section of the prismatic layer in the distal part. Proximal part with a step indicated by arrow; treated in HCl.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The inferred model of calcification of the organic shell of the ammonitella resembles the calcification of the larval shell in the archaeogastropod *Haliotis discus*, described by Iwata (1980).

In ammonitellae from Łuków the median layer of the first whorl displays usually a greater thickness and differs microstructurally from the corresponding layer in *Aconeceras*. Further differences concern the aggregation of crystals. In the wall of the first whorl of *Quenstedtoceras*, there are no pseudohexagonal trillings and the aragonite needles of the external layer do not go through the whole thickness of the wall and do not join the internal layers. These differences concerning the microstructure and aggregation of crystals in the wall of the first whorl in *Aconeceras* and *Quenstedtoceras* should be perhaps explained by different thickness of the primary organic shell wall and its physico-chemical structure, i.e., in ammonitellae of *Aconeceras* from Symbirsk it was thinner than in ammonitellae from Łuków.

Wall of initial chamber. — Umbilical walls of the initial chamber are calcified at the same phase as the external wall of the first whorl (cf. Bandel 1982). Differences in the thickness of the walls of the first whorl and initial chamber in the umbilical part and others may be due to: (1) different thickness of the primary organic wall undergoing calcification, or (2) secondary thickening of walls from the inside.

The importance of the first factor is suggested by the fact that the wall of the initial chamber in its apical part is much thinner than that of the first whorl. However, in the wall of the first whorl, the inner prismatic layer below the median represents a thickening from the inside of the original wall of ammonitella due to secretive-calcification activity of the mantle and not the secondary calcification of the primarily organic wall.

Within the initial chamber such thickening is behinde the proseptum and there it originated in a similar way as in the wall of the first whorl. The wrinkle-like elements belong to the dorsal wall and they subsequently were covered with laminae of the dorsal wall, as in the postembryonic shell (Kulicki 1979: Fig. 9).

The lack of a distinct boundary between the dorsal wall of the first whorl of the ammonitella and the wall of the initial chamber may result from

Fig. 8. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. Sections of ammonitellae. ❑A. Longitudinal section of ammonitella in the third stage of calcification. Visible nacreous primary varix and calcified proseptum; treated in HCl. Scale bar 50 µm. ❑B. Cross-section of ammonitella in the surroundings of seam dividing the umbilical wall of the initial chamber from the wall of the first whorl of ammonitella. The wall of the initial chamber dividing its interior from the inside lumen of the first whorl is well calcified. Dorsal wall of the first whorl is missing; treated in HCl. Scale bar 10 µm. ❑C. Longitudinal section of apertural margin of ammonitella shell with a well developed return section of prismatic layer in the distal part, and without traces of secretion of nacreous layer; prepared in H_2O_2. Scale bar 10 µm. ❑D. Longitudinal section of ammonitella wall near the proseptum base. Two laminae cover the inside of proseptum base; prepared in H_2O_2. Scale bar10 µm.


B
C
A
D

simultaneous calcification of the organic primary wall of the initial chamber and secretion of the dorsal wall of first whorl in the egg capsule. The disparity between the dorsal wall of ammonitella and that of postammonitella observed in *Quenstedtoceras* shortly before the caecum, is due to a dorsally thiner wall and tuberculous sculpture of the ammonitella wall.

Changes in thickness and structure of the dorsal wall of the first whorl before the nepionic varix and behind it are the probable reason of divergence in interpretations of the wedging out of the original wall of the initial chamber (Birkelund 1967; Birkelund & Hansen 1968; 1974; Erben *et al.* 1969; Bandel 1982; Tanabe 1989; Tanabe *et al.* 1993). As the nepionic varix is the last element of the embryonic shell, the sharply delimited dorsal wall must be a result of postembryonic developmental processes.

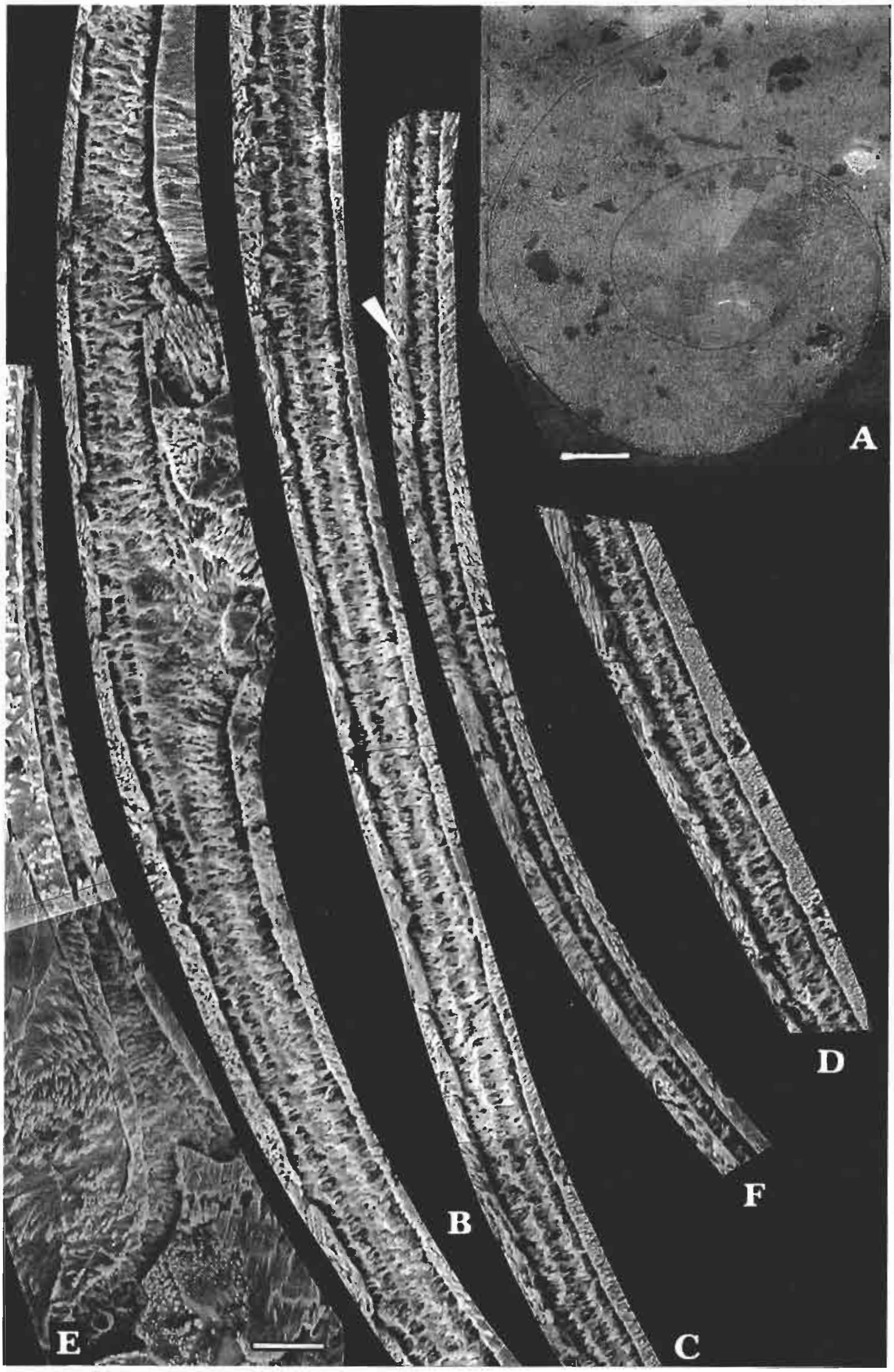
Proseptum. — Proseptum as an organic structure separating the initial chamber from the first whorl, existed before the surroundings of its ingrowing to shell walls were calcified. Fig. 8D shows that as soon as the ammonitella wall was calcified and started to thicken from the inside, the proseptum and its broad base ingrowing to the primary organic wall were not calcified yet.

As regards the moment of proseptum calcification and the formation of the nacreous layer of the primary varix, our data show that these events were almost simultaneous. An ammonitella from Łuków with a fully developed primary varix has two distinctly formed septa (proseptum and the first nacroseptum).

The presence of internal prismatic layer and thickening of the primary wall of the ammonitella from the inside, on both sides of the proseptum, indicates also the presence of soft tissues on both sides of the proseptum (Figs 8D, 13E). In extremely lateral sections (Birkelund & Hansen 1974, Fig. 2, Kulicki 1979, Fig. 10C) the inner prismatic layer is only present adoral the proseptum on the side of the first whorl.

Thus, it can be concluded, that the non-calcified and organic wall of the proseptum was formed and fixed also to an organic and non-calcified wall of the external ammonitella shell, when the soft tissues were partly withdrawn from the interior of the initial chamber. In the part of the initial chamber containing the whole breadth of the external saddle the soft tissues were most probably in touch with the shell wall during the formation of the proseptum (Fig. 1H).

Fig. 9. *Quenstedtoceras* sp., Late Callovian, *Quenstedtoceras henrici* Subzone, glacial drift, Łuków, Poland. Ammonitella, specimen treated in chromium sulfate + HCl. ❑A. General view of the longitudinal section. Scale bar 100 μm. ❑B–F. Longitudinal section of ammonitella wall in the vicinity of proseptum and second septum; a section of tuberculous ornamentation is visible; C – continuation of B; in the part closer to proseptum a section of tuberculous ornamentation is visible, in the following part, triangular wrinkle-like elements appear on the outer surface; D – continuation of C with visible wrinkle-like elements; E – section of dorsal part of the initial chamber; flange, proseptum, and posterior auxilliary deposit (also called cuff) (c) prove that caecum was developed although is not preserved; F – continuation of E with a short break and a distinct wrinkle-like element (indicated by arrow). Scale bars 10 μm.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Apertural edge of ammonitella shell. — The characteristic feature of the apertural edge of the ammonitella shell is its shape, deviating from normal in the distal portion of the apertural margin. In *Quenstedtoceras* from Łuków, the last part of the whorl (ca 140^0) does not indicate a radius increase and approximates a circle (Kulicki 1974). In the section, where primary prismatic layers are thinning out, the shell's curvature is bent more into the aperture, whereas the last distal section is flanged outwards (Figs 3A, 7A, 8C, 9A). The outside view shows a constriction across the whorl, parallel to the apertural edge (nepionic constriction or primary constriction).

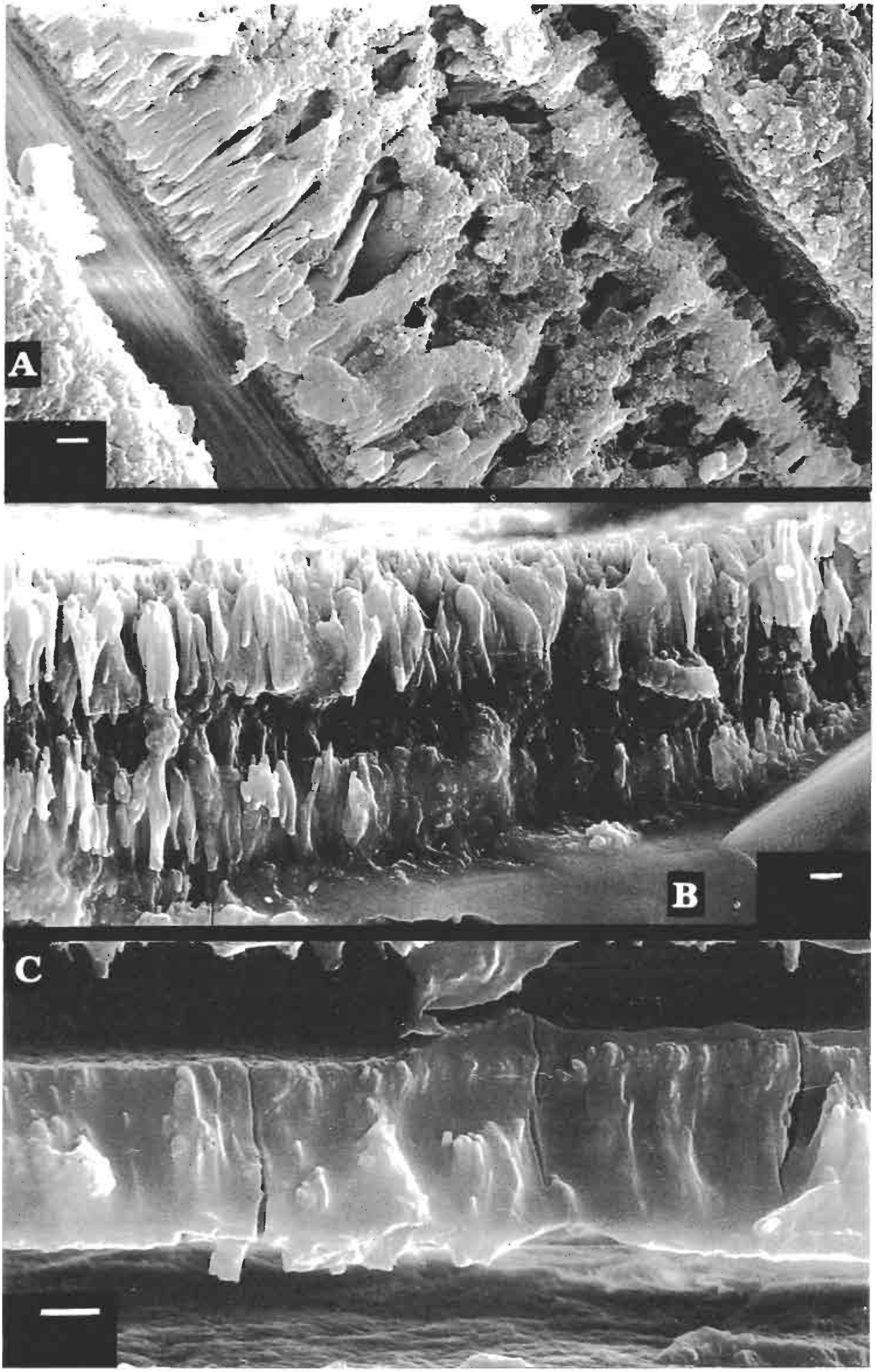
Such shape of adapertural surroundings as described above characterises the ammonitellae from Symbirsk, which do not have yet the nacreous primary varix and the wall of the initial chamber is not calcified. This is a diagnostic feature for determining the definitive aperture of the ammonitella.

The zone with observed thinning of shell near the aperture corresponds probably to the secretion zone of the primary organic shell. Epithelium cells of this zone must have been closely attached to the shell. The sharp thickening of shell wall from the inside observed in the posterior part of primary constriction (Figs 7B, F, 14D) was caused by gaining calcium secretory properties by the underlining epithelium, not observed before but connected with physiological reconstruction of not only epithelial cells but also of connective tissue (Kniprath 1977; Timmermans 1969). As a result of calcium secretory activity of epithelium behind the constriction zone itself, the primarily organic wall of embryonic shell was calcified and also grew thicker from the inside.

The short return section of prismatic layer observed in the distal part of the aperture (Figs 7B, 8C, 14D) should be connected with the formation of the free edge of the mantle and a characteristic furrow, in which the most external organic part of the shell – the periostracum is secreted.

The primary varix would be formed due to the secretion of free mantle edge, differentiated as usual into three secretion zones, but still in egg cover before hatching.

Fig. 10. *Quenstedtoceras* sp., Late Callovian, *Quenstedtoceras henrici* Subzone, glacial drift, Łuków, Poland. Ammonitella, sections of wall. Scale bars 1 µm. ❑A. Section of ammonitella wall before the primary varix; external layer (right side) relatively thin, made of thin needle-like crystallites, internal layer (left side) of greater thickness consists of similar elements as the external one, middle layer of irregular, granular structure (empty spaces giving it spongy appearance developed in result of preparation in H_2O_2 which removed organic matter and kerogen). ❑B. Section of wall of the initial chamber before proseptum. External layer (top) of similar thickness as the internal one (bottom). Both layers consisting of thin needle-like crystallites are divided by a thin middle layer. Prepared in H_2O_2. ❑C. Section of wall of the initial chamber of ammonitella in the vicinity of the apical one. The wall is uni-layered and the needle-like crystallites penetrate its whole thickness. Prepared in H_2O_2.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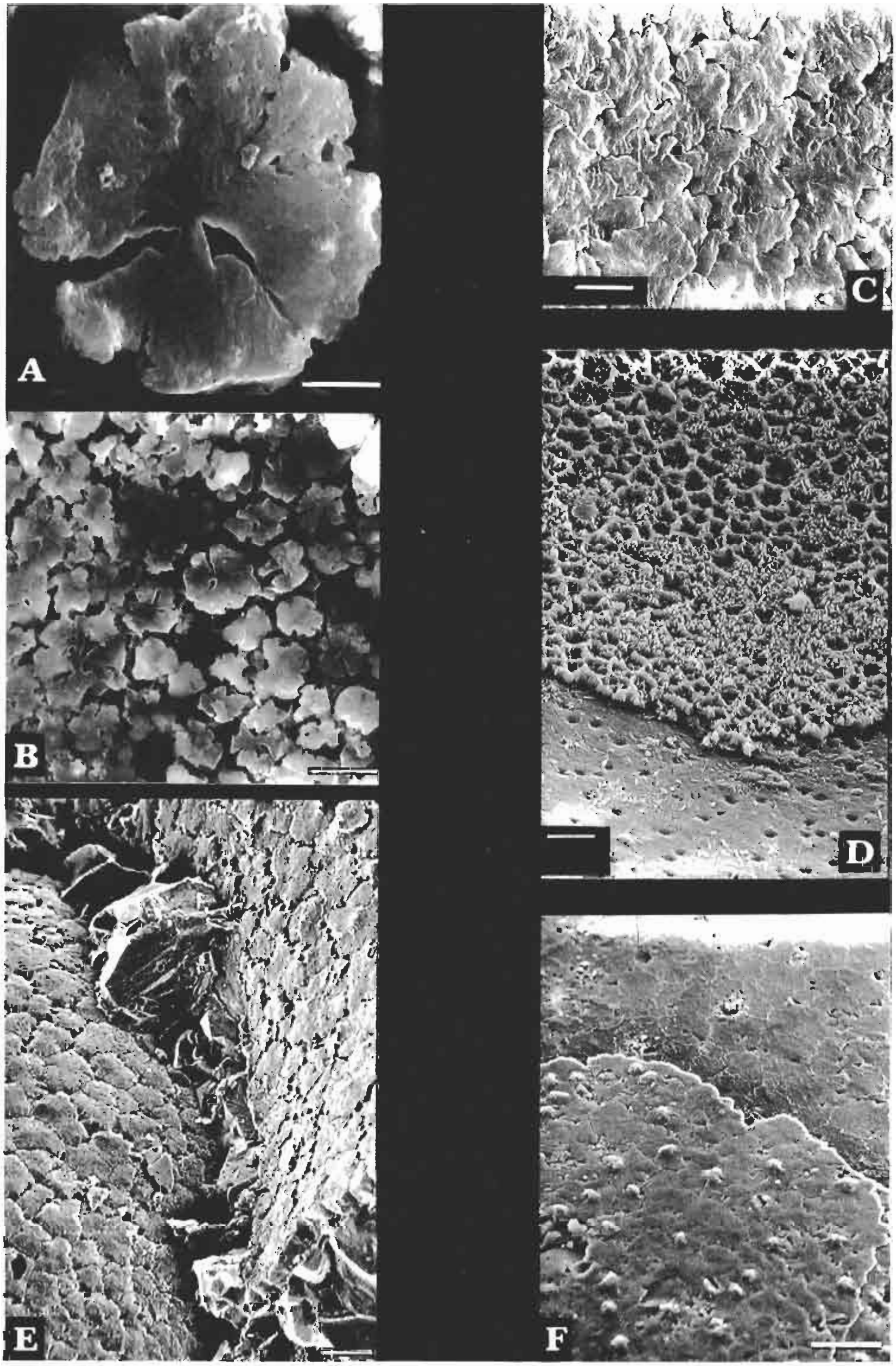
Structural diversity of ammonitellae and comparisons with gastropod protoconchs

In *Aconeceras trautscholdi* the thickness of the wall of first whorl after the proseptum is 3.8 μm, and before the primary varix 6.7 μm. The internal prismatic layer has some thickness, does not occur continuously, usually observed near the septa base. In *Deshayesites deshayesi* wall thickness near the proseptum is 6.7 μm, before the primary varix 16.7 μm, and after the primary varix 12.0 μm. The thickness of the internal prismatic layer in the proximal part of the primary varix is 10.0 μm. In *Quenstedtoceras* sp.the thickness of the wall the beyond proseptum is 9.3 μm, before the primary varix 11.3 μm and after the varix 11–13 μm. The thickness of the internal prismatic layer is slight, fluctuating between 1 and 2 μm.

In all three cases there is no disproportion at this stage as regards the thickness of the shell wall before the primary varix, and of early postembryonic shell. In the case of *Aconeceras* both walls have a small thickness as related to the two other genera. *Deshayesites* and *Quenstedtoceras* have similar thickness of walls of embryonic shell and of the first whorl. The difference in ammonitella wall at this stage is such that in *Deshayesites* there is a very thick internal prismatic layer, whereas in *Quenstedtoceras* this layer is very thin. Such disproportion in the thickness of internal prismatic layer suggests that in *Deshayesites* the primary organic wall of the first whorl was relatively thin, such as in *Aconeceras*, and the prismatic layer added from the inside balanced the disproportions in the thickness of both walls (Fig. 14A–C).

In *Quenstedtoceras* the organic primary wall of the first whorl of the ammonitella was probably much thicker, resembling the thickness of the postembryonic shell. Fig. 10A–C shows sections of the first whorl of ammonitella and initial chamber in *Quenstedtoceras*. Two prismatic layers are visible, and in between there is a middle layer of a less organized structure corresponding to the internal part of the primary ammonitella shell. In this case, the organic matrix limits probably the formation of full, undisturbed crystals and crystallites. In Fig. 10C there is a wall of the initial chamber of *Quenstedtoceras* ca 180° beyond the flange. Needle-like crystallites go there through the total wall thickness.

Fig. 11. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. All preparations in H_2O_2; ❑A–B. Pseudohexagonal trilling; view of delaminated ammonitella wall. Scale bars 5 and 1 μm, respectively. ❑C. View of outer ammonitella surface showing pseudohexagonal trillings. Scale bar 3 μm; ❑D. Inner side of delaminated ammonitella shell; external mould shows tuberculous ornamentation. Scale bar 10 μm. ❑E. View of outer surface of ammonitella at the umbilical seam. External outline of pseudohexagonal trillings of umbilical wall of the initial chamber does not differ from the outline of the same elements on the first whorl. Scale bar 10 μm. ❑F. Outer surface of ammonitella shell showing outline of pseudohexagonal trillings and tuberculous ornamentation; tubercles occur in the central part of the trilling, some of the trillings do not have tubercles. Scale bar 10 μm.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As regards the aggregation of crystallites in the external layer, thickness and structure of median layer, the wall of first whorl of *Aconeceras* differs from that of *Quenstedtoceras* (Figs 11C, E–F, 13E). According to the above interpretation (Fig. 4A), the layers – external, median and partly internal – correspond to the calcified organic wall of the primary organic shell. However, the internal layer was mostly formed by thickening from the inside of primary shell wall.

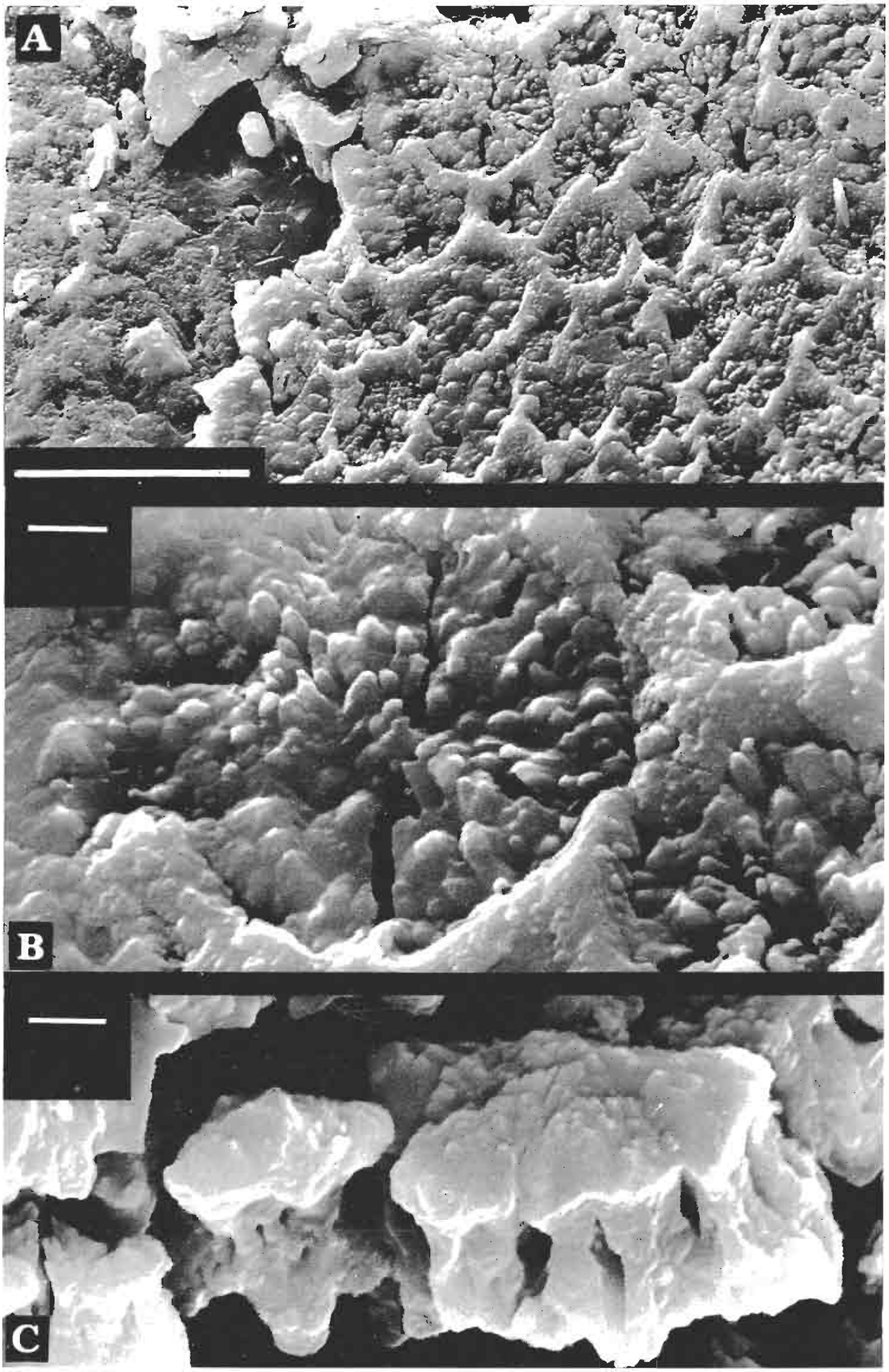
The external aragonite layer probably was not the most external shell element. This was probably the organic membrane, which was not calcified, which Iwata (1980) determined in the archaeogastropod *Haliotis* as periostracum, and on which he did not observe directly a deposition of aragonite crystallites. Nucleation of crystals in *Haliotis* occurs within organic spherules deposed under the external organic membrane. The orientation of crystallites is accidental, but crystallites contacting the external organic membrane are much more arranged and almost perpendicular to the shell surface (Iwata, 1980). As regards the microstructure, the external and middle layer of *Haliotis* larval shell resembles greatly the *Quenstedtoceras* embryonic shell (cf. Fig. 10A; Iwata 1980; Pl 5: 1)

The primary organic wall of the first whorl in *Aconeceras* and also in *Deshayesites* was thinner than in *Quenstedtoceras* (11 μm in *Quenstedtoceras* and 4–5 μm in *Aconeceras*, measured before primary varix without internal layer), This difference in thickness of the primary organic wall affected probably the aggregation of crystallites of external, middle and internal layers. Borders between external and internal plates overlap (Fig. 11F), and in places where external plates are connected with internal ones, aragonite needles consistently penetrate all three layers (Figs 6A, E–G). In the middle layer, in between aggregates there are free spaces originally filled with organic matter and then with secondary calcite or kerogen. The difference in the degree of filling the space between external and middle layers may coincide with the laminar structure of primary organic shell and different physico-chemical properties of its particular layers.

Kniprath (1977) has described in Recent pulmonate gastropod *Lymnea*, the ontogenesis of larval shell with several-layer external components and proposed reconstruction of epithelial cells responsible for the secretion of these laminae. He also found that in early ontogenesis the shell field produces some organic layers, which do not have an equivalent in later phases.

Dunachie (1953) has described a tri-layer periostracum in *Mytilus edulis*, the middle layer of which has a regularly vacuolar structure. In

Fig. 12. *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. Prepared in H_2O_2. ❑A–B. Delaminated ammonitella shell from inside showing pseudohexagonal trillings. Scale bar 10 and 1 μm, respectively. ❑C. Oblique view of pseudohexagonal trilling (right side) and its separated part (left side). showing full thickness of ammonitella shell wall; outer surface at the top, trillings are closely packed in external and internal parts, whereas in the middle part there are gaps. Scale bar 1 μm.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other *Mytilus* species vacuoles do not occur regularly and frequently do not occur at all.

The examples above have been given to support the thesis about the possibility of chemical and structural differentiation of particular layers of primary organic shell. Differences in the formation of the middle layer of the first whorl of ammonitellae of *Aconeceras* and *Quenstedtoceras* may be not only due to the difference in thickness of the primary organic wall but also to different physico-chemical properties of particular layers, or their structural diferentiation. Aggregation of crystallites in external, middle, and internal layers may depend on this.

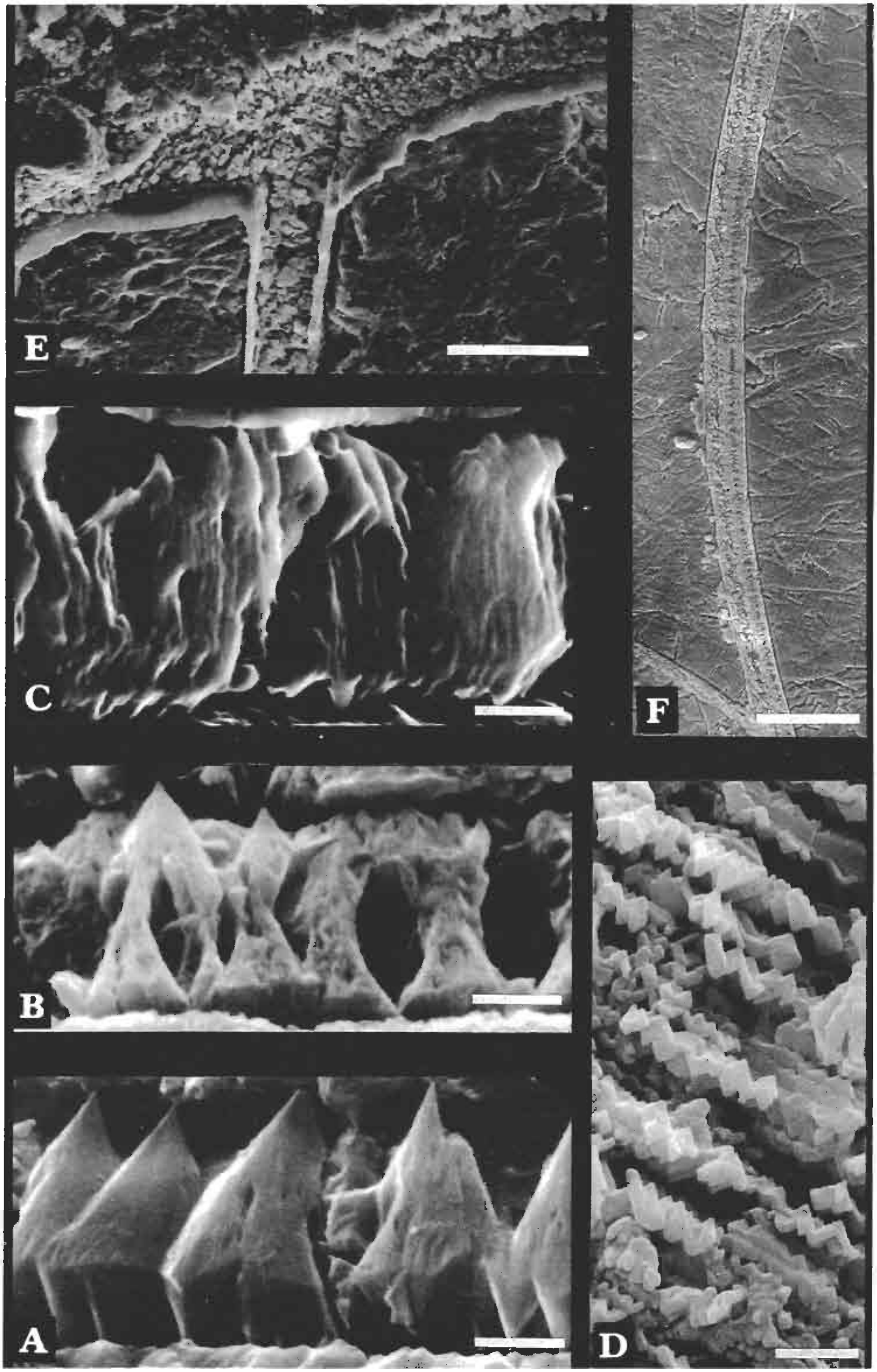
Tuberculous ornamentation of Mesozoic ammonitellae (Kulicki 1974; 1979; Bandel 1982; Bandel *et al.* 1982; Landman 1987; Tanabe 1989) caused the last author to formulate the endocochliate embryo model. The key-role in this model is played by an analogy to a similarly ornamented contemporary *Spirula* shell. A counterargument in the discussion may be a similarly ornamented archaeogastropod larval shell, such as *Haliotis* examined by Iwata (1980: Pl. 5: 3), or *Haliotis tuberculata* (Bandel 1982: Pl. 4: 7, 10) and many other Archaeogastropoda illustrated by Bandel (1982).

Conclusions

1. The primary ammonitella shell was made only of organic matter and consisted of the initial chamber and first whorl together with the primary constriction.

2. The primary organic shell was formed as a result of secretion in marginal zones of embryonic shell field. With the development of shell field the breadth and number of secretion zones of the organic shell changed and thus there was one or several layers and differences in their thickness.

Fig. 13. ❑A–C *Aconeceras* cf. *trautscholdi* (Sinzov 1870), Early Aptian, *Deshayesites deshayesi* Zone, vicinity of Symbirsk, Russia. Ammonitellae. Section of the wall of first whorl, external side of shell at the top; prepared in H_2O_2. Gaps develop in the middle part in effect of prolonged preparation (B), if preparation time was much shorter (C), on the surface of crystalline elements fine parallel stripes are visible, which indicate aggregates of thin needle-like crystallites. Scale bar 1 μm. ❑D–F. *Quenstedtoceras* sp., Callovian, *Quenstedtoceras henrici* subzone, glacial drift, Łuków, Poland. D. Nacreous layer of primary varix. Outer shell surface at the bottom, particular laminae consist of crystalline elements similar as in A. X Ray-analysis of nacreous layer of the specimen shows only the presence of aragonite. Scale bar 2 μm; E. Section of ventral wall of ammonitella (fourth stage) at the place of proseptum in growth. Border surface of proseptum form a discontinuity in internal prismatic layers and reach the primary wall of ammonitella shell. At the top the uncovered outer surface of primary shell visible with irregular borders between aragonite aggregates; treated in EDTA. Scale bar 10 μm. F. Longitudinal section of ventral wall of the initial chamber of ammonitella (fourth stage) before proseptum. In the dorsal wall of the first whorl visible totally incorporated, diagonal wrinkle-like elements: treated in EDTA. Scale bar 20 μm.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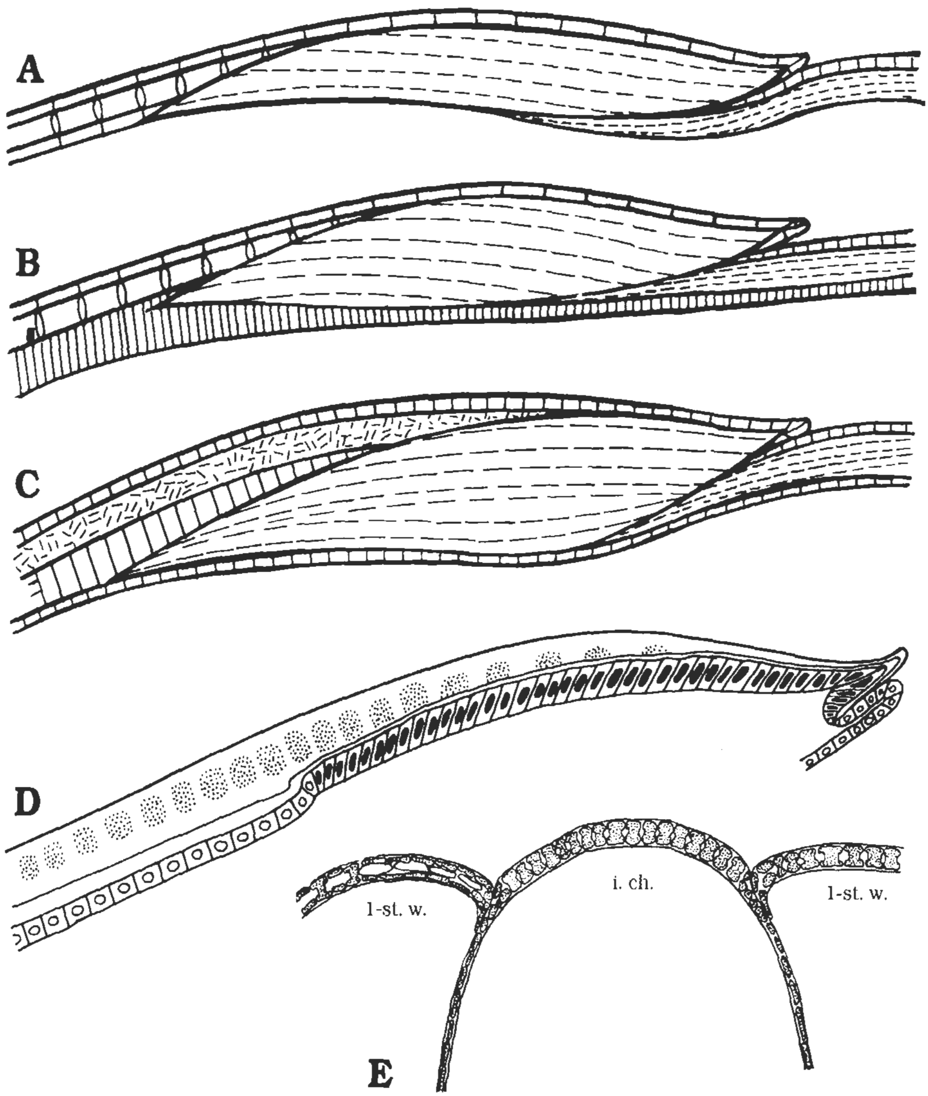

Fig. 14. ❑A–C Schematic section of primary varix in *Aconeceras trautscholdi* Sinzow 1870 (A), *Deshayesites deshayesi* (Leymerie 1841) (B), and *Quenstedtoceras* sp. (C). Sections differ in the thickness of internal prismatic layer in ammonitella wall before the primary varix, and by the relation of most internal laminae of nacreous layer to internal prismatic layers, best seen in the proximal part of nacrous primary varix. ❑D. Schematic longitudinal section of the distal part of ammonitella shell with the epithelium after the final phases of the first stage. The periostracal furrow is already developed (p.g.), whereas the epithelium in contact with shell developed biocalcification properties expanding towards the apical parts of the shell. The presence of a step-like thickening in the proximal part of constriction indicates difference properties of epithelium in different areas of the inner shell surface. ❑E. Cross-section of the initial chamber and first whorl of ammonitella of *Aconeceras* (third stage).

3. The proseptum is formed as a structure from organic matter before the calcification of the external shell of the ammonitella.

4. As soon as the finite aperture of the ammonitella is formed, secretion zones undergo reorganization: (a) Broad secretion zone responsible in its last phase for the secretion of organic wall of the first whorl is no longer active. Cells of this zone are in contact with the organic shell. (b) On the edge of the aperture a periostracum furrow forms – characteristic element for the free mantle edge. (c) The remaining part of the epithelium behind the secretion zone of the primary organic shell obtains biocalcifying properties. The zone of biocalcification properties broadens gradually the apical part of shell.

5. The result of biocalcification activity of the mantle epithelium is the calcification of the primary organic shell wall (external and middle layers form) and thickening of the shell to the inside (internal layer forms).

6. First of all the first whorl and umbilical walls of the initial chamber are calcified, and afterwards the remaining part of the wall of the initial chamber. In the last phase the proseptum becomes calcified and the nacreous primary varix is formed.

7. In the dorsal part of the living chamber of the ammonitella there is a wall showing wrinkle-like elements in the front part. The border between the dorsal wall and calcified primary wall is not sharp, crystallites of one layer are elongate as crystallites of the second one. With the end of the aperture of the ammonitella the thickness of the dorsal wall decreases, and the border between it and the ammonitella wall becomes very distinct. From this place the ventral wall is covered by microtuberculous ornamentation typical for ammonitellae.

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Streszczenie

Muszle embrionalne (amonitelle) *Aconeceras*, masowo występujące w konkrecjach aptu Symbirska, ukazują kolejne stadia kalcyfikacji ścianek. Pierwotna muszla amonitelli była niezmineralizowana, podobnie jak muszla larwalna dzisiejszych ślimaków Archaeogastropoda.