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Development of the Embryonic Shell Structure of Mesozoic Ammonoids

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ABSTRACT

Exceptionally well-preserved embryonic shells (ammonitellae) of the early Aptian ammonoid *Aconeceras* cf. *trautscholdi* Sinzov, 1870, preserved as coprolite remains from Symbirsk, Russia, were examined with scanning electron microscopy (SEM) to investigate the developmental sequence of the embryonic shell structure. Our SEM observations reveal that these shells can be classified into the following three groups with different wall microstructure: Group 1, with a thin (ca. 5 μm), double-layered shell wall, consisting of inner prismatic and outer homogeneous layers, the former of which is absent in the adapical portion and becomes thicker adorally; Group 2, with a three-layered shell wall that consists of inner prismatic, middle homogeneous, and outer prismatic layers, with tubercles on the outer layer; and Group 3, with a thick nacreous swelling (primary varix) on the anteroventral side near the aperture. The middle homogeneous layer of the embryonic shells of Group 2 is the same as the outer homogeneous layer in shells of Group 1 and may be composed of amorphous calcium carbonate (ACC). In embryonic shells of Group 3, the middle homogeneous layer is absent and there are voids instead. It may have been transformed into the inner prismatic layer or else dissolved during diagenesis.

In modern *Nautilus* and gastropods, embryonic or larval shell development is initiated by the secretion of a cap-shaped, fully organic shell prior to the deposition of calcium carbonate. This stage is not preserved in the material examined, but probably existed in the Ammonoidea. Based on our observations and data from extant *Nautilus* and gastropods, we propose a model for the development of the embryonic shell structure of Mesozoic ammonoids, starting from secretion of an organic primary shell, followed by deposition of ACC and its transformation into the inner prismatic layer, and terminating in the deposition of a primary varix on the inside of the ventral and ventrolateral position of the shell just adapical of the aperture.

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INTRODUCTION

Reconstruction of the early ontogeny of extinct organisms is an important subject in paleobiological research. However, this is usually difficult in invertebrates, because remains of embryos and larval soft tissues are very rarely preserved in the fossil record, except for special circumstances (e.g., phosphatized soft tissue remains of embryos of bilateralian animals from the Neoproterozoic Doushantuo Formation in southern China; Xiao et al., 1998; but see Bailey et al., 2007, for an alternative explanation). More commonly, only the mineralized hard parts of animals secreted at the embryonic stage are preserved as fossils. Ammonoids, which comprise an extinct group of cephalopod mollusks that flowered in the world's oceans during the early Devonian to the end of the Cretaceous, are examples of such animals. As in other mollusk shells, the aragonitic outer shell wall of ammonoids was formed by accretionary growth, so that the embryonic shell prior to hatching (synonymous with the ammonitella—defined as the initial chamber and part of the next whorl with a distinct constriction at the aperture—by Druschits and Khiami, 1970) is occasionally preserved in the apical shell portion, even in medium to large size shells. Based on microscopic observations of well-preserved fossil material, ammonoids were previously believed to have undergone a post-hatching larval stage before metamorphosis as do modern gastropods and bivalves (e.g., Erben, 1964; Erben et al., 1968, 1969). With increasing knowledge of the early ontogeny of modern cephalopods, especially of modern *Nautilus* (e.g., Uchiyama and Tanabe, 1999), recent authors believe that, like modern cephalopods, ammonoids developed directly without a larval stage (e.g., Druschits and Khiami, 1970; Druschits et al., 1977; Druschits and Doguzhaeva, 1981; Birkelund and Hansen, 1974; Kulicki, 1974, 1979, 1996; Tanabe et al., 1980; Tanabe and Ohtsuka, 1985; Tanabe, 1989; Landman, 1982, 1985, 1987; Bandel, 1982; Bandel et al., 1982; Westermann, 1996; Klug, 2001; Sprey, 2002). According to this theory, the early shell portion consisting of an initial chamber and a subsequent whorl with a nacreous swelling near the aperture was formed within the egg capsule as the embryonic shell, and the ammonoid hatched almost simultaneously after the formation of the primary constriction. This theory of direct development is supported by a number of morphological features including synchronous changes of ornament, shell microstructure, and whorl growth at the primary constriction, as well as discoveries of ammonitellae (e.g., Bandel, 1982, 1986; Landman, 1982, 1985; Kulicki and Wierzbowski, 1983; Kulicki and Doguzhaeva, 1994; Tanabe et al., 1993, 1995).

Opinions, however, are still unsettled concerning the sequence of embryonic shell development, as indicated by three different models: (1) accretionary growth model similar to the embryonic shell development of modern *Nautilus* (see Druschits et al., 1977; Druschits and Doguzhaeva, 1981; Kulicki, 1979; Tanabe et al., 1980, 1993); (2) "archaeogastropod"-type development model emphasizing that the embryonic shell was originally organic (= nonmineralized) (Bandel, 1982, 1986; Kulicki and Doguzhaeva, 1994); and (3) endocochliate embryo model arguing that Mesozoic ammonoids were temporarily enveloped by the outer reflected mantle late in embryonic development (Tanabe, 1989; see Landman et al., 1996: fig. 18). In addition, the process of biomineralization of the tubercles on the embryonic shells of Mesozoic ammonoids has not yet been clearly addressed. To solve these problems, development of the embryonic shell structure was examined based on exceptionally well-preserved ammonitellae of Early Cretaceous ammonoids that retain their original aragonitic shell mineralogy and microstructure.

MATERIAL

Exceptionally well-preserved ammonoid embryonic shells from the lower Aptian of Symbirsk, Volga River Basin, Russia, were examined in this study. They were preserved as coprolite remains, together with small bivalves, gastropods, and fish scales in a clayey calcareous concretion (fig. 1). Immature and mature specimens of *Aconeceras trautscholdi* Sinzov, 1870, and fewer specimens of *Deshayesites deshayesi* (Orbigny, 1840) are also present in the same concretion. Overall

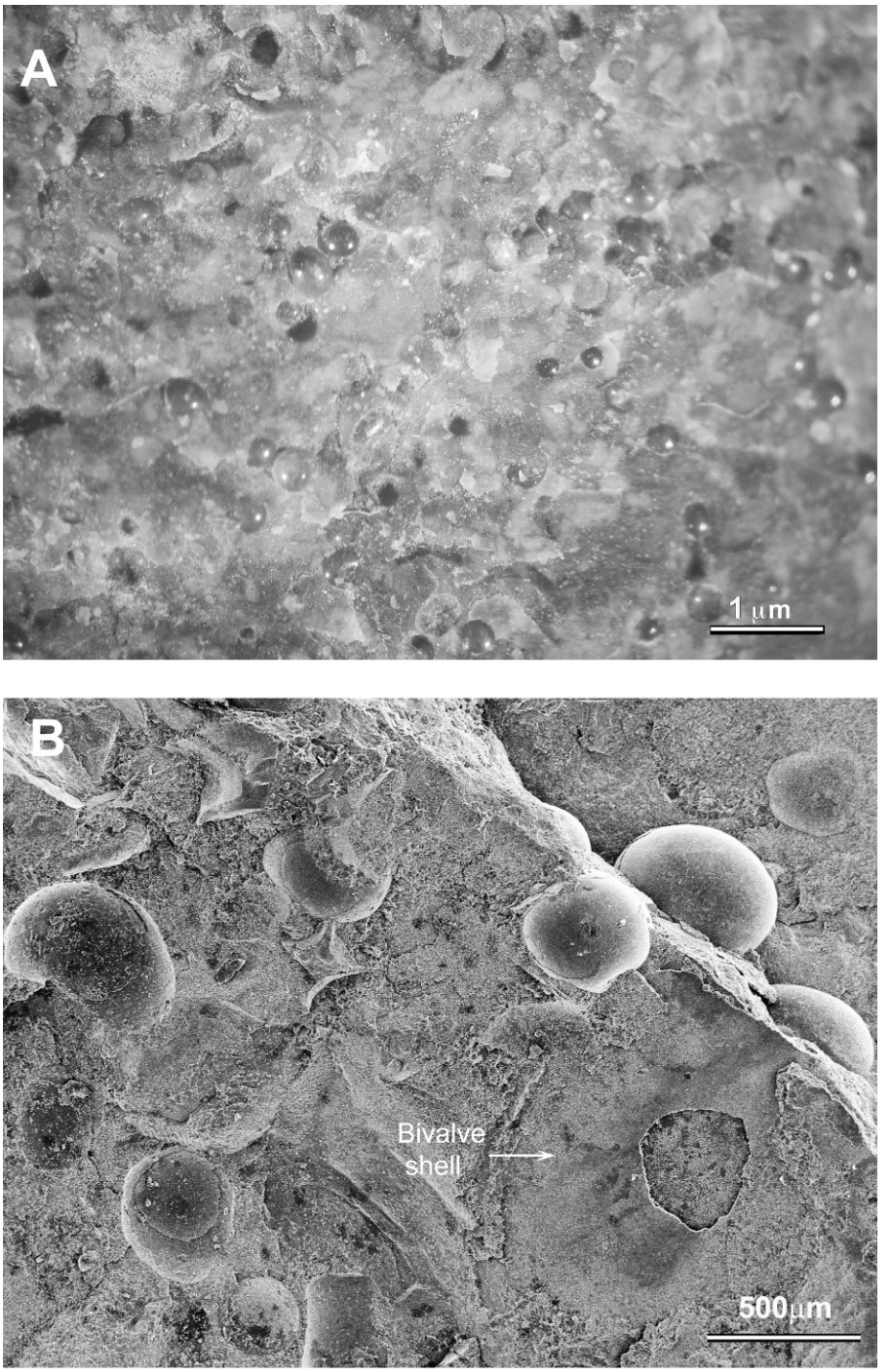


Fig. 1. Embryonic shells of *Aconeceras* cf. *trautscholdi*, lower Aptian, Symbirsk, Volga River Basin, Russia. **A**. Optical micrograph of part of a calcareous concretion, showing the mode of occurrence of embryonic shells preserved as coprolite remains. UMUT MM 29439-1. **B**. SEM of embryonic shells on the broken surface of the concretion. UMUT MM 29440-1.

shape and tuberculate micro-ornamentation of the ammonoid embryonic shells are similar to those of embryonic shells described by Kulicki and Doguzhaeva (1994) as *A.* cf. *trautscholdi* from the same locality. The shells were assigned to this species on the basis of their similarity in overall morphology and internal structure to juvenile and adult shells of this species. Accordingly, we refer our ammonoid embryonic shells from Symbirsk to *A.* cf. *trautscholdi*.

All specimens examined are preserved in the University Museum, University of Tokyo (UMUT).

METHODS

In most previous studies, the embryonic shell microstructure of ammonoids was examined in median and cross section after polishing and etching with weak acidic solution (e.g., Erben et al., 1968, 1969; Kulicki, 1979; Kulicki and Doguzhaeva, 1994; Tanabe et al., 1980, 1993; Druschits and Doguzhaeva, 1981; Landman, 1982). This method is useful in tracing the change in shell wall microstructure from the initial chamber to subsequent whorls, but the details of shell wall microstructure are difficult to observe even in excellently preserved specimens. For this reason, surface ornamentation and wall microstructure in our study were mostly observed by scanning electron microscopy (SEM) (Hitachi S2400 and Philips XL-20) using only naturally fractured embryonic shells without any chemical or physical treatment. SEM images were imported to a desktop computer, where measurements of embryonic shell size, rotation angle (= the angle between line segments from the center of an imaginary circle inscribed inside the embryonic shell and extending to the adapical and adoral edges of the shell wall), shell wall thickness, and tubercle size were made using image analyzing software (Quartz PCI Ver. 4).

To determine the mineralogy of the embryonic shell layers, we also made quantitative elemental analyses of shell microstructure by means of an energy dispersion X-ray microanalyzer (EDAX) attached to the Philips XL-20 SEM.

OBSERVATIONS

Based on the microstructure of the shell wall, the absolute thickness of each layer at different shell sites, the total rotation angle of the preserved shell in medially broken specimens, and the presence or absence of tuberculate micro-ornamentation, the embryonic shells of the present species can be roughly classified into the following three groups.

Group 1

This group is represented by poorly mineralized embryonic shells, all of which possess the following features: (1) absence of a calcified initial chamber wall and tuberculate micro-ornamentation, (2) shell wall consisting of a homogeneous layer in the adapical portion, and an outer homogeneous layer and an inner prismatic layer in the adoral portion, and (3) a short spiral length of the shell without a proseptum, primary varix, or dorsal shell layer. We observed the shell microstructure and mineralogy of two representative specimens in detail.

UMUT MM 29441-1 (fig. 2A) is a more or less medially broken shell with a spiral length of approximately 240 degrees. Its maximum diameter is 653 μm, which is comparable to that of more well-developed embryonic shells. A calcified initial chamber wall and a dorsal shell wall are both absent. In addition, this specimen lacks a constricted aperture and an associated nacreous deposit (primary varix). The ventral shell wall in the adapical (posterior) portion is extremely thin (1–2 μm) and consists only of homogeneous material (h, fig. 2B). This homogeneous layer gradually thickens adorally (ca. 4 μm thick, point C, fig. 2A), and, simultaneously, a prismatic layer develops underneath it (ip, fig. 2C). The inner prismatic layer also gradually increases in thickness adorally (fig. 2D). The shell wall in the adoral portion is approximately 5 μm thick (fig. 2D).

UMUT MM 29439-2 (fig. 3) is an approximately medially broken shell with the outer surface partly exposed (fig. 3B). The preserved maximum diameter is 640 μm and the spiral length of the shell is approximately 300 degrees, which is slightly longer than that of UMUT MM 29441-1(fig. 2A). The shell wall at the

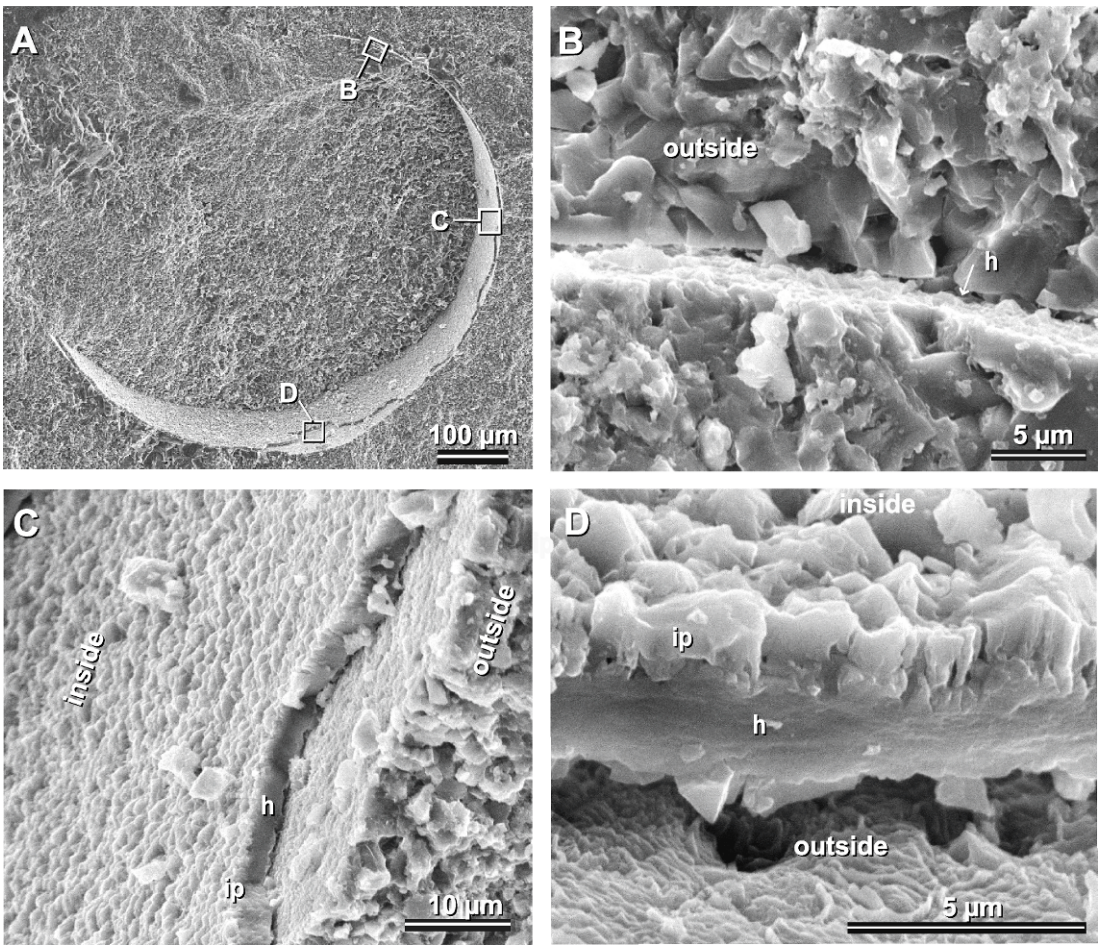


Fig. 2. SEMs of an embryonic shell of *Aconeceras* cf. *trautscholdi* belonging to Group 1. UMUT MM 29441-1, lower Aptian, Symbirsk, Russia. **A**. Lateral view of medially broken embryonic shell. **B–D**. Shell wall of the embryonic shell at adapical (B), middle (C), and adoral (D) portions. Note that the shell wall at the adapical portion consists of a very thin homogeneous layer, whereas that at the middle and adoral portions is made up of homogeneous and inner prismatic layers. Abbreviations: h, homogeneous, possibly amorphous calcium carbonate layer; ip, inner prismatic layer.

apical portion (fig. 3B) is approximately 3 µm thick and consists of a single thin homogeneous layer in the same position as in UMUT MM 29441-1 (fig. 2B). A thin (ca. 2 µm thick) inner prismatic layer appears adorally underneath the homogeneous layer (ip, fig. 3C), which can be traced to the preserved apertural end, and maintains a constant thickness (fig. 3D). The outer shell surface is slightly rough but lacks any trace of tubercles (fig. 3C).

The elemental composition of the inner prismatic and outer homogeneous layers in UMUT MM 29444-1 is presented in table 1.

Group 2

Embryonic shells of this group are incompletely mineralized and have approximately 1.0–1.5 whorls. A calcified initial chamber wall is not present in specimens representing earlier growth stages, but a very thin, calcareous initial chamber wall and a proseptum are both present in specimens representing later growth stages. The shell wall is thicker than that of the specimens of Group 1 and consists of three layers: outer prismatic, middle homogeneous, and inner prismatic layers, in asso-

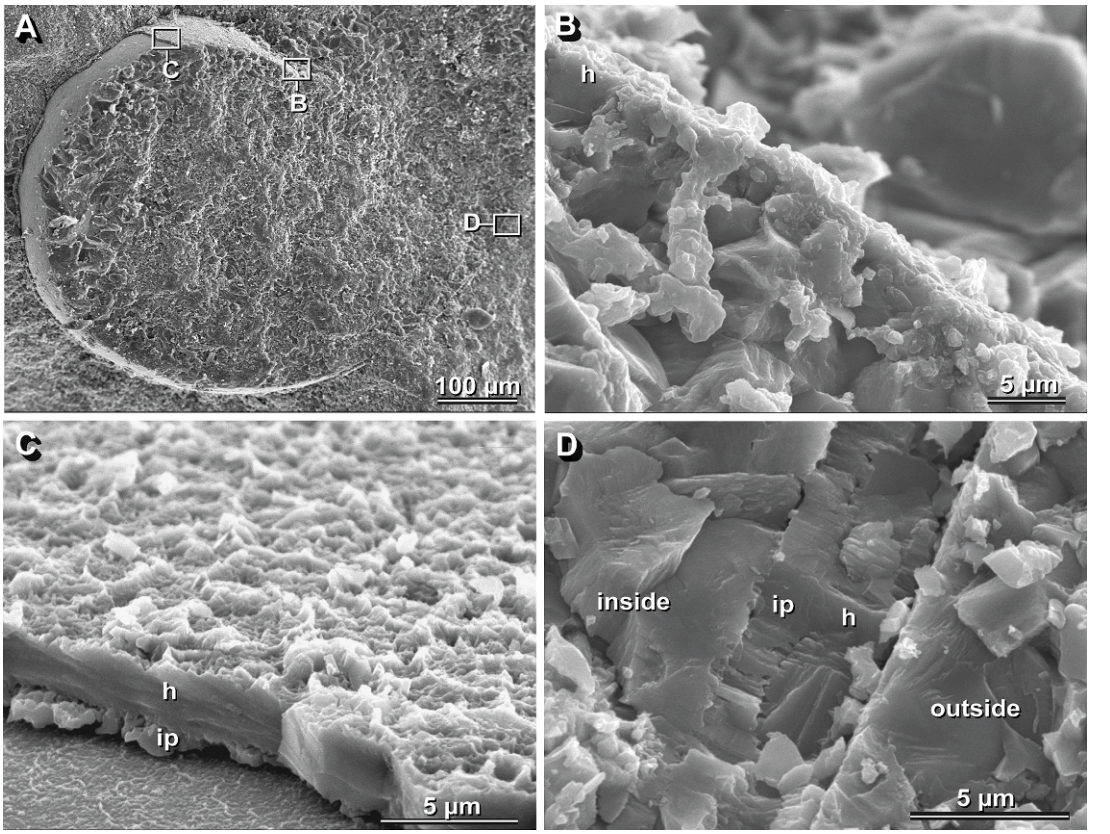


Fig. 3. SEMs of an embryonic shell of *Aconeceras* cf. *trautscholdi* belonging to Group 1. UMUT MM 29439-2, lower Aptian, Symbirsk, Russia. **A**. Lateral view of medially broken embryonic shell. **B–D**. Shell wall of the embryonic shell at adapical (B, C) and adoral (D) portions. Note that the shell wall at the adapical end (B) consists of a very thin homogeneous, possibly amorphous calcium carbonate layer, whereas that at the other portions is made up of outer homogeneous and inner prismatic layers. The outer surface of the shell wall is bumpy but lacks tubercles. For abbreviations, see the explanation of figure 2.

TABLE 1

Elemental composition of embryonic shells of *Aconeceras* cf. *trautscholdi*. Results of EDAX analysis (all amounts given as a percentage of total weight, wt)

	Specimen of Group 1 (UMUT MM 29444-1)		Specimen of Group 2 (UMUT MM 29444-2)			
Element	Inner layer (prismatic)	Outer layer (homogeneous)	Middle layer (homogeneous)	Outer layer (prismatic)	Tubercle (spherulitic)	Clayey matrix
C	9.81	10.27	10.79	10.40	9.72	8.80
O	59.01	59.70	59.11	59.49	51.33	50.36
Na	0.25	0.33	0.40	0.31	0.49	0.26
Mg	0.45	1.94	1.50	0.58	1.56	1.83
Al	0.13	—	0.19	—	0.27	0.54
Si	0.13	0.28	0.28	0.26	0.33	0.78
S	0.14	0.10	0.08	0.08	—	0.24
Ca	28.81	27.17	27.46	28.66	36.20	36.89
Fe	1.27	0.21	0.19	0.21	0.10	0.30
Total (wt %)	100.00	100.00	100.00	99.99	100.00	100.00

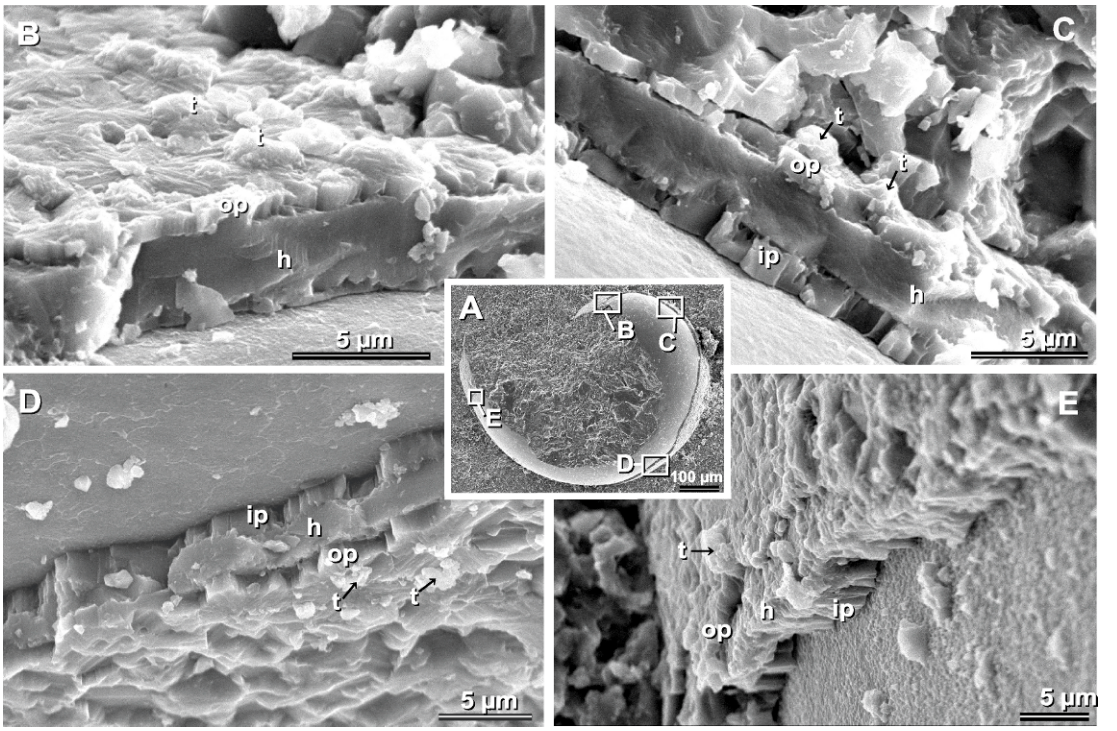


Fig. 4. SEMs of an embryonic shell of *Aconeceras* cf. *trautscholdi* belonging to Group 2. UMUT MM 29441-3, lower Aptian, Symbirsk, Russia. **A**. Lateral view of the embryonic shell. **B–E**. Close-up views of the embryonic shell wall at four different portions. The wall consists of inner prismatic, middle homogeneous, and outer prismatic layers. Abbreviations: op, outer prismatic layer; t, tubercles. For other abbreviations, see the explanation of figure 2.

ciation with tubercles on the outer layer. The embryonic shells belonging to this group are the most abundant ones in the concretion slabs examined. Four representative specimens showing slightly different stages of shell development are described below.

UMUT MM 29441-3 (fig. 4) is a medially broken shell, whose spiral length is approximately 320 degrees, which is slightly longer than that of the embryonic shells of Group 1. Its maximum diameter is approximately 645 µm. As in specimens of Group 1, neither a calcified initial chamber wall nor a dorsal shell of the first whorl is present. In addition, this specimen lacks a constricted aperture and a nacreous deposit (primary varix). The shell wall near the adapical (posterior) margin is relatively thin (ca. 4.5 µm) and consists of a thin, outer prismatic and thicker, inner homogeneous layer, 1.0 µm and 3.5 µm thick, respectively (fig. 4B). An inner prismatic layer appears adorally underneath the homogeneous layer; accordingly, the ventral shell wall at this stage is built up of three layers, i.e., outer prismatic, middle homogeneous, and inner prismatic layers (fig. 4C–E). The shell wall thickness gradually increases adorally to 7–8 µm near the apertural portion (fig. 4E). The outer surface of the embryonic shell is ornamented with tubercles. The tubercles, each about 2 µm in basal diameter and 0.7 µm in height, rest upon underlying prisms showing pseudohexagonal trilling, and consist of irregularly oriented, minute spherulites (fig. 4B, D).

UMUT MM 29439-3 (fig. 5) and UMUT MM 29439-4 (fig. 6) are almost complete specimens with a primary constriction at the aperture (arrows, figs. 5A, 6). In UMUT MM 29439-3, the lateral side of the shell near the aperture was partly removed, allowing us to document that the shell wall at this point

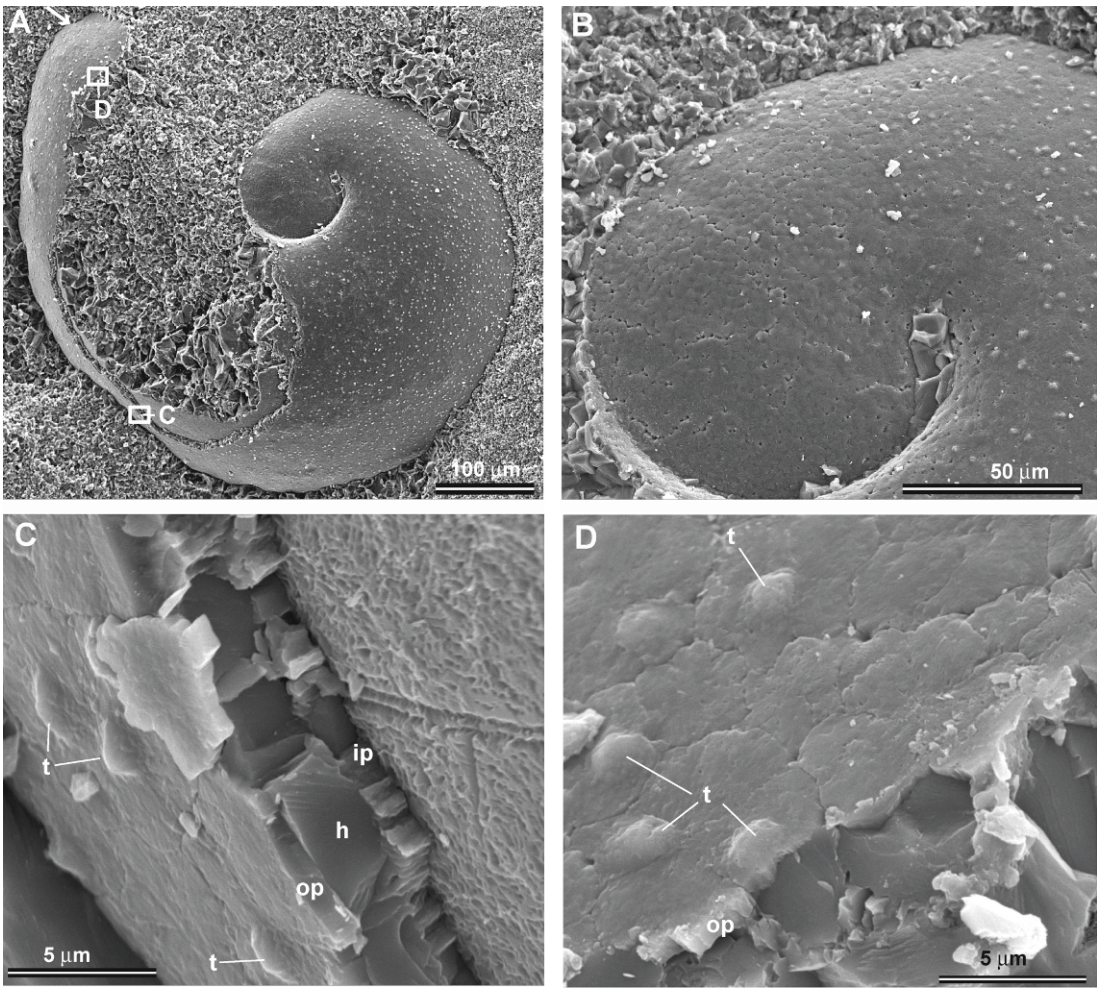


Fig. 5. SEMs of an embryonic shell of *Aconeceras* cf. *trautscholdi* belonging to Group 2 with a constricted aperture. UMUT MM 29439-3, lower Aptian, Symbirsk, Russia. **A**. Lateral view of the embryonic shell partly exposed on the fractured surface of a carbonate concretion. The arrow points to the constricted aperture. **B**. Close-up of the lateral side of the initial chamber portion without tubercles. **C**. Shell wall microstructure consisting of inner prismatic, middle homogeneous, and outer prismatic layers on the ventral side of the first whorl. **D**. Shell wall microstructure consisting of a thin outer prismatic layer near the primary constriction. For abbreviations, see the explanations of figures 2 and 4.

consists only of a thin outer prismatic layer (op, fig. 5D), and lacks a nacreous primary varix. As in UMUT MM 29441-3 (fig. 4C–E), the ventral shell wall of this specimen is triple layered, consisting of outer prismatic, middle homogeneous, and inner prismatic layers (fig. 5C). Tubercles occur irregularly on the exposed surface of the shell, but they are absent on the lateral surface of the initial chamber in UMUT MM 29439-3 (fig. 5B) and on the venter near the aperture in UMUT MM 29439-4 (fig. 6).

UMUT MM 29442-1 (fig. 7) attains 760 μm in median diameter and consists of an initial chamber and a subsequent whorl of approximately 230 degrees spiral length (fig. 7A). The initial chamber wall is extremely thin (ca. 0.6–0.8 μm thick) and consists of a single prismatic layer (ip, fig. 7B–D). This prismatic layer extends adorally and is the inner

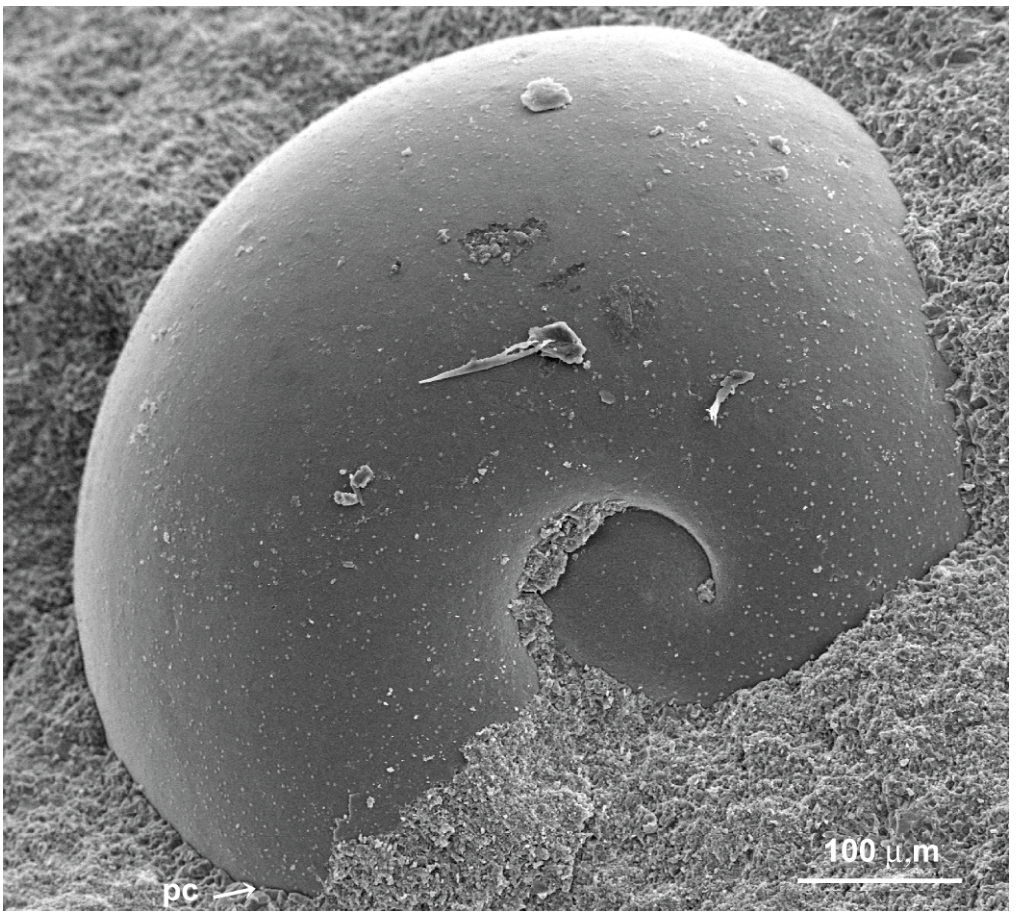


Fig. 6. SEM of an embryonic shell of *Aconeceras* cf. *trautscholdi* belonging to Group 2 with a constricted aperture (ventrolateral view). UMUT MM 29439-4, lower Aptian, Symbirsk, Russia. Note that minute tubercles are absent on the ventrolateral side of the first whorl. Abbreviation: pc, primary constriction.

prismatic layer of the succeeding shell wall (fig. 7F, G). At the base of the initial chamber, a distinct proseptum is visible (ps, fig. 7F). The shell wall abruptly thickens on the adapical side of the proseptum (fig. 7E) and, thereafter, maintains a constant thickness (ca. 5 μm) in the succeeding first whorl (fig. 7F–H). This specimen appears to represent a later growth stage than UMUT MM 29441-3 (fig. 4), in having a longer spiral length and in the presence of a proseptum. In this specimen, only inner and outer prismatic layers in association with tubercles on the outer layer are visible, and a middle homogeneous layer cannot be distinguished (fig. 7E–H).

UMUT MM 29443 (fig. 8D–F) lacks a complete aperture and may also belong to this group. In this specimen, a single tubercle does not always cover an individual prism, and two contiguous tiny tubercles are occasionally developed on a single prismatic tablet showing pseudohexagonal trilling (fig. 8F).

The elemental composition of UMUT MM 29444-2 is presented in table 1. The results are similar to those for the embryonic shell belonging to Group 1 (UMUT MM 29444-1).

Group 3

Embryonic shells of this group consist of an initial chamber and a subsequent whorl with a

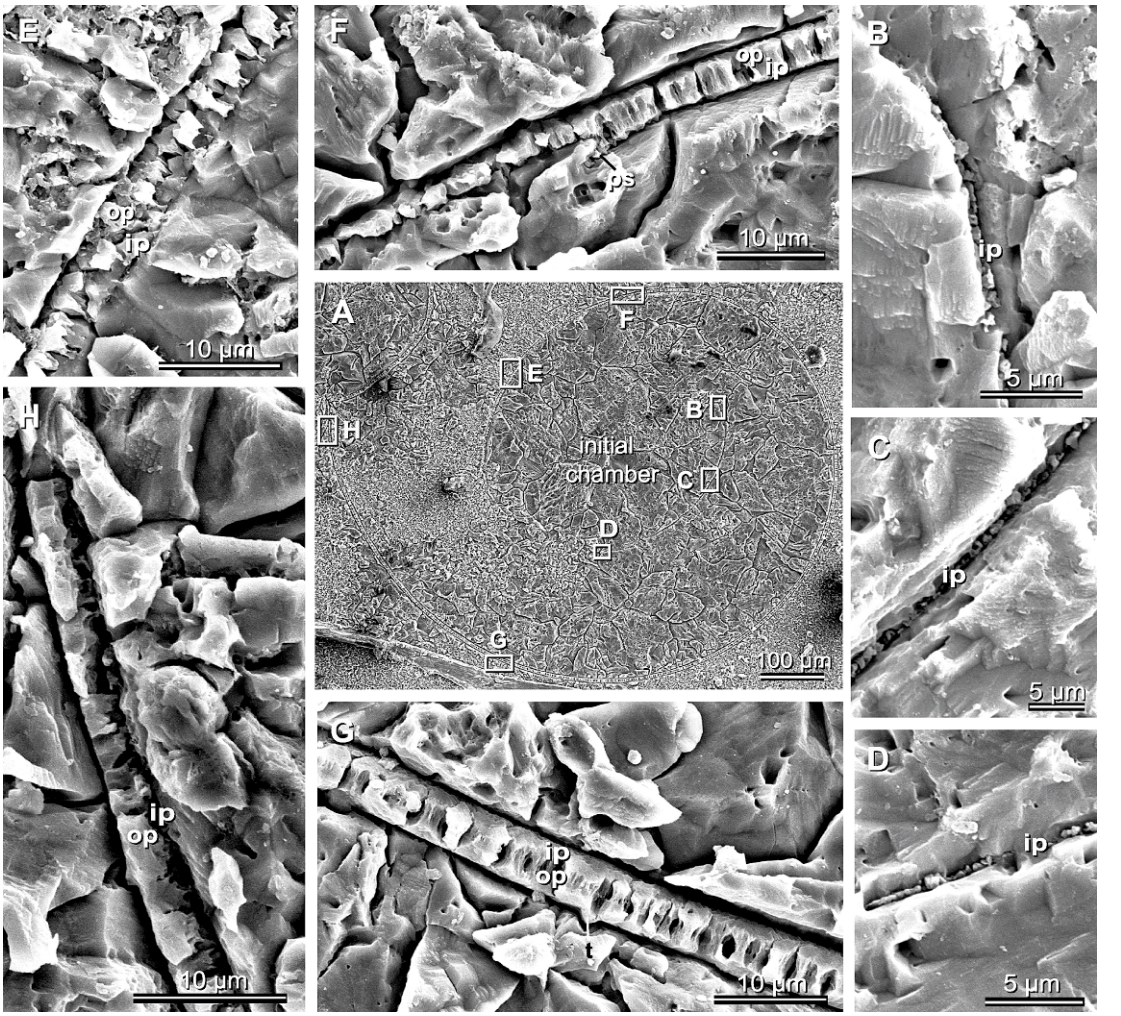


Fig. 7. SEMs of an embryonic shell of *Aconeceras* cf. *trautscholdi* belonging to Group 2 in medial section. UMUT MM 29442-1, lower Aptian, Symbirsk, Russia. **A**. Overall view of the medially sectioned embryonic shell. **B–H**. Close-up views of the embryonic shell wall at seven different portions. The shell wall of the first whorl is fully mineralized and consists of inner and outer prismatic layers, while that of the initial chamber is poorly mineralized, consisting only of a very thin inner prismatic layer. The proseptum (ps) is developed at this stage (see F); for other abbreviations, see the explanations of figures 2 and 4.

constricted aperture in association with a nacreous varix. They are relatively rare in the concretion slabs examined. Microstructural features of one representative specimen are described below.

UMUT MM 29442-2 (fig. 9) appears in oblique cross section on the polished concretion slab. The initial chamber wall is extremely thin (ca. 1 µm thick) in the adapical portion but rapidly increases in thickness adorally (ca. 4 µm) at the connecting portion (= umbilical shoulder) with the subsequent whorl (fig. 9B). A dorsal prismatic layer and a nacreous deposit (primary varix) near the aperture are both observable (dp and n, respectively, fig. 9B). The ventral shell wall of the first whorl, approximately 6 µm thick, is double layered, consisting of outer and inner prismatic layers, without any trace of a middle homogeneous layer. UMUT MM 29440-2

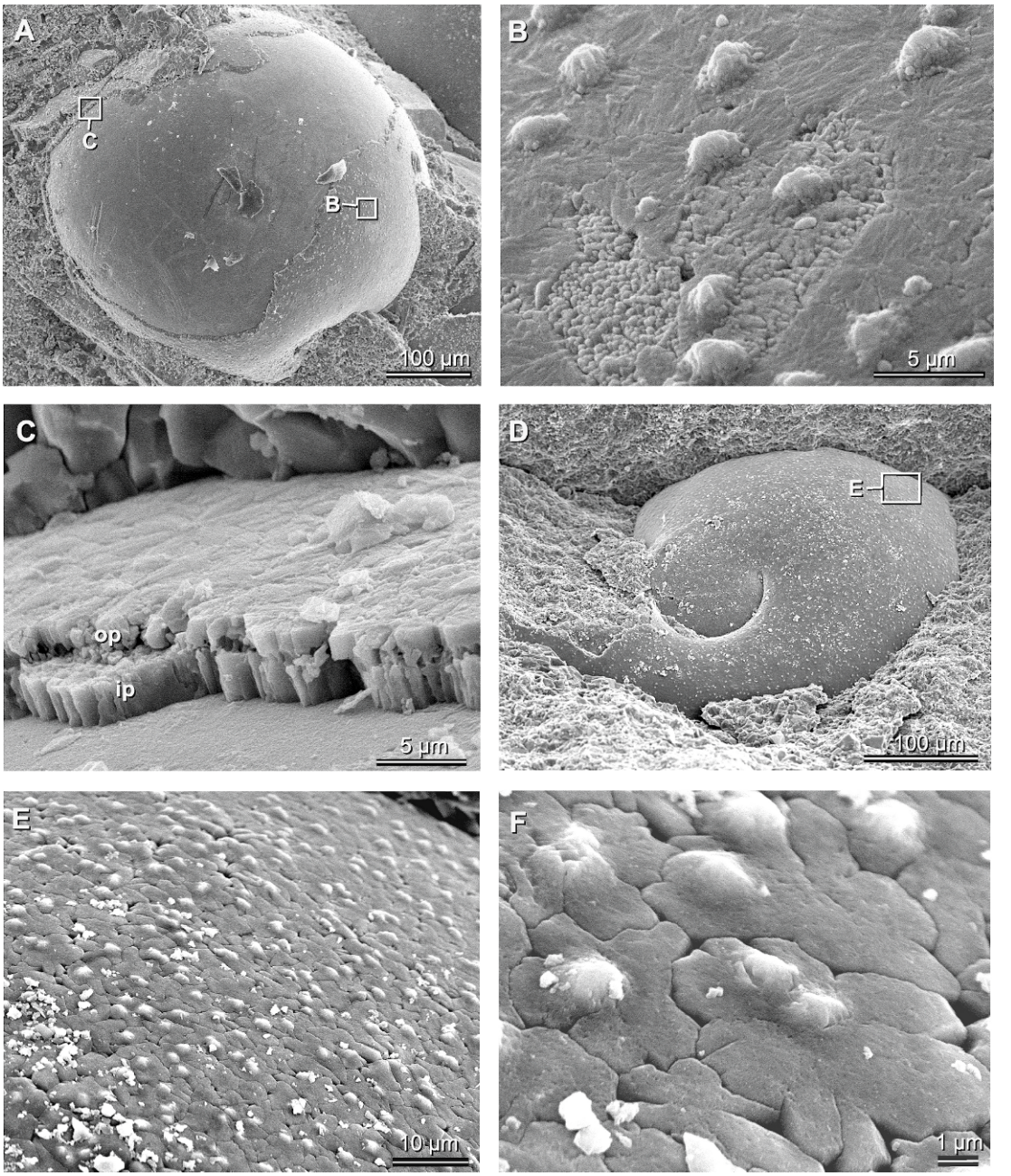


Fig. 8. SEMs of two embryonic shells of *Aconeceras* cf. *trautscholdi* partly exposed on the fractured surface of a carbonate concretion, lower Aptian, Symbirsk, Russia. **A–C**. UMUT MM 29440-2. This specimen possibly belongs to Group 3, though its aperture is not exposed. Ventral view (A), close-ups of the outer shell surface with tubercles (B), and shell wall microstructure, consisting of inner and outer prismatic layers with tubercles on the outer layer (C). **D–F**. UMUT MM 29443. This specimen may belong to Group 2. Lateral view (D) and close-ups of the outer shell surface with tubercles (E, F). Note that tubercles rest on the underlying outer prismatic layer, and occasionally a couple of tubercles occur on a single prismatic crystal showing pseudohexagonal trilling (F).

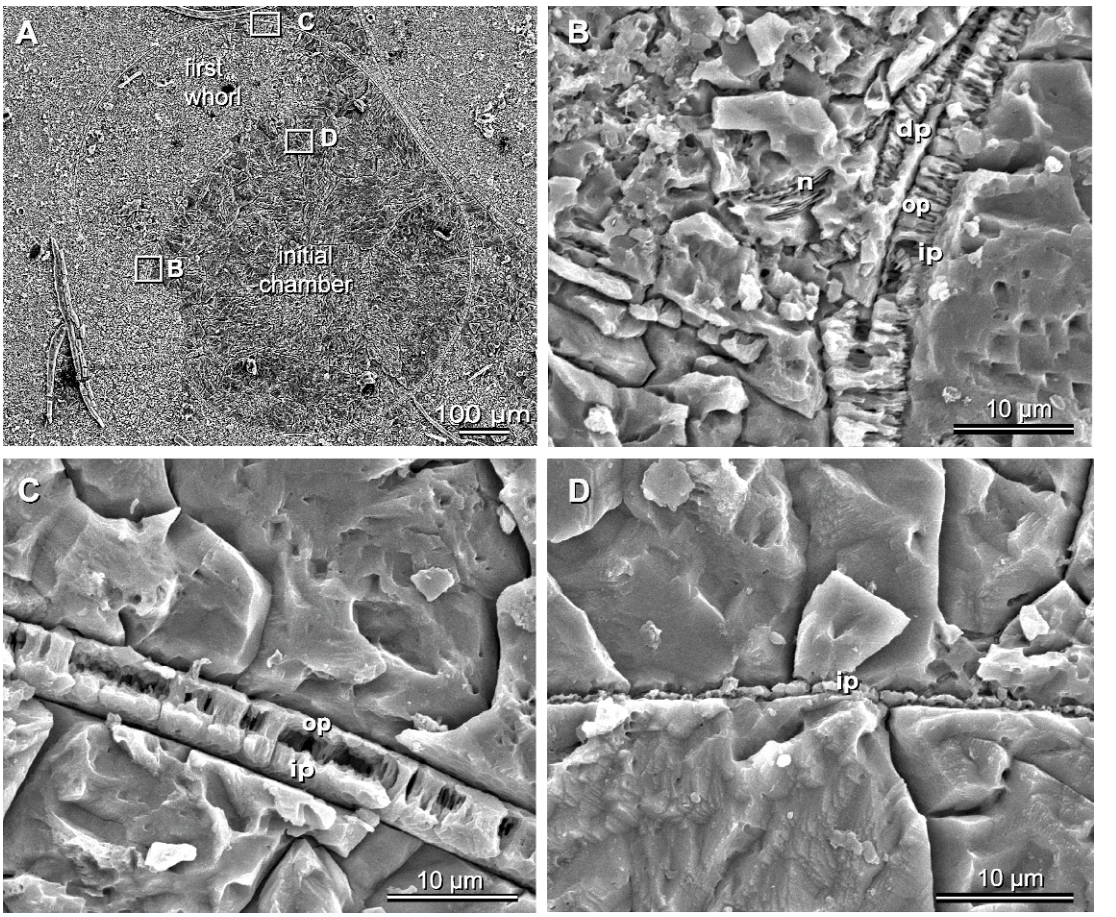


Fig. 9. SEMs of an embryonic shell of *Aconeceras* cf. *trautscholdi* belonging to Group 3 in oblique cross section. UMUT MM 29442-2, lower Aptian, Symbirsk, Russia. **A**. Overall view of the oblique cross-sectioned embryonic shell. **B**. Close-up view of umbilical seam showing the relationship between the walls of the initial chamber and first whorl. **C**. Shell wall of the first whorl on the ventral side, consisting of outer and inner prismatic layers. **D**. Initial chamber wall consisting of a very thin prismatic layer. Abbreviations: n, nacreous layer developed as the primary varix at the flank of the first whorl; dp, dorsal prismatic layer of the first whorl. For other abbreviations see the explanations of figures 2 and 4.

(fig. 8A–C) may also belong to this group, because its shell wall lacks a middle homogeneous layer and consists only of thinner outer and thicker inner prismatic layers.

Similar to the tubercles in the embryonic shells of Group 2, those on UMUT MM 29440-2 are built of irregularly oriented, elongate crystallites extending outward (fig. 8B). They rest directly on the underlying outer prismatic layer (fig. 8C), indicating that the tubercles form an integral part of the outer prismatic layer.

DISCUSSION

Our SEM observations of well-preserved embryonic shells of *Aconeceras* cf. *trautscholdi* from Symbirsk, Russia, have revealed the presence of three groups (Groups 1–3), each with different wall microstructure. Comparison of the number of layers in the shell wall and the spiral length of the embryonic shell demonstrates that these three groups represent successive stages of embryonic shell development.

The results of EDAX analysis (table 1) show that the prismatic and homogeneous layers and tubercles of the embryonic shells of *A.* cf. *trautscholdi* from Symbirsk are all rich in calcium (27.17–36.20 wt%). The amount of magnesium in the homogeneous layer (1.50–1.94 wt%) is, however, three times larger than that in the outer and inner prismatic layers (0.45–0.58 wt%). Kulicki and Doguzhaeva (1994: 19) cited unpublished data by I.V. Pochtareva that ammonoid shells preserved in sideritic concretions from this locality are composed of 95–99% aragonite. In the similarity of the microstructure to the inner and outer prismatic layers of postembryonic ammonoid shells with aragonitic mineralogy from the same concretion, it seems reasonable to conclude that the inner and outer prismatic layers of the embryonic shells are made of aragonite.

The middle homogeneous layer in the embryonic shells of Group 2 undoubtedly corresponds to the outer homogeneous layer in the embryonic shells of Group 1, in which an outer prismatic layer with tubercles is not yet developed. The homogeneous layer in the embryonic shells of *A.* cf. *trautscholdi* is similar in microstructure to amorphous calcium carbonate (ACC), which appears in the early larval shells of modern bivalves (Weiss et al., 2002) and gastropods (Marxen et al., 2003). On the basis of combined analysis by infrared spectrometry, Raman-imaging spectrometry, thermogravimetry, synchrotron powder diffraction, CaK-edge X-ray absorption spectrometry, and scanning electron microscopy, Weiss et al. (2002) demonstrated that ACC represents a precursor phase for aragonite deposition in larval shells of the bivalves *Mercenaria mercenaria* and *Crassostrea gigas*. According to these authors, in *M. mercenaria*, the prodissoconch I of a three-day-old larval shell consists of three layers: a thin outer prismatic layer (ca. 0.3 μm thick), a thick middle ACC layer (ca. 1.5 μm thick), and a thin inner prismatic layer (ca. 0.5 μm thick). The middle layer became thinner (ca. 0.5 μm thick) in the prodissoconch I of a nine-day-old larval shell, because part of it had been transformed into the inner prismatic layer (see Weiss et al., 2002: fig. 6 a, b). Biologically formed ACC is also known to occur in other major invertebrate phyla (see Weiner et al., 2002: table 1). We, therefore, conclude that the homogeneous layer that occurs in the embryonic shells of *A.* cf. *trautscholdi* consists of ACC.

There are currently three different models for ammonoid embryonic shell development (see Landman et al., 1996: 369–374, fig. 18, for a recent review; fig. 10). The first one, proposed by Druschits et al. (1977: fig. 6), Kulicki (1979: fig. 9), Tanabe et al. (1980: fig. 4; 1993: fig. 8), and Druschits and Doguzhaeva (1981: fig. 57), stresses that like those of modern *Nautilus*, embryonic shells of ammonoids were formed by accretionary growth, starting from the secretion of a calcified initial chamber, followed by subsequent deposition of the shell of the first whorl, and ending by deposition of a nacreous primary varix on the inner side of the shell wall just adapical of the aperture (''accretionary growth model''; fig. 10A).

The second model, proposed by Bandel (1982, 1986) and Kulicki (1989), relied on the embryonic shell formation of modern ''archaeogastropods'' as an analogy to explain ammonoid embryonic shell development. According to this archaeogastropod-type development model, an ammonoid embryonic shell was initially entirely organic, and later its mineralization proceeded from the adoral side to the adapical side (fig. 10B). Biomineralization of the initial chamber wall after the formation of the shell of the first whorl was based on observations of well-preserved embryonic shells of *Aconeceras*, *Quenstedtoceras* (see Kulicki, 1989; Kulicki and Doguzhaeva, 1994), *Baculites* (see Landman, 1982) and *Scaphites* (see Landman, 1985). According to Bandel (1982: 56, fig. 46), the tubercles and the underlying thin prismatic layer were secreted by the shell gland after the formation of the organic shell (fig. 10B-1), but the majority of the initial chamber wall was still unmineralized at this stage.

The third model was proposed by Tanabe (1989), who assumed that the embryo of Mesozoic ammonoids might have temporarily had an endocochliate body plan late in embryonic development during which the outer prismatic layer with tubercles was secreted from the outer reflected mantle

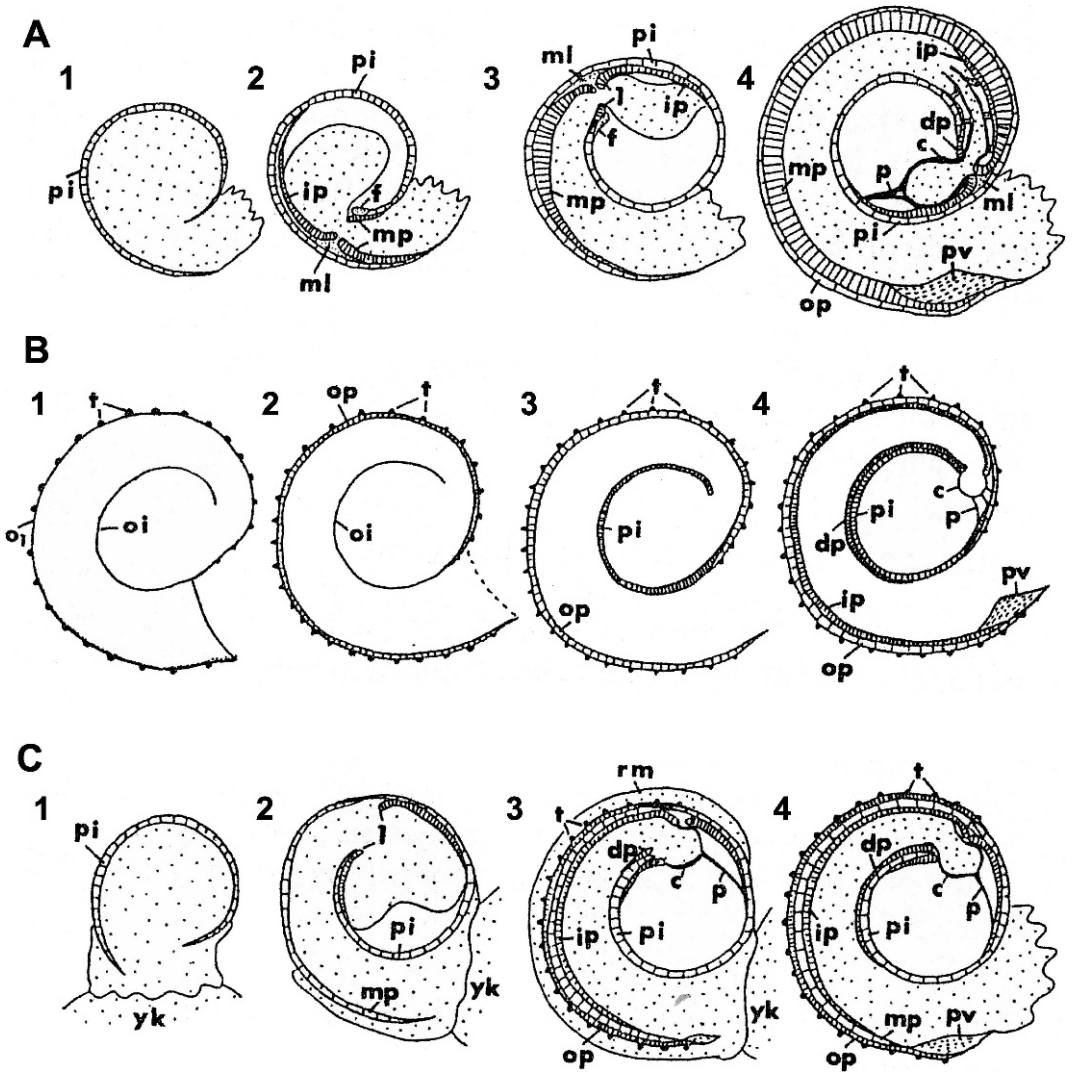


Fig. 10. Three models (A–C) depicting the sequence of ammonoid embryonic development (1–4) (partly adapted from Landman et al., 1996: fig. 18). Animals are represented in median cross section with soft tissue shaded for A and C. **A**. Kulicki (1979: fig. 7) emphasized a *Nautilus*-like mode of embryonic shell development. **B**. Bandel (1982: figs. 40, 46, 47) argued that the embryonic shell originally consisted of an organic, unmineralized shell, and that mineralization proceeded from adoral to adapical sides. **C**. Tanabe (1989: fig. 7) proposed that the embryonic shell was temporally enveloped by the outer mantle late in embryonic development. Abbreviations: c, caecum; dp, dorsal prismatic layer of the first whorl; f, flange; ip, inner prismatic layer of the initial chamber or of the first whorl; ml, middle prismatic layer of the first whorl; oi, organic wall of the initial chamber; o1, organic wall of the first whorl; op, outer prismatic layer of the first whorl; p, prosiphon; pi, prismatic layer of the initial chamber; pv, primary varix; rm, reflected mantle; t, tubercles; yk, yolk mass.

("endocochliate embryo model"; fig. 10C-3). This model also hypothesized that after the secretion of this outer prismatic layer, the mantle was thought to have migrated back toward the aperture, resuming its earlier position (fig. 10C-4).

In the embryonic shell development of modern *Nautilus*, a spherulitic prismatic layer

composed of calcium carbonate is deposited on the inner side of the already formed organic layer (Arnold et al., 1987; Tanabe and Uchiyama, 1997: fig. 8B). Initial secretion of an organic primary shell by undifferentiated mantle (shell gland) has also been confirmed in the embryonic and/or larval shell development of extant gastropods (Iwata, 1980; Bandel, 1982; Collin and Voltzow, 1998; Hickman, 1992). These data strongly support the view of Bandel (1982: fig. 40) and Kulicki and Doguzhaeva (1994: fig. 1A, B) that the original embryonic shell was entirely organic, although this has not yet been confirmed by fossil evidence. As suggested by Bandel (1982: 49), the ammonoid embryonic shell was presumably cap-shaped at the earliest stage, as in the embryonic shells of modern *Nautilus* and early larval shells of gastropods, and was subsequently enlarged with the development of the shell gland.

Based on our SEM observations of *Aconeceras* embryonic shells, the sequence of embryonic shell development can be summarized as below (see fig. 11):

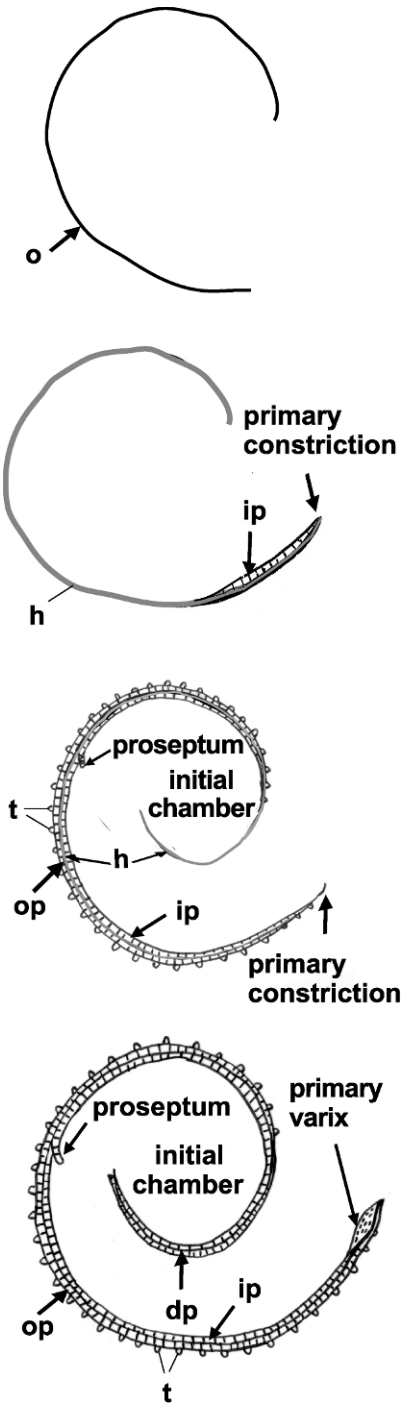
Stage 0 is marked by secretion of an entirely organic shell. It was enlarged marginally with the development of the shell gland. This stage is not confirmed by fossil evidence. This stage corresponds to the completed organic stage hypothesized by Kulicki and Doguzhaeva (1994: fig. 1A, B).

Stage 1 is defined by deposition of amorphous calcium carbonate followed by deposition of an inner prismatic layer adorally. The inner prismatic layer exhibits geometrical selection of crystals toward the inner side of the shell wall (fig. 2D), indicating that this layer was deposited by the shell gland of the embryonic body that occupied the inner space of the shell (for details of geometrical selection of the prismatic structure, see Ubukata, 1994). Embryonic shells at this stage are poorly mineralized, less than one whorl in spiral length, presumably with a constricted aperture where the soft body was attached, but without a calcified initial chamber wall nor a nacreous swelling (primary varix); the shell wall is thin and consists of two layers, i.e., an outer homogeneous layer (ACC) and an inner prismatic layer; tuberculate micro-ornamentation is absent at this stage of development. This stage roughly corresponds to the end of the first calcification stage defined by Kulicki and Doguzhaeva (1994: fig. 1C, D).

Stage 2 is characterized by secretion of an outer prismatic layer associated with tubercles. The tubercles and the outer prismatic layer must have been deposited from the outside, in view of the microstructural relationship with the already formed middle homogeneous (ACC) and inner prismatic layers. Embryonic shells at this stage have approximately 1.0–1.5 whorls terminating at the primary constriction, without a calcified initial chamber wall in earlier substages but with a very thin calcareous initial chamber wall and a proseptum at later substages; the ventral shell wall is thicker than that at stage 1 and consists of three layers, i.e., outer prismatic, middle homogeneous (ACC), and inner prismatic layers, with associated tubercles on the outer layer. This stage is comparable to the end of the second calcification stage defined by Kulicki and Doguzhaeva (1994: fig. 1E, F).

Stage 3 is defined by completion of a fully mineralized embryonic shell. The embryonic shell at this stage consists of an initial chamber and a subsequent whorl with a constricted aperture. There is a dorsal shell consisting of a thin prismatic layer. The middle homogeneous layer (ACC) that was present in stage 2 is missing. It either merged with the inner prismatic layer or has been destroyed due to dissolution leaving occasional void spaces. In addition, a thick nacreous swelling termed the primary varix is present on the inner ventral side of the shell wall near the aperture. This stage corresponds to the end of the third calcification stage defined by Kulicki and Doguzhaeva (1994: fig. 1G, H).

The embryonic shell structure of *Aconeceras* differs in the number and position of shell layers from that of other ammonoids described by previous authors (Erben et al., 1968, 1969; Birkelund and Hansen, 1968, 1974; Kulicki, 1979; Bandel, 1982; see also Landman et al., 1996: fig. 14), but it is unclear whether these differences are due to the incorrect recognition of shell layers, taxonomic variation, diagenesis, or sample preparation. However, in embryonic shells of *Aconeceras* cf. *trautscholdi*, Kulicki and



Stage 0 (hypothetical)

Secretion of an unmineralized organic shell (o) (not observed; analogy from the embryonic shell formation of modern *Nautilus*).

Stage 1

Initial mineralization of a homogeneous layer (h), possibly consisting of amorphous calcium carbonate (ACC). Subsequent transformation of the inner portion of ACC into an inner prismatic layer (ip) on the adoral side. The aperture is distinctly constricted.

Stage 2

Secretion of an outer prismatic layer (op), followed by deposition of irregularly distributed tubercles (t) on top of it.

Stage 3

Secretion of a dorsal prismatic layer (dp) and a nacreous swelling (primary varix) on the inner side near the aperture. The middle homogeneous layer (ACC) that occurred in stage 2 is mineralized and merged with the inner prismatic layer (ip).

Fig. 11. Diagrams showing the sequence of embryonic shell development in Mesozoic ammonites. See the text for details.

Doguzhaeva (1994: 22, figs. 6C–G, 7, 8) documented the same pattern that we observed. For example, they noted that the wall of the first whorl and the lateral wall of the initial chamber have a trilayered structure at the end of the first calcification stage (= our stage 2). The middle layer is homogeneous and appears to consist of ACC. Furthermore, they showed that the shell wall of embryonic shells with a primary varix at the aperture (= our stage 3) consists of only outer and inner prismatic layers. These facts are consistent with our model of the development of the structure of the ammonoid embryonic shell.

Our model is basically the same as that of Bandel (1982) and Kulicki and Doguzhaeva (1994), but differs with regard to the timing of formation of the outer prismatic layer and tubercle formation. Our observations indicate that in the development of the embryonic shell of *Aconeceras*, the outer prismatic layer and the overlying tubercles were not formed at an early stage of calcification (stage 1), but were deposited instead at a later stage of calcification (stage 2), from the outside. However, it is still unclear whether the outer prismatic layer and overlying tubercles were secreted by means of an overlying reflected mantle, as postulated by Tanabe (1989) in his endocochliate model, or by other processes, for example, nonepithelial mineralization under weak biological control, as hypothesized by Hickman (2004) to explain the formation of tuberculate and reticulate micro-ornamentation on some gastropod larval shells. Further microstructural observations of well-preserved specimens of various Mesozoic ammonoid taxa are needed to resolve this issue.

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