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Pre-mortem septal crowding and pathological shell wall ultrastructure of ammonite younglings from the lower Aptian of Central Volga (Russia)

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Abstract: The mass death of younglings of the pelagic nectic ammonite *Aconeceras*, which inhabited the early Aptian epicontinental sea of the East-European Platform, has been investigated. The sedimentary environment, the absence of benthic communities and the status of preservation of the ammonites indicates oxygen-deficient conditions in the basin. Whether the unfavourable ecological factors affected ammonite shell secretion has been investigated, using observations on septal disposition and shell wall ultrastructure. About 200 small shells with preserved living chambers have been examined. In approximately 25–30%, the last chamber of the phragmocone has been considerably shortened. The external whorl of many shells shows the pathology of the shell wall structure, revealed in the uneven outer surface, bearing some kind of scabs caused by varying shell wall thickness and irregular ultra-structure. When the growth lines of the nacreous layer, which forms the bulk of the wall, are irregular, then the inter-lamellar organic sheets are unusually thick and often interrupted, standard stock packing of nacreous tablets is not constant or missing, the thickness of the nacreous tablets varies strongly, and the nacreous layer sometimes looses its typical appearance.

The considerable chamber shortening observed near the living chamber, followed by the pathological shell wall structure, has been interpreted as retardation of shell secretion preceding mass mortality of the ammonite younglings due to stressed living conditions. The chamber shortening must have disturbed the buoyancy, making the diurnal vertical migration impossible, so that even at night the younglings were unable to leave the lower water column, where the oxygen shortage was more acute than in the upper water column. Further, the shell wall pathology observed reduced its solidity. This is also interpreted as an indication of the stressed physiological condition of the younglings prior to death. The study showed that approximately 25–30% of the total number of dead younglings underwent gradual, but unsuccessful adaptation to the unfavourable environments; the remainder were completely unable to adapt to the conditions.

Keywords: Lower Cretaceous, Aptian, Volga Area, Ammonites, Ecology, Oxygen-deficient Environments, Pathology.

1. INTRODUCTION

The paper deals with an analysis of mass mortality in the early ontogenetic stages of the pelagic nectic ammonite *Aconeceras* in the early Aptian epicontinental sea on the East-European Platform (Fig. 1). The work has been focused on small-sized (up to

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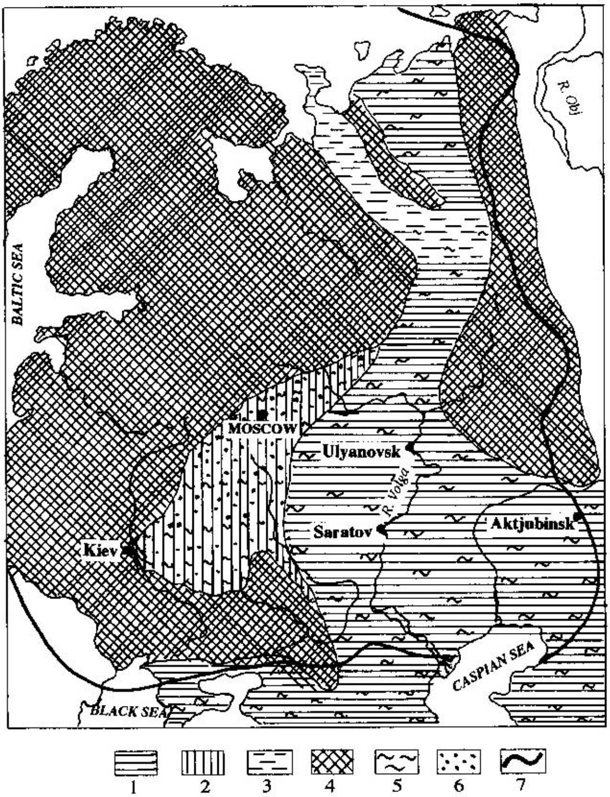


Fig. 1:
Paleogeographic scheme of the East-European Platform during Aptian (after GERASIMOV et al., 1962: Text-Fig. 44, p. 157). Legend : 1 – domain of marine sedimentation; 2 – domain of continental sedimentation; 3 – domain of supposed marine sedimentation; 4 – domain of erosion; 5 – clay deposits; 6 – sand deposits; 7 – boundary of the East-Europeanian Platform.

15 mm in diameter) oxyconic shells; their septal disposition and shell wall ultrastructure have been examined with an SEM. This approach requires a large number of shells with well preserved living chambers and apertural parts and buried with minor or no transportation. Such material was collected from the Lower Aptian in the Ulyanovsk region, Middle Volga, Central Russia. In this region, where the Aptian sections are the most complete in Central Russia (maximum thickness is about 80 m), the lower and middle substages are characterized by a large number of ammonite species (SAZONOVA, 1958a, b; GLAZUNOVA, 1973).

The Lower Aptian is represented by dark bituminous rich claystones alternating with black bituminous shales, marls and interbeds of fine-grained, sometimes glauconitic sandstones. The succession contains calcareous concretions with remnants of pelagic fish, teuthids and ammonites, floating wood plant fragments and a poor benthic fauna.

Due to the exceptionally good preservation of the ammonites in this region, rarely observed morphological structures, such as soft body/shell attachment scars, jaws and radulae have been described (DOGUZHAEVA & MUTVEI 1991, 1992, 1993). KULICKI & DOGUZHAEVA (1994) reconstructed the biomineralization at the pre- and post-hatching stages, whilst the aberrant helicoidal shell of *Deshayesites* was illustrated and commented on by DOGUZHAEVA *et al.* (1990).

2. MATERIAL AND METHODS

Approximately 200 small shells (up to 15 mm in diameter) with preserved living chambers, conventionally assigned to *Aconeceras sp.* and *A. trautsholdi* SINZOW, 1870, were examined. The species was later described as *Sinzovia trautsholdi* SAZONOVA, 1958, but a further work is needed to resolve this taxonomic problem, which is beyond the scope of this paper.

The small shells, together with larger ones, were collected near the village of Shilovka, about 40 km south of Ulyanovsk, on the right bank of the Volga River, where the total thickness of the Lower Aptian is about 50 m. The ammonites were collected from siderite and ankerite-siderite concretions lying within claystone beds (about 2 m thick) corresponding to the *Deshayesites deshayesi* Zone. The beds are situated above the "Aptian Plate", a ca.2 m thick marker horizon in the middle part of the Lower Aptian section. This represents an interval of dark-grey claystones, pyritized glauconitic laminated aleurite limestones and marls, filled with extremely compressed (so that the lateral sides of the shells touch each other) iridescent ammonite shells assigned to *D. deshayesi* and *Aconeceras sp*. The concretions from the claystone beds yielded numerous small- to medium-sized (up to 60 mm in diameter) shells of *Aconeceras* and *Deshayesites* and rarely the heteromorph *Toxoceratoides.* Above this part of the section, the claystones contain numerous clusters of gypsum crystals, dispersed pyrite, small concretions of marcasite and organic matter. The large (up to 300 mm in diameter) shells of *Deshayesites* and of the heteromorphs *Ancyloceras, Australiceras, Pseudoaustraliceras* and *Hamiticeras* reported by SAZONOVA (1958a, b) and GLAZUNOVA (1973) were collected from this part of the section.

The preservation of living chambers has been used to indicate that the selected shells belonged to dead younglings and are not the internal whorls of fully-grown shells. The comparative length of last chambers of the phragmocone has been observed in longitudinal sections and on the phragmocone surface, if it is exposed. The shell wall ultrastructure has been studied with the aid of median shell sections. To avoid loosing the outermost portion of the shells, small blocks of the concretions containing the shells were cut and material carefully ground down to the median shell section position, polished, etched by 1–5 per cent HCl for 5–10 s., coated with gold and examined with a CamScan SEM instrument.

3. STATUS OF PRESERVATION OF AMMONITE SHELLS AND SEDIMENTARY ENVIRONMENTS

The ammonite fossilization process was different inside and outside the concretions. The siderite and ankerite-siderite concretions with ammonites are a very dense, dark-grey, often with rusty marks on dry surfaces, large (0. 2–0. 5 m in large diameter), usually oblate, but sometimes swollen, prolate and laminated. The uniformity of the sediment outside and inside the concretion proves their early diagenetic formation. Approximately 10 to 12% of concretions contain ammonites; their exceptionally good preservation indicates a very early lithification. In some concretions, the shell wall and siphuncular tube are slightly pyritized.

The medium-sized (50–60 mm in diameter) ammonite shells show no preferred orientation and usually lie in different planes. In some concretions, the shells are not sorted by size (range is 0.7–60 mm), so that large, small and embryonic shells and also aptychi were accumulated together. Some other concretions include only embryonic shells, or embryonic and immediate post-hatching shells (diameter up to 15 mm). There are also concretions which contain only aptychi. The largest specimen is about 30 mm in length, but commonly they are about 15 mm long.

The small ammonite shells either accumulated along the surface of laminations (Pl. 1, Fig. 2) or lie in different planes, as the large shells do. Apart from ammonites, the concretions also contain rare gladii of teuthids (Hecker & Hecker, 1955), abundant plates, vertebrae and gill covers of pelagic fish, rare inoceramids. The latters sometimes occur inside the living chamber or in the umbilicus and around and between the small shells of the ammonites (Pl. 1, Figs. 1, 3; Pl. 2, Fig. 1). Nuculids, gastropods, floating pieces of wood up to 0.3 m in length, and rarely wings of terrestrial insects are found in concretions as well.

The level of preservation of the ammonite shell matter gives some indications of an oxygen-deficient depositional environment. X-ray analysis showed that approximately 90–95% of the shell matter of the Lower Aptian ammonites from the Ulyanovsk region has not been diagenetically recrystallized (Doguzhaeva et al., 1990). The nacreous layer of the ammonite shell, which forms the bulk of the shell wall and is the only layer of the septa, represents an alternation of aragonite and conchioline lamellae. Thus, the ammonite shells contain much organic matter preserved due to the oxygen deficient conditions, which would otherwise have easily disintegrated. Finds of hard parts of the buccal apparatus within the living chambers and soft body/shell attachment scars also indicate that after death the ammonite shells sank into the silt before their soft tissues had decayed. This would only have been possible if the sea floor was covered by soft silt and

Plate 1

Aconeceras trautsholdi; Lower Aptian; Middle Volga, Ulyanovsk Region, v. Shilovka.

Fig. 1: 3871/93. Shell with preserved peristome, side view; tiny inoceramids are in the umbilicus; x 4.7

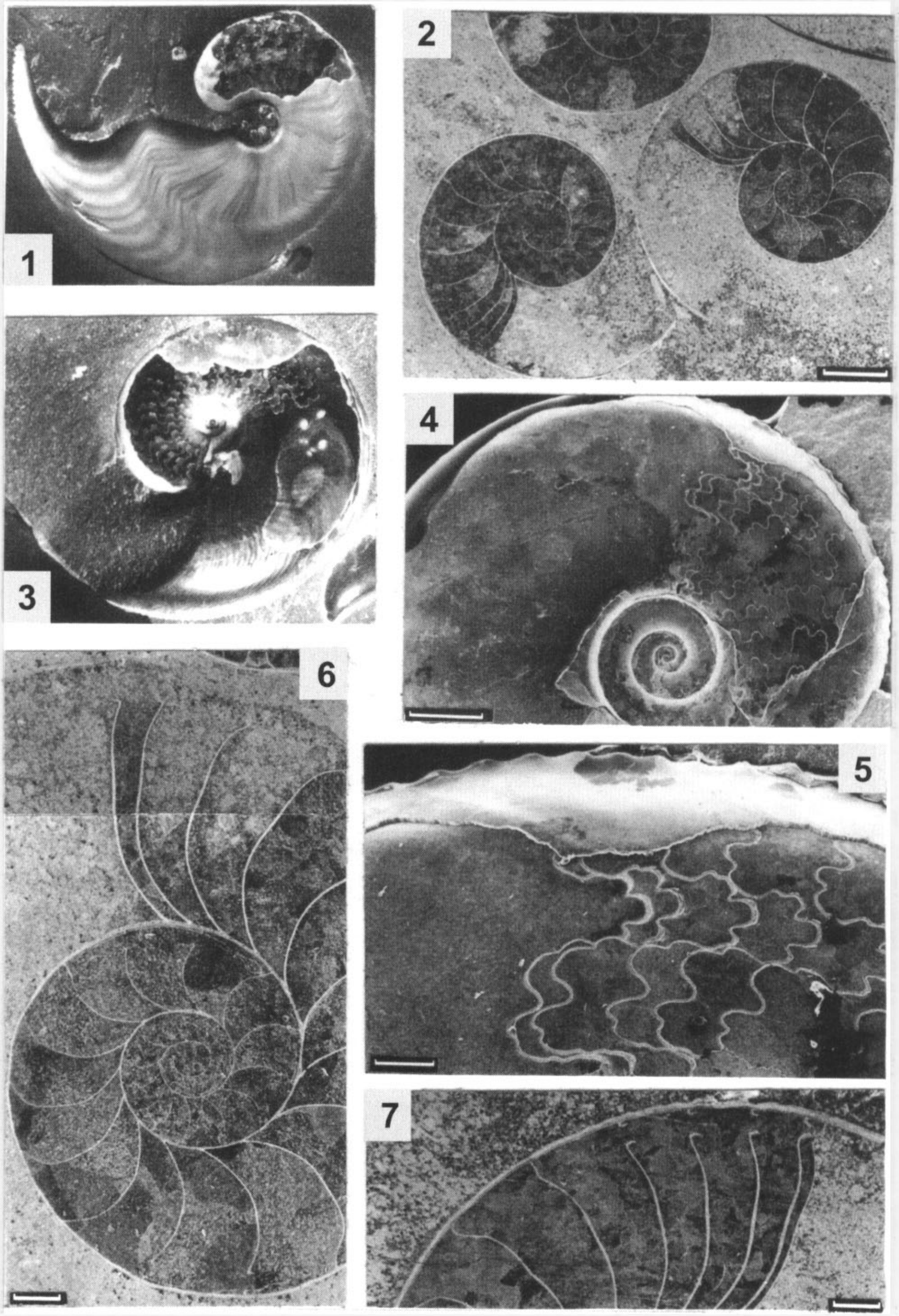
Fig. 2: 3871/94. Median section of three adolescent shells buried close each other; last chambers of the phragmocone are short; scale bar – 1 mm

Fig. 3: 3871/95. The adolescent shell with a large ventro-lateral muscle scar on the nodule of the living chamber; white spots are small shells of inoceramids buried in the living chamber near last septum; x 5

Fig. 4: and 5: 3871/96. Shell with extremely short last chamber near living chamber, lateral view; 4: scale bar – 1 mm; 5: Close-up of Fig. 4 to show that the last suture line lies at a very short distance from the preceding one; scale bar – 0. 3 mm

Fig. 6: 3871/97. Median section of shell with short last chamber of the phragmocone at the end of the third whorl; scale bar – 0.3 mm

Fig. 7: 3871/98. Median section of shell with short four last chambers; scale bar – 0.3 mm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if the necrophagouses were absent or rare, the sea water oxygen content low and disintegration slow. Such a conclusion fits with the lithologies, which indicate a disoxygenated environment (dark bituminous organic matter rich claystones and shales with numerous clusters of gypsum crystals, dispersed pyrite, concretions of marcasite and dark-grey siderite and ankerite-siderite concretions). The lamination in the calcareous concretions and claystones, interlayered with beds of fine-grained glauconitic sandstones, laminated aleurite limestones and marls, indicate generally shallow water depths.

4. OBSERVATIONS ON SHELL MORPHOLOGY AND ULTRASTRUCTURE OF *ACONECERAS* YOUNGLINGS

4.1. Inner shell structure at the first four whorls

The inner shell structure of the first four whorls (see also Druschitc & Doguzhaeva, 1981: P. 109–112, 160–161; Text-Fig. 4, 6, 10, 39, 44; Pl. 42, Figs 1–7) comprises a small, spindle-like protoconch, with a width of 0. 41–0. 47 mm; in median section rounded or oval, large diameter is 0. 34–0. 38 mm, small diameter 0. 27–0. 35 mm. Prosiphon is of short to medium length (0. 08–0. 17 mm). Primary constriction and primary varix are

Plate 2

Aconeceras sp.; Lower Aptian; Middle Volga, Ulyanovsk Region.

Fig. 1: 3871/99. Specimen with two adolescent ammonite shells and numerous tiny inoceramids shells; note that some of the latters are inside the living chamber of the larger ammonite shell; they are visible through transparent calcite; x 14

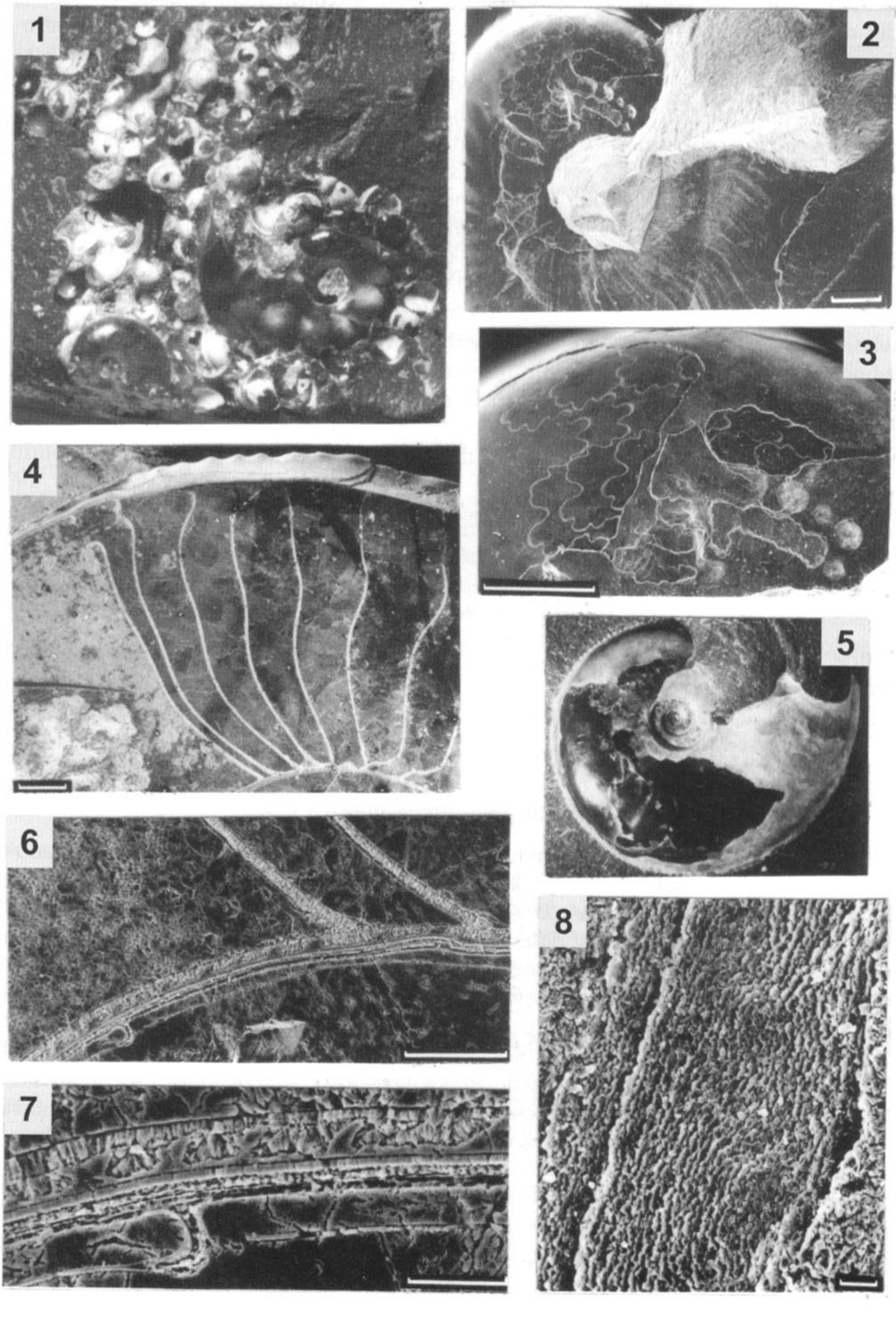
Fig. 2 and 3: 3871/100. Shell with biting punctures on the phragmocone; 2: scale bar – 1 mm; 3: Close-up of Fig. 2 to show 11 punctures; scale bar – 1 mm

Fig. 4: 3871/101. Para-median section of shell with a remarkably shortened last chamber of phragmocone; scale bar – 0. 3 mm

Fig. 5: 3871/102. Adolescent shell with living chamber occupying approximately the fourth whorl; the two last sutures lie extremely close to each other; the length of the living chamber is less than 3/4 of the whorl; large ventro-lateral muscle-scar is about 2/5 of the living chamber length; serrated keel and apertural edge are well preserved; x 5

Fig. 6 and 7: 3871/103. Shell wall between the third and fourth whorls near the last two approached septa; 6: scale bar – 0. 1 mm; 7: Close-up of Fig. 6 – ventral wall of the third whorl (close to the septal neck and siphonal tube) is thin and consists of nacreous and outer prismatic layers; the dorsal wall of the fourth whorl is thick and is formed by wrinkle and inner pismatic layers; scale bar – 0. 03 mm

Fig. 8: 3871/104. The disordered shell wall near the aperture of the adolescent shell (the outer shell surface is on the left) showing two nacreous layers; the outermost one is thin and shows uneven surface; nacreous layers lack regular column pattern, growth lines are wavy; scale bar – 0. 03 mm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located at the angle equal to 275–360 degrees from the proseptum. Ammonitella small, the diameter is 0. 64–0. 9 mm. Siphuncle subcentral on the first whorl and ventromarginal after the end of the whorl. Septal necks short, the first five septal necks retrochoanitic, the rest prochoanitic. First whorl is 0.7–0.9 mm in diameter; the second 1.81–2.36 mm; the third 5.15–7 mm; and the fourth 13.0–16 mm. Rostrum first appears at the beginning of the third whorl; serrated. Living chamber occupies about one whorl, or even a little more at the ammonitella stage; during ontogeny it becomes shorter (slightly less or equal half of the whorl). Shell oxyconic starting from the fourth whorl, the whorl height becomes much large than the width. The inner height of the whorl (measured at median sections) is 0. 06–0. 08 mm at the beginning of the first whorl and 0. 21–0. 32 mm at the end; 0. 57–0. 94 mm at the end of the second whorl; 1. 88–2. 80 mm at the end of the third whorl; 5. 1–6. 5 mm at the end of the fourth whorl. Protoconch and ammonitella smooth, or with minor tubercles. On the second whorl the growth lines are not distinct; on the third and fourth whorls they become more distinct; on the fifth whorl the growth lines are crescent-shaped, repeating the configuration of the aperture having the pronounced ventral keel and lateral lappets. 10–14 septa are at the first whorl, 12–18 the second, 15–23 the third, 19–26 the fourth whorls. In some shells they are arranged more regularly than in others. Generally the irregular placement of the septa is a typical feature of the *Aconeceras* shells from the Ulyanovsk region.

4.2. Peristome

In the studied shells (Pl. 1, Fig. 1; Pl. 2, Figs. 2, 5), the simple peristome, or apertural margin is replaced by a modified one at approximately the end of the fourth whorl, when lateral lappets and the ventral rostrum appear. The apertural edge is extremely thin and may be transparent.

4.3. Jaws and radula

The lower and upper jaws (aptychi and countraptychi), sometimes together with radulae, have been observed inside the living chambers, or between small shells (see also Kulicki et al., 1988: Text-Fig. 2A; Doguzhaeva & Mutvei, 1991: Pl. 8, Fig. 1; 1992). They have been preserved in shells of different sizes, starting from the ammonitella stage with a shell diameter of about 1 mm; more often they were found in larger shells.

4.4. Muscle-scars

The muscle scars (Pl. 1, Fig, 3; Pl. 2, Fig. 5; Doguzhaeva and Mutvei, 1991: Pl. 2, Figs. 2–4; PL. 3, Fig. 2) have no relief, being visible due to the distinct contour formed by a thin strip of shell wall matter, sometimes with a thin film of shell matter inside the contour. The presence of large muscle scars in small-sized shells suggests that in *Aconeceras* the younglings had a nectonic mode of life, like fully-grown individuals (see reconstructions in Doguzhaeva & Mutvei, 1991: Text-Fig. 9).

4.5. Chamber shortening preceding the living chamber

In approximately 25–30% of the small-sized shells with the living chamber preserved, the last chamber of the phragmocone (but sometimes two or more chambers) is considerably shortened (Pl. 1, Figs. 2–7; Pl. 2, Figs. 4, 5). In bigger shells, with the phragmocone exceeding 15 mm diameter, the remarkable shortening of the chamber is not observed in the ontogenetic stages when shell diameter is less than 15 mm. The last chamber of the phragmocone is two to five times shorter than the preceding one and, in extreme cases, the last shortened chamber looks like a slit in median sections (Pl. 1, Fig. 7; Pl. 2, Fig. 4), so that the last suture is attached to the preceding suture line (Pl. 1, Figs. 4, 5). In some shells, the gradual shortening of chamber length involves up to 1/3 to 1/2 of the whorl (Pl. 1, Figs. 2, 6, 7).

4.6. Pathological shell wall ultrastructure

Many shells (Pl. 2, Fig. 8; Pl. 3, Figs. 1–8) have no lustre, in contrast to the rainbow-tinted fully-grown shells; the shell surface is often uneven, with numerous 'scabs' of different sizes and irregular shapes, formed by irregularly packed crystals of smaller size than the nacreous tablets, but similar to them. In longitudinal shell sections, they look like additional portions of shell matter irregularly distributed on the outer surface, above the nacreous layer, with no outer prismatic layer between them. The shell wall shows frequent abnormal ultra-structure of the main nacreous layer, such as irregular bio-mineralization, with cavities inside the layer, irregular packing of nacreous tablets, irregular growth lines, irregular change of layer thickness and the occasional replacement of nacreous tablets by prisms. Septa and septal necks show rare minor abnormalities; in several cases, the septal necks observed suddenly became longer.

4. 7. Marks of exogenous injuries

4.7.1 Biting punctures

A series of punctures looking like inwardly crushed nearly circular undulations of the test were observed on a single shell (Pl. 2, Figs. 2, 3). The shell is small, about 8 mm in diameter, oxyconic and the aperture has pronounced lateral lappets and protruded ventral rostrum. The growth lines on the outer surface repeat the configuration of the aperture and have a crescent shape. The living chamber is about 3/4 of the whorl along the ventral side, where the tip of the rostrum is remarkably protruded forward but is a bit shorter on the lateral sides. Where the shell wall is removed, the four to five suture lines preceding the living chamber are exposed. The last chamber is little shorter than the preceding one. These data indicate the precise location of the bite marks on the shell in its living position. They occur in front of the aperture, dorsally to the head and at a short distance from it.

The bites are represent by two longitudinal, parallel, weakly arched rows of rounded punctures in the middle of the lateral side, separated by a short interval. The outer row is formed of four punctures, three of which are of approximately of the same size, although the anterior one is a bit larger than the others, and the one before the last being smaller than the others. In the second row, there are five punctures, four of them being of equal size with the punctures of the first row but the last one is as small as the smallest in the first row. Along the line through the anterior punctures of the two rows towards the umbilicus there are two more single punctures situated at a short distance from each other and from the second row. These two punctures do not belong to rows, as behind them there are no visible scars, although indistinct undulations of the shell wall occur. The portion of the shell just behind the marks is not exposed, so it is uncertain if there are more punctures in each row. Moreover, the shell wall near the marks is partly destroyed, making the precise number of punctures uncertain. The length of the row is about the length of the fourth to fifth chambers.

The identity of the puncture-causing predatory animal remains problematic. However, it is significant that the punctures have regular linear alignments, making it scarcely possible that they are gastropod borings. In some respects, the punctures are comparable to the punctures of the Kendrick (Lower Pennsylvanian) nautiloid from Kentucky, interpreted as biting marks of a shark (Mapes & Hansen, 1984). In both cases, the punctures are nearly circular, linearly oriented, inwardly crushed; none of them exhibit shell repair. The described punctures seem to be traces of the teeth of a small fish attacking the *Aconeceras* youngling. As noted above, the plates, vertebrae and gill covers of pelagic fish are common in Lower Aptian concretions containing ammonites.

4.7.2. Linear scratch-like scars

The apertural part of the shell with the series of the punctures bears two long tangential scars running from the ventro-lateral side to the apertural edge. One of them extends from above the lappet, and the other from below it (Pl. 2, Fig. 2). They look like slightly curved scratches accompanied by weak undulations of the shell wall; the latter is not crushed and the growth lines are not interrupted. There is no evidences that these two

Plate 3

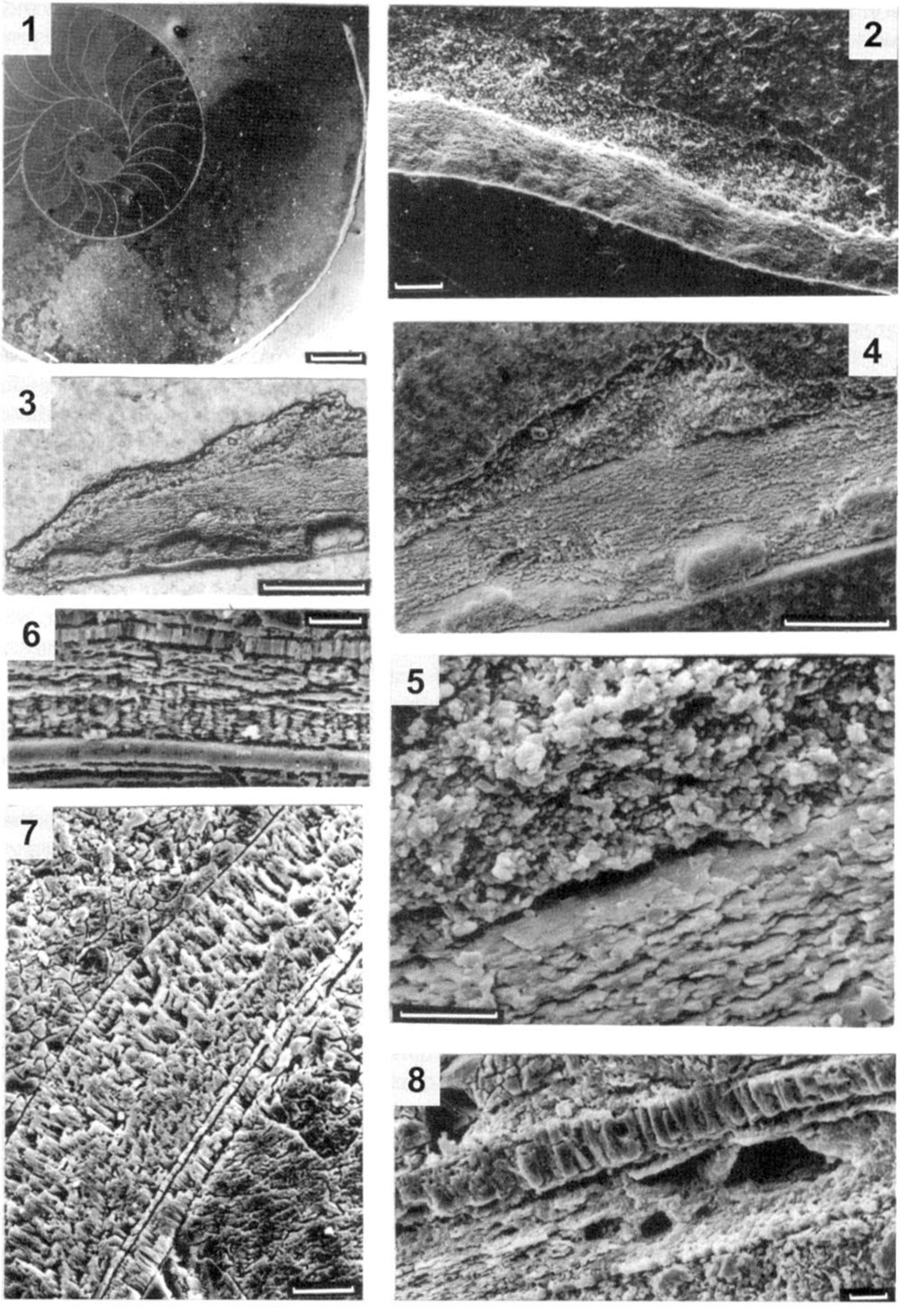
Aconeceras sp.; Lower Aptian; Middle Volga, Ulyanovsk Region

Fig. 1–5: 3871/105. Median section of the adolescent shell to show pathological shell wall structure; 1: general view, phragmocone consists of three first whorls, the living chamber occupies half of the fourth whorl; the shell wall near the aperture is of irregular thickness, with the uneven outer surface; scal bar – 1 mm; 2–5: Close-up of Fig. 1 to show the details of pathological ultrastructure: the outer prismatic layer is missing; the outer surface with a kind of large scabs showing 'irregular nacreous' ultrastructure; the principle nacreous layer with wavy growth lines and blocks; scale bar: 2 – 0. 3 mm; 3 – 0. 1 mm, 4 – 0. 3 mm, 5 – 0. 01 mm

Fig. 6: 3871/106. Shell wall with minor aberrant structure: the nacreous layer has different inner and outer portions; the latter has no columnar nacre; scale bar – 0. 01 mm

Fig. 7: 3871/107. The portion of the shell wall with the nacreous layer of the aberrant ultrastructure; its outer portion consists of vertical elements; scale bar – 0. 01 mm

Fig. 8: 3871/108. Shell wall fragment with irregularly biomineralized nacreous layer; black spots seemed to be originally non-mineralized; scale bar – 0. 03 mm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injuries appeared as a result of the one and the same cause and it is uncertain if they formed in connection with the biting marks. However, the scratches look as if the shell wall was deeply damaged, nearly cut through by a narrow acute talon or pointed jaw.

5. DISCUSSION – MASS LOSS OF *ACONECERAS* YOUNGLINGS IN THE OXYGEN-DEFICIENT ENVIRONMENTS OF THE EARLY APTIAN EPICONTINENTAL SEA ON THE EAST-EUROPEAN PLATFORM

Two characteristic features of the investigated mass occurrences of small-sized ammonite shells have been revealed: 1) approximately 25–30% of the shells show one or more considerably shortened chambers preceding the living chamber; 2) many of shells have aberrant shell wall surfaces and ultrastructures.

The 25–30% of dead younglings which show a pronounced crowding of sutures underwent shell secretion retardation in the process of a gradual but unsuccessful adaption to the oxygen-deficient environment. The remainder were unable to continue shell secretion, even in a retarded manner. Previously, a less dramatic septal approximation than in the present case has been observed in various ammonoid taxa. This phenomenon occurred in shells showing characteristic signs of the terminal stage of growth, in shells showing repairing of a large injure, and in forms with regular repeated structures like ribs, one of which was larger than others, lappets and collars (DOGUZHAEVA, 1982, 1990). In all these cases, the formation of the chamber, which is remarkably shorter than normal chambers fitting genetically controlled pattern of shell growth, was caused by the temporary (with the exception of the terminal stage of growth) retarding of the shell tube growth. Keeping in mind that the younglings under consideration inhabited dysoxygenated environments, one can assume that the low oxygen content could be the primary reason for retarding shell secretion. The formation of the shortened chambers led to an increase in the animal's weight and a decrease in buoyancy. Recent teuthids inhabiting dysoxic environments overcome the lack of oxygen by regular nightime migrations to the oxygenated surface waters. On the asssumption that *Aconeceras* younglings had a similar behaviour, then the disturbance of their bouyancy caused by the shortened last chambers would have inhibited their rise to the surface water. Hence they perished because of their incapacity to escape from the dysoxigenated conditions, at least for a short time. The younglings which had no septal crowding fully stopped the secretion processes and died.

KAMMER et al. (1986) observed the close packing of the sutures near the living chamber in small-sized ammonoids from Mississippian strata. The authors noted that this feature was a character of late ontogenetic stages and supposed that at least some of the small-sized ammonoids "have been stunting associated with oxygen-deficient conditions" (KAMMER et al., 1986: 117). These authors believed that some of the small-sized ammonoids studied did not die as younglings but lived for some period after, being dwafs. However, no detailed information on the shell walls was given by KAMMER et al. (1986).

Accepting that in the small-sized shells under study, the extremely short phragmocone chambers preceding the living chamber indicates the lethal physiological condition of the younglings, does the shell wall show notable signs of lethal pathological secretion ? As shown above, some of the studied shells exhibit pathological signs on the external whorl, expressed in the uneven 'sick' surface, with scabs, varying shell wall thickness and irregular ultrastructure (Pl. 2, Fig. 8; Pl. 3, Figs. 1–8). The nacreous layer, which is the main bulk of the wall, has been damaged in a such way that the growth lines are irregular, the interlamellar organic sheets are unusually thick and suddenly wedge out, standard stock packing of nacreous tablets is missing, and the thickness of the tablet is strongly variable. The whorl before the last one shows a more regular ultrastructure and consists of three layers: inner prismatic, nacreous (with minor infringments when standard stock packing of nacreous tablets is missing here or there and the thickness of the tablet is changable) and outer prismatic; the wall is coated by the standard dorsal wall of the next whorl formed by the wrinkle layer and inner prismatic layer (Pl. 2, Figs. 6, 7).

The nacreous layer is a complicated shell structure known in molluscs only. This layer contains a lot of organic matter – organic sheets separate the sublayers and organic capsules coat aragonitic structural units. The organic sheets define the shape of aragonite skeleton elements. Thus, in *Aconeceras*, the oxygen-deficient environment affected secretion of organic matter. The aberrant shell wall of the external whorl seemed to result in diminishing of shell solidity. Thus, the extraordinary septal crowding accompanied by the pathological shell wall of the external whorl revealed in small-sized *Aconeceras* shells must have been of lethal significance for younglings.

In Recent *Nautilus*, shell secretion affected by environmental changes was documented in two animals in an advanced ontogenetic stage. They were captured in the Philippines, transferred to Germany and kept in an aquarium for two years (Spaeth & Hoefs, 1986). The replacement of food, water, temperature, pressure, light and probably some other parameters of the natural habit resulted in aberrant secretion of the shell wall. The portions of the shell secreted in aquarium show irregular layering of aragonitic sheets interlaminated by thick conchyoline lamellae. As a result, the outer surface became uneven and lost a color pattern which was present in parts formed under natural environments.

Starting from the embryonic stages, the investigated *Aconeceras* lived in a pernicious disoxygenated environment in a shallow epicontinental sea. It co-existed with *Deshayesites,* characterized by ribbed and less involute shell, and the small ribbed heteromorph *Toxoceratoides*. *Aconeceras* disappeared in the basin earlier than these two genera. The latter forms seem to have inhabitated shallower depths (Westermann, 1996; Tsujita & Westermann, 1998) which must have been better aerated. Further, possibly they were better adapted for vertical migrations. Later, the basin became shallower (the upper part of the Lower Aptian has more sandstone interbeds). At this time both *Deshayesites* and heteromorphs evolved into species characterized by considerably large size, the former being up to 250–300 mm in diameter and the latter up to 400 mm in length. So far, the reasons for this phenomenon have remained obscure.

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