A New Type of Shell Malformation Caused by Epizoans in Late Jurassic Ammonites from Central Russia

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A new type of shell malformation caused by epizoans in Late Jurassic ammonites from Central Russia

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A new type of shell damage on Late Jurassic ammonite *Kachpurites fulgens* is described. The new type of shell malformation consists of small elongated pits, arranged in groups on the surface of ammonite shell and concentrated near the terminal aperture. The examination of the pits demonstrated no signs of drilling, biting, or healing of punctures. The shell layers in the pits are bent downward without changing in thickness. At the same time the pits, in some cases, significantly distort the shape of the shell walls. Deformed growth lines are associated with some of the pits. All of this supports the hypothesis that the pits had been formed by epifauna located at a flexible uncalcified part of the periostracum in the apertural region of the growing ammonite shell. It is likely that epizoan attachment led to the deformation of the thin periostracum film and to the distortion of the growing shell wall. The nature of epizoans is discussed, but remains unclear due to their rather poor preservation. The relationship between epizoans and ammonites is also an open question: they could have been parasites, but other types of biotic relationships cannot be entirely ruled out.

Key words: Ammonoidea, Craspeditidae, *Kachpurites*, parasites, epifauna, Jurassic, Russia.

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Introduction

The shells of live ammonites, swimming in the water column, often have been used as a substrate for the attachment and growth of different invertebrate animals (i.e., epifauna). Lifetime attachment of serpulids (Keupp 2000, 2012; Seltzer 2001; Larson 2007; Andrew et al. 2011), bivalves (Seilacher 1960; Seltzer 2001; Larson 2007), limpets (Akpan et al. 1982; Kase et al. 1994, 1998; Seilacher 1998), bryozoans (Davis et al. 1999), and cirripedes (Drushchits and Zevina 1969; Ifrim et al. 2011; Keupp 2012) to the ammonite shells are well known. Ammonoid shells provided not only substrate for attachment: the flow of water, which arose during the ammonite swimming, could have supplied some epizoans with food/nutrients. Limpets could have eaten algae growing on the ammonite shells in the photic zone (Kase et al. 1994, 1998; Seilacher 1998). In some cases the epizoans did not affect their hosts (see Ifrim et al. 2011), but in others they were the cause of distortion of shell shape and even the inhibition of growth of the ammonites (Seltzer 2001; Checa et al. 2002; Larson 2007; Andrew et al. 2011; Keupp 2012).

Although previously described epizoans are considered as parasites due to the harm caused to their hosts (Andrew et al. 2011), they did not feed on the ammonite soft-tissue or “rob” ammonite food. Parasites, which had lived inside the ammonite body chamber and apparently fed on the soft-tissues of ammonites, are known because of blister pearls (House 1960; Keupp 1986, 2000, 2012; Hengsbach 1996; De Baets et al. 2011, 2013, 2015). These small hemispherical protrusions were formed by ammonites on the inner walls of the body chamber for protection against parasites which lived between the shell and mantle, on the mantle surface (see De Baets et al. 2011; Keupp 2012). The blister pearls left imprints on the internal moulds of ammonoid shells, but they have no traces on the outer ammonoid shell surface. Very likely, ammonites, as well as modern coleoids and nautilids (see De Baets et al. 2015 for review), could have had parasites on the surface of their arms and cephalic complex, but such parasites have never been found in a fossil record and this assumption is hypothetical.

The epizoans, which lived on ammonoid shells, often led to a distortion of shell shape (Keupp 2000, 2012; Seltzer 2001; Checa et al. 2002; Larson 2007; Andrew et al. 2011). However, in general, these malformations were caused by bioimmuration: the ammonite was forced to grow over the epizoan located on the previous shell whorl. Another type of epizoan-produced shell damage is a bioerosion: borings of ammonoid shell which were made by different groups of epizoans. However, available information about syn vivo bioerosion of ammonoid shells is relatively scarce, in many cases the boring traces were likely formed postmortem (see Keupp 2012 and De Baets et al. 2015 for review).

This paper describes a new type of anomalous structures in ammonite shells likely related with epizoans. They are in a form of small elongated pits located on the shells of the Upper Jurassic ammonite *Kachpurites fulgens* (Trautschold, 1861) belonging to the Craspeditidae. These pits were previously interpreted as casts of blister pearls (Mironenko 2012), but new better preserved findings allowed author to propose a new interpretation of these shell abnormalities. The nature and mechanism of formation of these pits is discussed in the present paper.

Institutional abbreviations.—MSU, Moscow State University Museum.

Other abbreviations.—EDS, dispersive spectroscopy detector.

Geological setting, material and methods

The present study is based on ammonite shells from the Late Volgian (latest Jurassic, corresponding to Late Tithonian, see Houša et al. 2007; Rogov 2014a) *Kachpurites fulgens* Zone from the Moscow region in Central Russia. Specimens studied herein were collected by the author in the summers of 2011–2014 in two localities in the Moscow area (Fig. 1): Eganovo (55°32'08.28" N; 38°03'10.47" E) and Mnevniki (55°46'4.12" N; 37°28'4.67" E) (Rogov and Starodubtseva 2014).

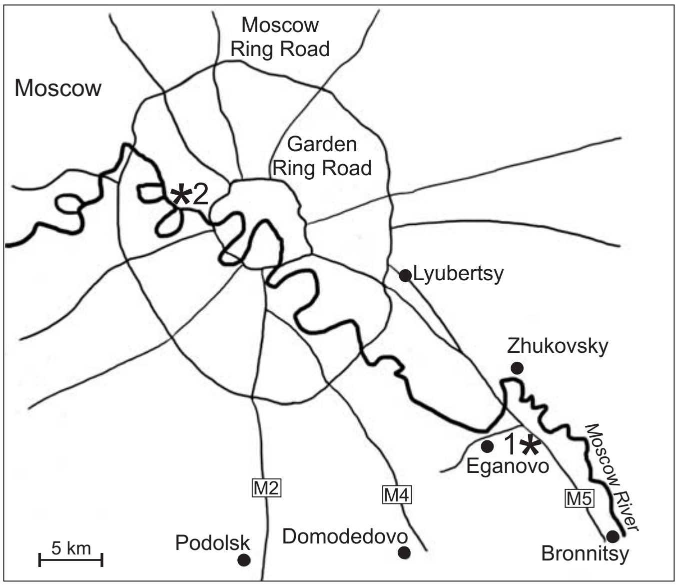

Fig. 1. Map of Moscow area with localities: 1, Eganovo (55°32'08.28" N; 38°03'10.47" E); 2, Mnevniki (55°46'4.12" N; 37°28'4.67" E).

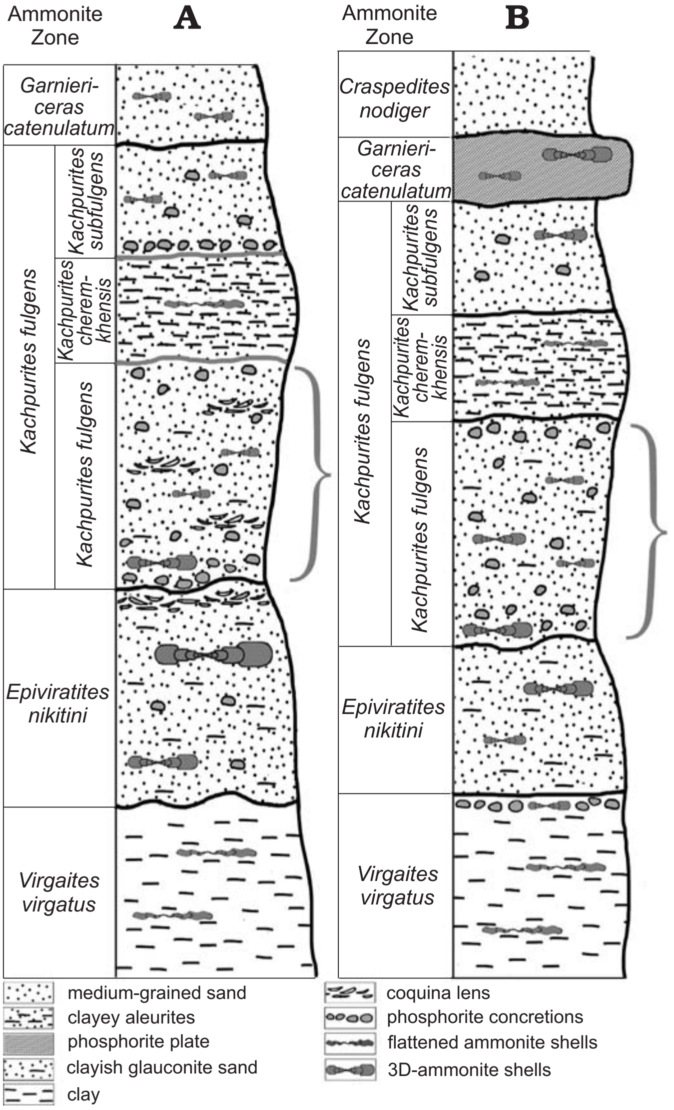

Fig. 2. Stratigraphic column of the localities. **A**. Mnevniki, Moscow. **B**. Eganovo, Moscow area. The braces mark the horizon from which the described ammonites have been collected. Ammonite zones (see Rogov and Starodubtseva 2014). The total thickness of the layers is about 2 m.

In these localities the strata, which belong to several ammonite zones, are available for study (Fig. 2). The beds of the *Kachpurites fulgens* Zone have been studied briefly and its division into subzones and biohorizons is not yet widely accepted (see Rogov and Starodubtseva 2014). The author uses herein a division into three subzones which are clearly separated lithologically and by ammonite species: *K. fulgens*, *K. cheremkhensis*, and *K. subfulgens* subzones (Figs. 2, 3).

K. fulgens Subzone beds are composed of dark green clayish glauconite sand with phosphatic nodules and contain well-preserved three-dimensional ammonite shells. *K. cheremkhensis* Subzone deposits in the Moscow region are represented by clayey aleurites; *K. subfulgens* Subzone deposits are composed of medium-grained yellowish-green sand (Figs. 2, 3). In Mnevniki and Eganovo, *K. fulgens* Subzone beds are slightly different. In Mnevniki coquina interlayers are present in clayish sand, consisting of fragments of small bivalves, brachiopods, and crinoids, but there are no such coquina layers in Eganovo. Similar coquina layer containing also fragments of ammonite shells in the uppermost part of *Epiviratites nikitini* Zone underlies *K. fulgens* sediments in Mnevniki, but not in Eganovo. These layers of fragmented shells indicate that Mnevniki was located closer to the seashore than Eganovo at the time of formation of these strata. Nevertheless, the ammonite species and their mode of preservation in these localities are identical.

Ammonites studied herein come from the *Kachpurites fulgens* Subzone of the eponymous ammonite zone (Figs. 2, 3). In the strata of the *E. nikitini* and *Virgaites virgatus* zones, as well as in the *K. subfulgens* Subzone, well-preserved ammonite shells are extremely rare in both localities: most shells are poorly preserved, fragmented or devoid of shell layers. In the *K. cheremkhensis* Subzone ammonites are flattened and their shells are dissolved. Only in the phosphorite plate of the *Garniericeras catenulatum* Zone in Eganovo relatively numerous solid ammonite shells with preserved aragonite layers occur. However, they are usually fragmented and deprived of body chambers. Therefore only ammonites from *K. fulgens* Subzone are sufficiently numerous and well-preserved for examination. Only shells of three genera of the family Craspeditidae: *Kachpurites*, *Craspedites*, and *Subcraspedites* can be found in the beds of the *Kachpurites fulgens* Zone (Rogov and Starodutseva 2014).

Ammonites for this article were studied at various angles under incident illumination with the naked eye and were examined with a binocular microscope. Several specimens were examined under a scanning electronic microscope TESCAN/VEGA with BSE detector at the Paleontological Institute of the Russian Academy of Sciences in Moscow. The specimens were inspected in low vacuum conditions at 30 kV. Images were generated using backscattered electrons (BSE). Data on elemental composition of the preserved structures were obtained using the SEM-coupled energy dispersive spectroscopy detector.

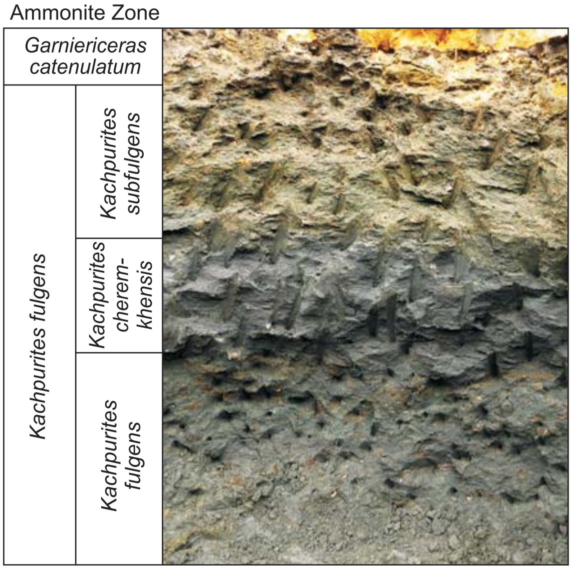

Fig. 3. Upper Volgian strata in Eganovo locality. Three subzones of *Kachpurites fulgens* Zone. The thickness of all layers is about 1.4 m. The traces on the surface of the layer have been left by the excavation knife.

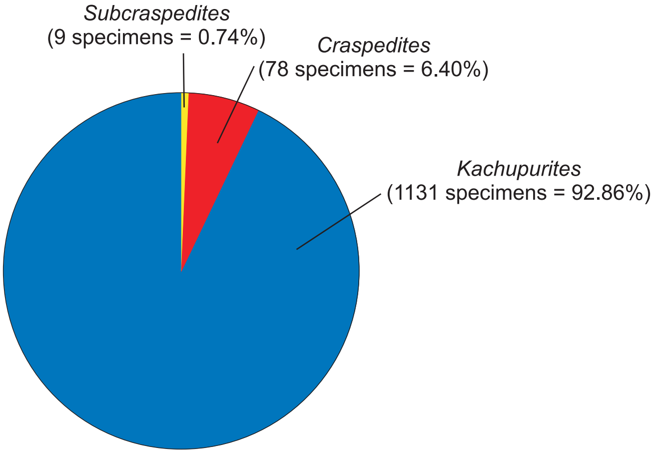

Fig. 4. The circular diagram of the frequency of the genera distribution in *Kachpurites fulgens* Zone.

Results

1218 whole and fragmentary shells of *Kachpurites*, *Craspedites*, and *Subcraspedites* ammonites were examined in this study. On 15 specimens (approximately 1.23% of studied ammonites) numerous small elongated pits were found. These pits are mostly arranged in groups on the surface of ammonite body chambers and are concentrated near the terminal aperture. All ammonites with pits belong to the *Kachpurites fulgens* (Trautschold, 1861), the most abundant species (Fig. 4) in the *K. fulgens* Subzone in Central Russia (Mitta 2010; Rogov and Starodubtseva 2014). Ammonites with pits make up 1.32% of studied *Kachpurites* shells (1133 specimens), they were found in different layers throughout the sediments of *K. fulgens* Subzone.

Most shells of *Kachpurites fulgens* in the Moscow area are relatively small: 5–6 cm in diameter (Mitta 2010; Rogov and Starodubtseva 2014). Body chambers of studied ammonites are filled with finely dispersed glauconite sand and sometimes contain ammonite jaws (Mironenko 2014a), whereas the phragmocones remain empty and often crushed during excavation. If phragmocones remain intact, they usually contain phosphatized siphuncular tubes and occasionally cameral membranes (Schindewolf 1968; Mironenko 2014b). Broken shells and their isolated fragments can also be found. Since they are mixed with intact shells and bear no traces of abrasion, they had been likely fragmented by predators or scavengers before they were buried. However, some damages may have resulted from non-biological factors (e.g., transportation by water currents).

Most of the ammonites in the *K. fulgens* Subzone, as well as their fragments, have more or less preserved shell layers: it is commonly the transparent inner prismatic layer only, but in some specimens other layers are preserved (Fig. 5A).

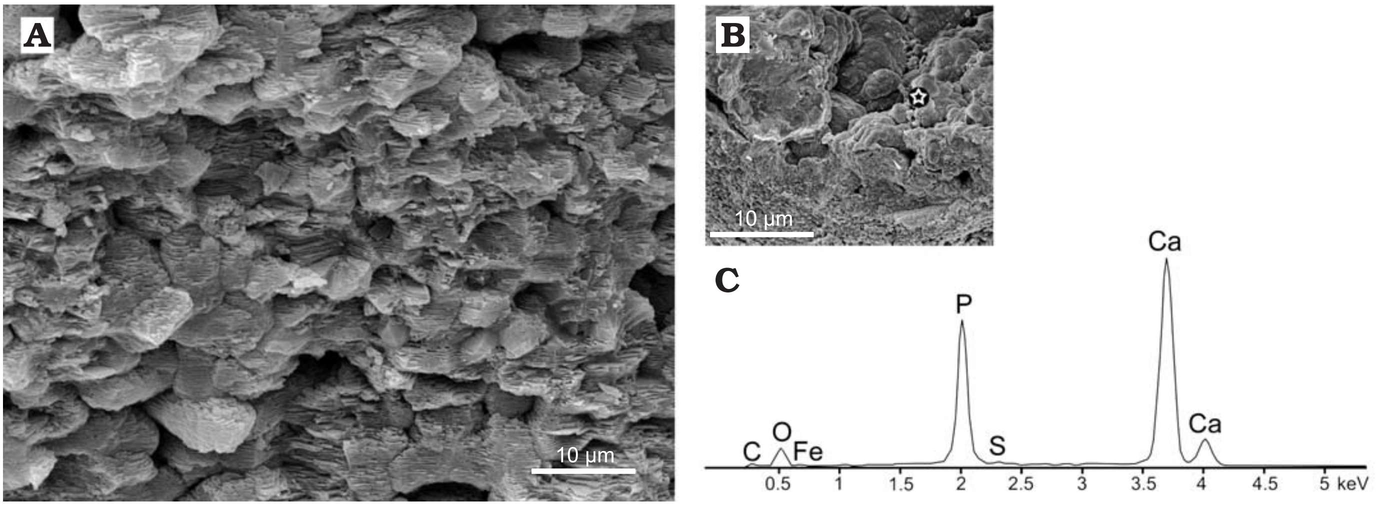

Fig. 5. Craspeditid ammonite *Kachpurites fulgens* (Trautschold, 1861) from the Late Volgian, *Kachpurites fulgens* Zone, Moscow region, Eganovo locality, Central Russia; shell structure and chemical composition of the filling of pits, MSU 118/1. **A**, **B**. Aragonite layer of the shell. **C**. EDS (Energy Dispersive X-ray Spectroscopy) analysis of the brown mineral in the pit on the surface of specimen (asterisk in B).

The pits are observed on internal moulds of the body chambers, covered by a thin inner shell layer, as well as on the surface of preserved aragonitic shell layers.

The number of pits on different *K. fulgens* pit-bearing specimens varies greatly, but in most cases it is impossible to establish their exact number on each shell as many of them merged with each other and small pits are barely visible. It is also impossible to calculate the total number of pits on each ammonite due to preservation of the studied specimens: most of them are body chamber fragments.

In all cases (except MSU 118/6) the size of the pits is less than 1 mm and their shape is longitudinally elongated. In several cases (MSU 118/1, 9, 10), the shell layers of the previous whorl are partially preserved on the dorsal side of body chamber. These layers bear convex structures which reflect the pits, located on the penultimate shell whorl.

As the number of studied pit-bearing ammonites is very small, a detailed description of the most interesting specimens is included below:

MSU 118/1 (Figs. 5–7): A fragment of the *Kachpurites fulgens* body chamber with preserved aragonitic shell layers on one lateral side (Fig. 5A). Numerous elongated pits are visible on the specimen (Fig. 6A). The size of the pits is less than 1 mm, they are elongated in an apertural direction. The two small tubercles on the dorsal side of the specimen reflected the pits which were formed on the penultimate shell whorl (Fig. 6B). Several abnormally curved growth lines are connected with some of pits (Fig. 6C, D). At the front end of the specimen there are 5 pits, located on the preserved portion of the outer shell layer, filled with brown calcium phosphate (Fig. 5) as indicated by the EDS analyses (Fig. 5B).

MSU 118/2 (Fig. 8A): The fully preserved *Kachpurites fulgens* body chamber is 30 mm in diameter. Only the inner semitransparent shell layer is preserved in this specimen. The pits appear at a distance of about 40° behind the aperture on the ventral and lateral sides. Their number increases near the aperture.

MSU 118/3 (Fig. 8B): *Kachpurites fulgens* shell with a 17 mm diameter. At a distance of about 70° behind the aperture the pits merge together and form a deep constriction on the body chamber (although normal *Kachpurites* shells have no constrictions). Three more pits are arranged in a row in front of the constriction, however, there are no pits directly near the preserved part of the aperture.

MSU 118/4 (Fig. 8C): The fully-preserved *Kachpurites fulgens* body chamber, 24 mm in diameter. A lateral muscle attachment scar, which is visible on one side of the body chamber, is smaller than such scars in other *K. fulgens* specimens. The length of the muscle scar of this ammonite is about 1/4 of the length of the body chamber whereas *Kachpurites,* in general, have lateral attachment scars which occupy 1/3 of the body chamber (Mironenko 2015). First pits appear on the ventral side at 90° behind the aperture, their concentration dramatically increases adorally. While they are located on both the lateral and ventral sides, most of them are situated on the ventral side near the aperture.

MSU 118/5 (Fig. 8D): *Kachpurites fulgens* shell with a diameter of 17 mm. At 40° behind the aperture on the ventral and ventrolateral sides the pits are visible and their concentration increases adorally (though the apertural edge is not preserved). The pits are located asymmetrically: most of them are on one lateral side and on the venter.

MSU 118/6 (Fig. 8E): The *Kachpurites fulgens* body chamber fragment of 30 mm in diameter without aperture and phragmocone. At the end of the first third of the body chamber there is one large (about 1 mm in diameter) round pit. This pit is different from all other studied pits by its larger size, round shape, and by the fact that it is the only pit on this shell.

MSU 118/7 (Fig. 9A): Unusual "scaphitoid" *Kachpurites fulgens* shell, 29 mm in length. The hook-like deformation is the effect of a relatively large epizoan shell attached to the venter of a previous whorl (see Keupp 2000, 2012; Seltzer 2001; Larson 2007). Such deformations, likely caused by bi-

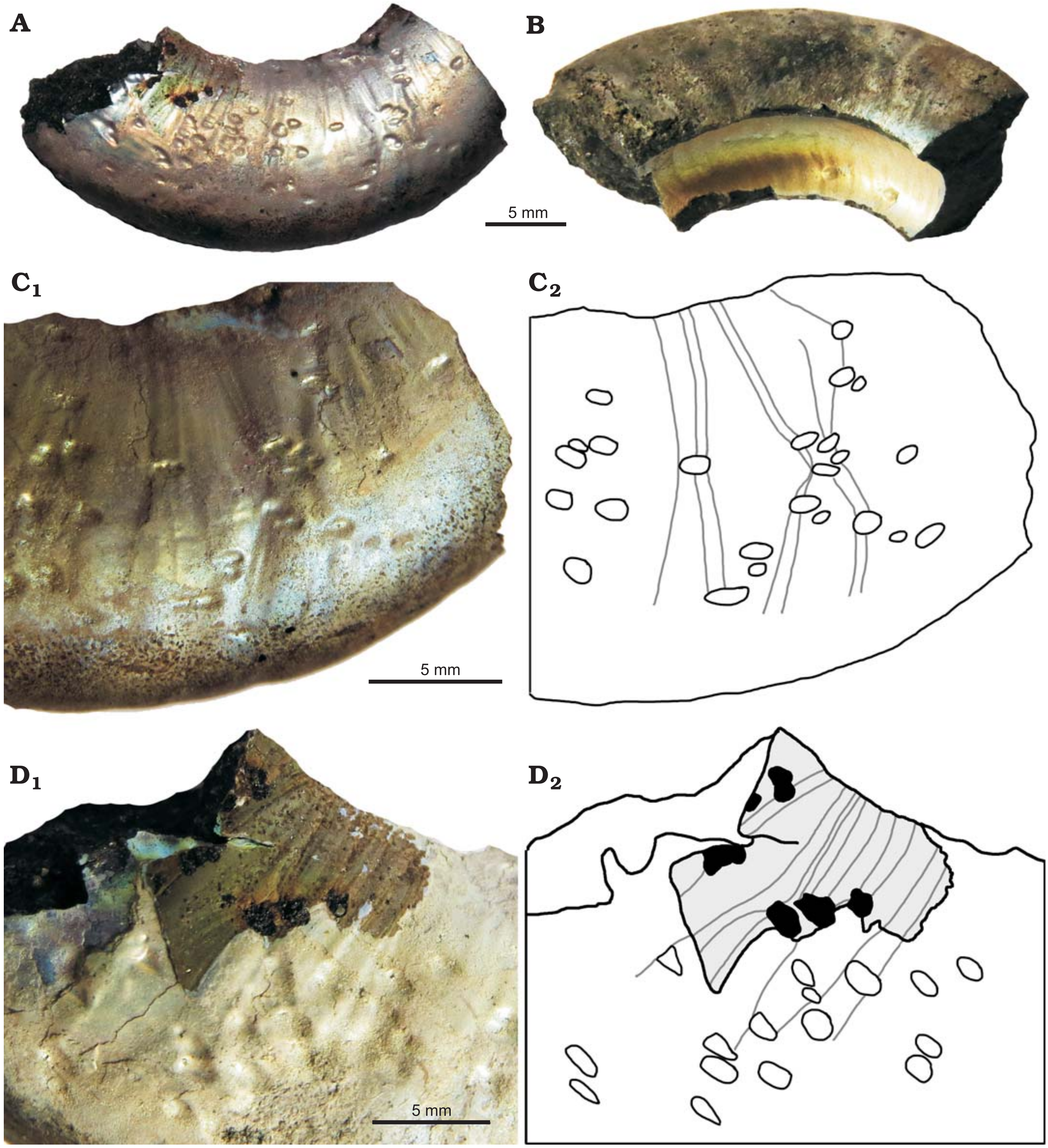

Fig. 6. Craspeditid ammonite *Kachpurites fulgens* (Trautschold, 1861) from the Late Volgian, *Kachpurites fulgens* Zone, Moscow region, Eganovo locality, Central Russia; shell with pits and deformed growth lines, MSU 118/1. **A**. General lateral view. **B**. Dorsal view, two tubercles located on the dorsal side of the body chamber, reflecting pits which are located on the previous shell whorl. **C**. The pits and deformed growth lines, which are related with pits, on the lateral surface of the specimen. **D**. Outer shell layer with phosphatic mineral inside pits and curved growth lines connected with these pits. Photographs (A, B, C_1, D_1), explanatory drawings (C_2, D_2).

valves (see Fig. 9B) very rarely occur on *Kachpurites* shells (Mitta et al. 1999) and are not related to the studied pits. However, pits are located on the body chamber of this specimen (Fig. 9A_2). They are scattered throughout the surface of the body chamber and their number increases towards the aperture (though the apertural edge is not fully preserved).

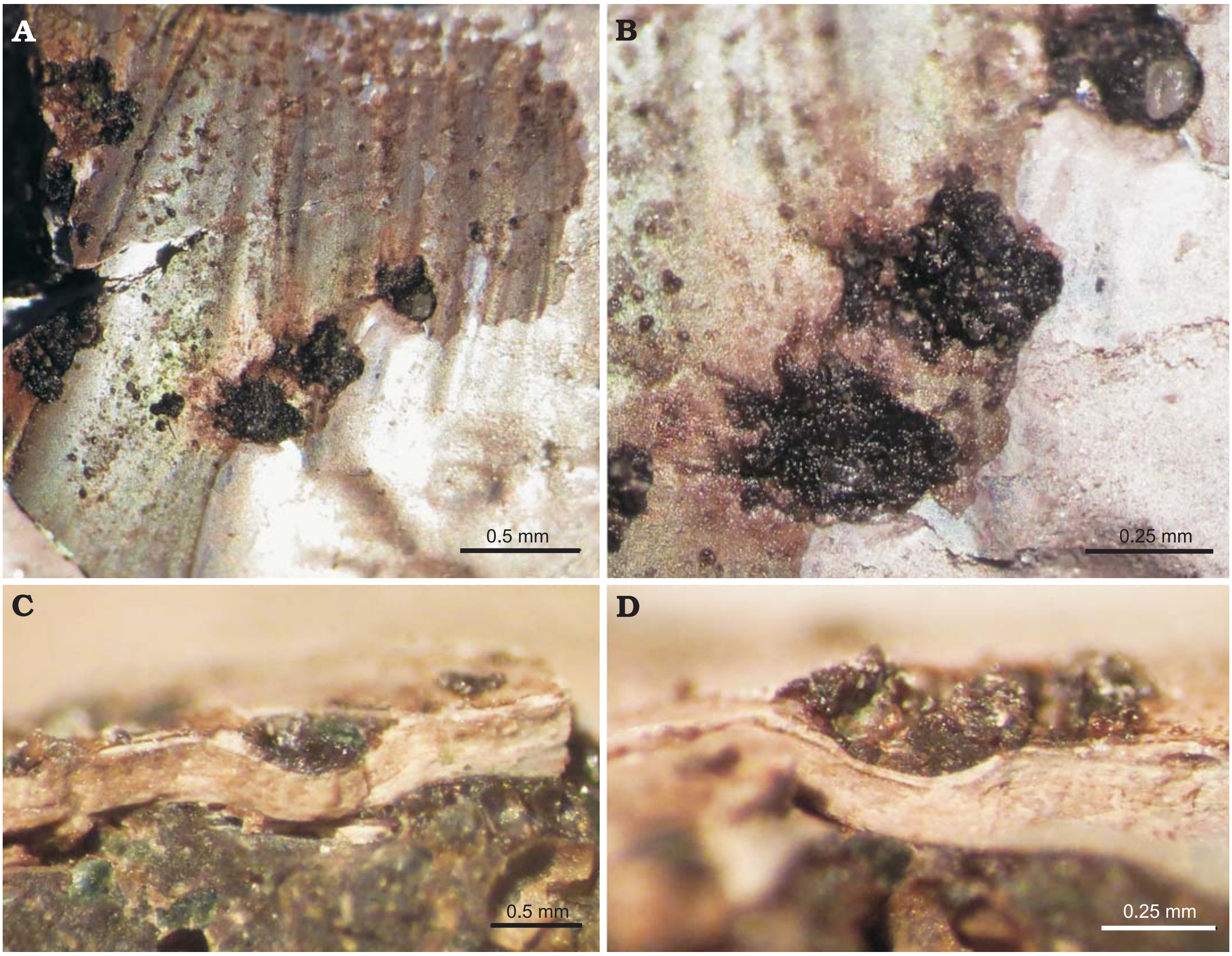

Fig. 7. The pits with preserved phosphatic remnants on the shell of craspeditid ammonite *Kachpurites fulgens* (Trautschold, 1861) from the Late Volgian, *Kachpurites fulgens* Zone, Moscow region, Eganovo locality, Central Russia; MSU 118/1. **A**, **B**. Three pits with phosphatic filling on the well-preserved surface of the specimen. **C**, **D**. Transverse cross-sections of the two pits with phosphatic remnants located on the well-preserved part of the shell of the specimen. Note the thin outer prismatic and thick nacreous layers. The photos were taken using an optical binocular microscope.

MSU 118/8 (Fig. 9C): The nearly intact *Kachpurites fulgens* body chamber (28 mm in diameter) with partially preserved shell. The pits start to emerge at 80° behind the aperture. The distribution of the pits is asymmetric: most of them being near the aperture on one side (Fig. $9C_1$), two on the venter and two on the opposite side (Fig. $9C_2$).

MSU 118/9 (Fig. 9D): *Kachpurites fulgens* body chamber fragment, 25 mm in diameter. The aperture bears numerous poorly preserved merging pits on lateral sides. On the ventral side, there are not many pits. Several bulges (the pits which are located on the previous shell whorl) are visible on the dorsal side of the specimen.

MSU 118/10 (Fig. 10): The *Kachpurites fulgens* body chamber fragment is 26 mm in diameter. Slightly dissolved outer shell layers are preserved. The pits are very numerous on both the ventral and lateral sides of the entire surface of the specimen (Fig. $10A_1$, A_2). On the dorsal side remnants of the shell layers of the previous whorl are preserved and several bulges reflecting the pits, which are located on the previous shell whorl, are visible here (Fig. $10A_3$).

Five more pit-bearing specimens (MSU 118/11–15, three from the Eganovo locality and two from Mnevniki) are poorly preserved and display no new data. Therefore, a detailed description of these specimens has been omitted.

Discussion

The phosphatic structures inside the pits.—The majority of the pit-bearing specimens is poorly preserved and their outer prismatic and nacreous shell layers are dissolved (for example Fig. 8A–C, E). In the three specimens (Figs. 8D, 9C, 10) the nacreous layer is preserved, although its surface is partially eroded while in the one of specimens (Figs. 5–7) the shell layers on the one side of the body chamber are relatively well-preserved (Figs. 5A, 7).

Fig. 8. Craspeditid ammonites *Kachpurites fulgens* (Trautschold, 1861) from the Late Volgian, *Kachpurites fulgens* Zone, Moscow region, Central Russia, Mnevniki (A) and Eganovo (B–E) locality; shells with pits. **A**. MSU 118/2, fully preserved body chamber with pits, which are clearly visible not far from the aperture; lateral view. **B**. MSU 118/3, shell with abnormal constriction on the body chamber; in ventral (B_1) and lateral (B_2) views. **C**. MSU 118/4, shell with fully preserved body chamber; in lateral (C_1) and ventral (C_2) views. There are abnormally small lateral attachment scars (on the top of the C_1) and pits on the apertural part of the shell. **D**. MSU 118/5, shell without aperture and with pits which are located ventro-laterally; lateral view. **E**. MSU 118/6, body chamber fragment without aperture and phragmocone; ventral view (E_1), enlarged view of the pit (E_2). There is only one relatively large pit on this fragment.

The pits are visible in all these types of preservation because they are located not only on the shell surface: all shell layers are bent downward within the boundaries of each pit (Fig. 11A, B). Inside the pits located on the surface of specimens MSU 118/1 (Figs. 6, 7) and MSU 118/10 (Fig. 10) the dark material is visible. Examination using a binocular microscope shows that in the MSU 118/10 this dark material is just clay particles, whereas in the MSU 118/1 it is spherical formations of a brown mineral (Fig. 7). The EDS analyses have shown that it is a phosphate mineral, most likely apatite (Fig. 5B). Identical spherical formations were found inside the pit enclosed between shell layers on the dorsal side of

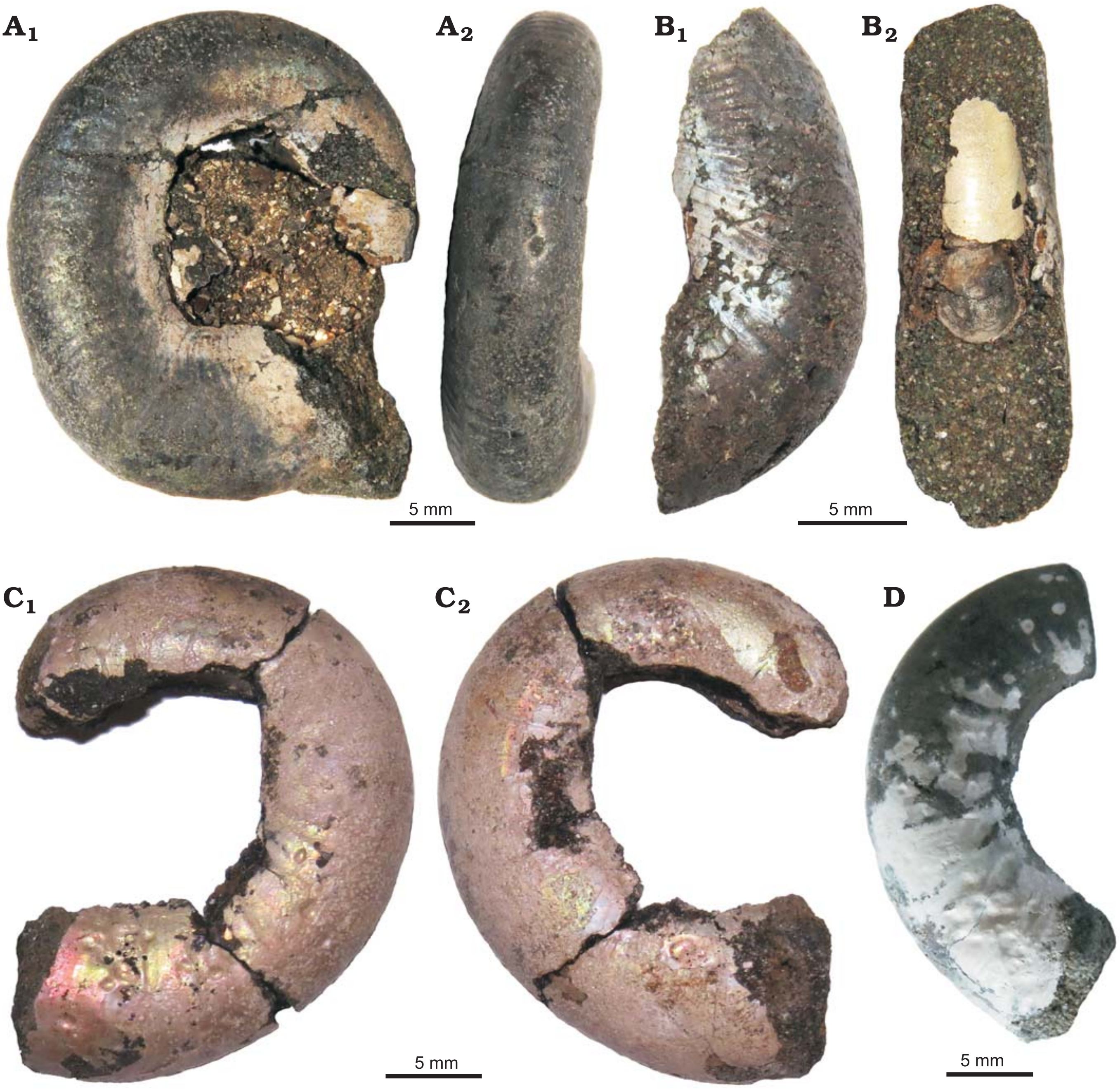

Fig. 9. Craspeditid ammonites *Kachpurites fulgens* (Trautschold, 1861) from the Late Volgian, *Kachpurites fulgens* Zone, Moscow region, Central Russia, Eganovo (A, B) and Mnevniki (C, D) localities; shells with pits and epizoans, lateral (A_1, B_1, C, D) and dorsal (A_2, B_2) views. **A**. MSU 118/7, abnormal "scaphitoid" shell shape. There are several pits on the ventral side of the shell (A_2). **B**. MSU 118/16, fragment of the abnormal shell. The fragment of bivalve shell which caused distortion of the shell growth can be seen on the dorsal side (B_2). There are no pits on this specimen. **C**. MSU 118/8, body chamber with pits on both sides of the shell. **D**. MSU 118/9, fragment of the body chamber with pits, many of them are merged with each other.

specimen MSU 118/9 (Fig. 11C, D). This pit is located on the surface of the penultimate whorl and had been overlapped by the terminal body chamber. Apatite replaces the organic parts of the ammonite shell such as membranes of phragmocone, siphuncle tubes, and blood vessels of Upper Volgian ammonites including *Kachpurites* and *Craspedites* from the Russian Platform (Schindewolf 1968; Mironenko 2014b). There is little doubt that apatite inside pits formed during microbial decomposition of organic tissues. However, the nature of these organic tissues is uncertain. These tissues could have been produced by the ammonite: probably they were remnants of a thick organic periostracum. On the other hand, it could originate from the soft bodies of epizoans which lived in the pits on the ammonite shell surface. The SEM-study of the mineral filling these pits (Fig. 11) did not help to reveal the nature of replaced tissues. No traces of any epizoan remnants were found, nonetheless, they could have been very thin and could have disappeared due to the decomposition.

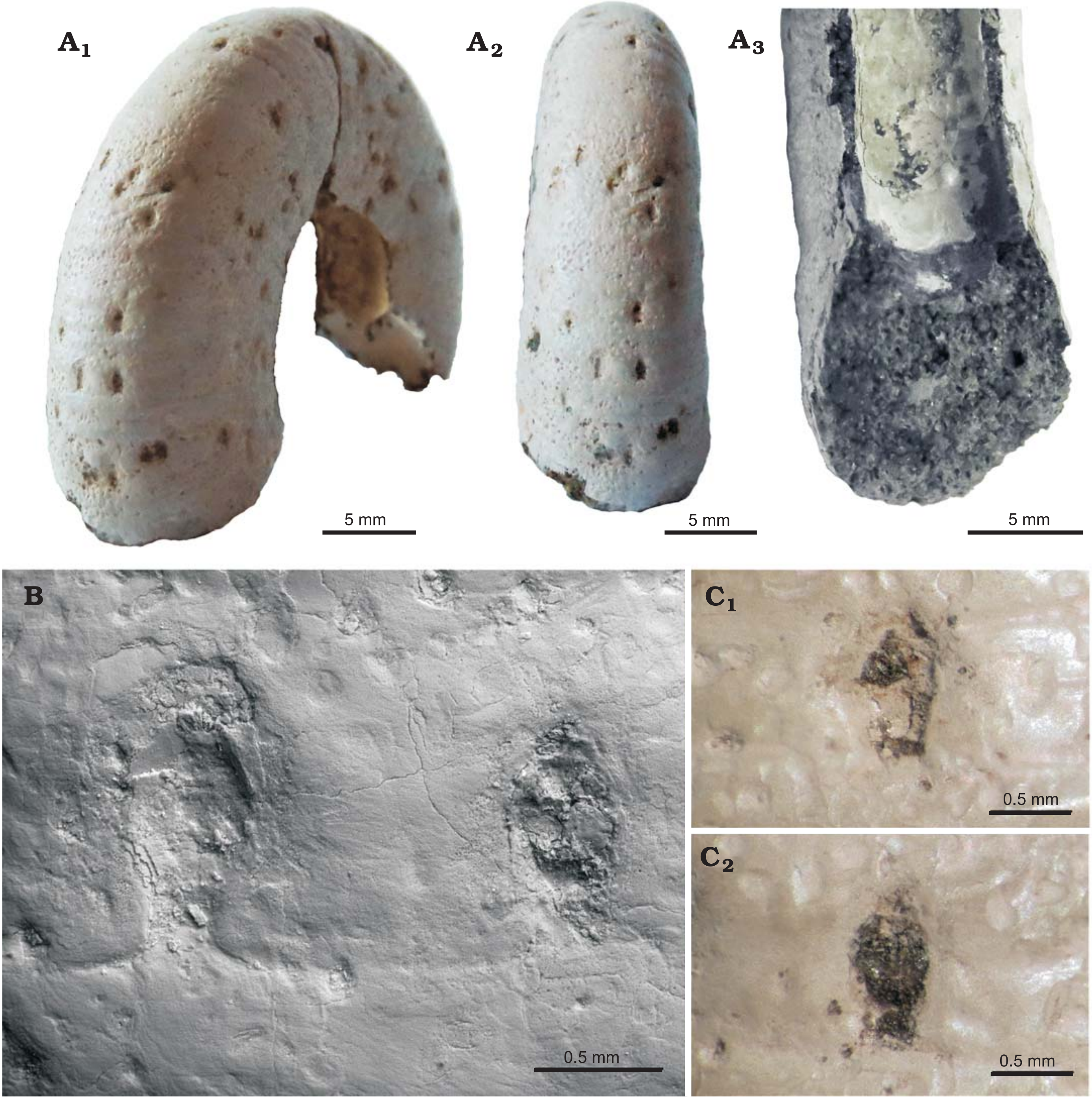

Fig. 10. The pits on the aragonitic shell layers of the craspeditid ammonite *Kachpurites fulgens* (Trautschold, 1861) from the Late Volgian, *Kachpurites fulgens* Zone, Mnevniki, Moscow region, Central Russia; MSU 118/10. **A**. Body chamber with slightly dissolved shell layers. General view in ventro-lateral (A_1), ventral (A_2), and dorsal (A_3) views; on the dorsal side the small tubercle is visible, which reflect the pit on the previous whorl. **B**. Two pits on the specimen, SEM photograph. **C**. Two pits on the specimen, optical binocular microscope photographs.

The mechanism of formation of pits.—The following hypotheses are herein proposed to explain the mechanism of formation of observed pits on the *Kachpurites fulgens* shells. First findings did not allow author to test all of these hypotheses, but with the accumulation of material their testing was possible.

Hypothesis 1: The pits are a result of post-mortem diagenesis, more precisely they are traces of sand grain incisions or some borings. In certain circumstances the aragonitic ammonite shells could have been plastically deformed during diagenesis. In this case imprints of surrounding objects can be incised onto the shell surface. However, ammonite shells in the *K. fulgens* Subzone are not plastically deformed. A lot of completely undamaged shells were found near the shells bearing pits. Outer shell layers of many ammonites are completely or partially dissolved, but not deformed. Lastly and most importantly, the pits are located not only on both lateral and dorsal sides of the shells, but also on the previous shell whorl, which is covered by the body chamber (Figs. 6B, 10A$_3$, 11C, D). The suggestion that the pits are traces of post-mortem drillings is also excluded as the pits are usually associated with abnormal growth lines and the thickness of the shell layers inside these pits is the same as around it (the shell in these pits is bent downward but not drilled or dissolved). Due to these lines of evidence this hypothesis is rejected.

Hypothesis 2: Syn vivo origin of the pits. The pits are imprints of the blister pearls, similar to the structures which have been described on the internal moulds of the Devonian and Jurassic ammonoids by House (1960), Keupp (1986, 2000, 2012), and De Baets et al. (2011, 2013, 2015) and named "forma aegra concreta" by Hengsbach (1996). The blister pearls are hemispherical "half-pearls" which are located on the inner surface of the shell wall. These pearls were formed by ammonoids to isolate the parasites which lived between the shell wall and ammonoid mantle (House 1960; De Baets et al. 2011, 2015). When only internal moulds of *Kachpurites* shells with no outer shell layers were available this hypothesis was considered as most plausible (Mironenko 2012). However, when the specimens with preserved shell layers became available, it turned out that the pits are located on the outer surface of the shell. Therefore this hypothesis could be rejected for the majority of specimens. Only the specimen MSU 118/6 (Fig. 8E) could be related to blister pits as it was previously suggested (Mironenko 2012), since there is only one pit on the ammonite and it is significantly different from the others in a larger size and accurate round shape. This pit is very similar to imprints of the blister pearls on the ammonite internal moulds depicted by Keupp (1986, 2000, 2012). However, it is not possible to prove the relationship of these pits to the blister pearls without outer shell layers preserved (compare Keupp 1986; De Baets et al. 2011, 2013, 2015).

Hypothesis 3: The pits are healed punctures. Keupp (2006, 2012) described healed punctures in body chambers of Mesozoic ammonites (forma aegra fenestra). It could be suggested that the pits on *Kachpurites fulgens* shells could represent similar healed holes. This hypothesis was difficult to disprove based solely on internal moulds, but detailed examination of specimens with preserved shell layers (Figs. 6, 8D, 10) has revealed that there are no traces of healing as well as no boundaries between walls and bottoms of the pits while in the healed punctures such boundaries between old (pre-damaged) and new (post-damaged) parts of the shell wall should be visible (see e.g., Keupp 2006: figs. 3, 4). The lack of boundaries is clearly visible on cross-sections of the pits observed under the SEM (Fig. 11A, B). Therefore, this hypothesis can also be rejected.

Hypothesis 4: The pits are traces of bioerosion: borings of epizoans or predators, which did not end up puncturing the shell. Such boreholes are sometimes found on ammonite shells: there are limpet "home scars" (Kase et al. 1994, 1998; Seilacher 1998). Bioerosion is also known in Recent *Nautilus* shells (Seuss et al. 2015). Not only epizoans, but also predators can produce boreholes in cephalopod shells. For example, the bore holes which are made by octopuses are described from the shells of living nautilids (Saunders et al. 2010). It can be assumed that not all drilling events were successful and the pits could have been a result of such attempted attacks. However, in the case of octopods and limpets, the drilling usually displays traces of the radula which are absent on the studied specimens. Moreover, the observations under SEM (Fig. 11A, B) showed that the aragonite layer is not damaged or eroded, it appears to be only bent downwards (Fig. 11A). The bioeroders or drilling predators are able to destroy the shell layers, but it is unlikely that they could have bent all the layers of the shell downward without changing their thickness. Therefore this version also does not explain forming of the pits.

Hypothesis 5: The pits are a result of illness or injury of the mantle tissue, which formed the shell wall. Ammonites like other animals have been exposed to infectious and parasitic diseases (Keupp 2000, 2012; De Baets et al. 2011, 2015). It can be assumed that some kind of illness or parasitic infestation could have caused a mantle distortion which in turn produced pits on the newly formed parts of the shell. However, all known mantle injuries caused spiral "scars" on the shell corresponding to the damaged site of the mantle. If the pits are in fact a result of mantle illness or injury, they would have lined up in rows, but this is not observed. Therefore, this hypothesis cannot explain the occurrence of pits.

Hypothesis 6: The pits are traces of a predator attacks which occurred at the time of the development of a new part of the shell. Theoretically the attack of predators (e.g., fish or hook-armed belemnites) could have led to the deformation of the soft apertural edge. However, the pits on several specimens (Figs. 6, 9C, 10A) are located too far from each other to be the result of a single attack. In three specimens pits are located even in penultimate whorls (Figs. 6B, 9A$_3$, 11C, D). If the pits are result of predatory attack, we would need to assume that several ammonites were attacked repeatedly. However it is difficult to imagine a series of pit-producing attacks on the same ammonites because of the paucity of the shells with pits (1.23% of studied ammonites). Moreover, it is widely known that predators caused several types of traces on ammonoid shells such as bite marks and the following spiral "scars", produced by damaged mantle edge (see Hengsbach 1996; Keupp 2012). However, on ammonites with pits there are no such traces whereas during attacks the damage of the mantle leading to the appearance of such scars is likely. Therefore, the hypothesis which explains the appearance of pits by predator attacks has to be rejected.

Hypothesis 7: The pits are traces of organisms (epizoa) which were attached to the flexible uncalcified edge of the periostracum during the development of new part of the shell. This hypothesis is similar to the previous one, but different in that the animals which were responsible for the

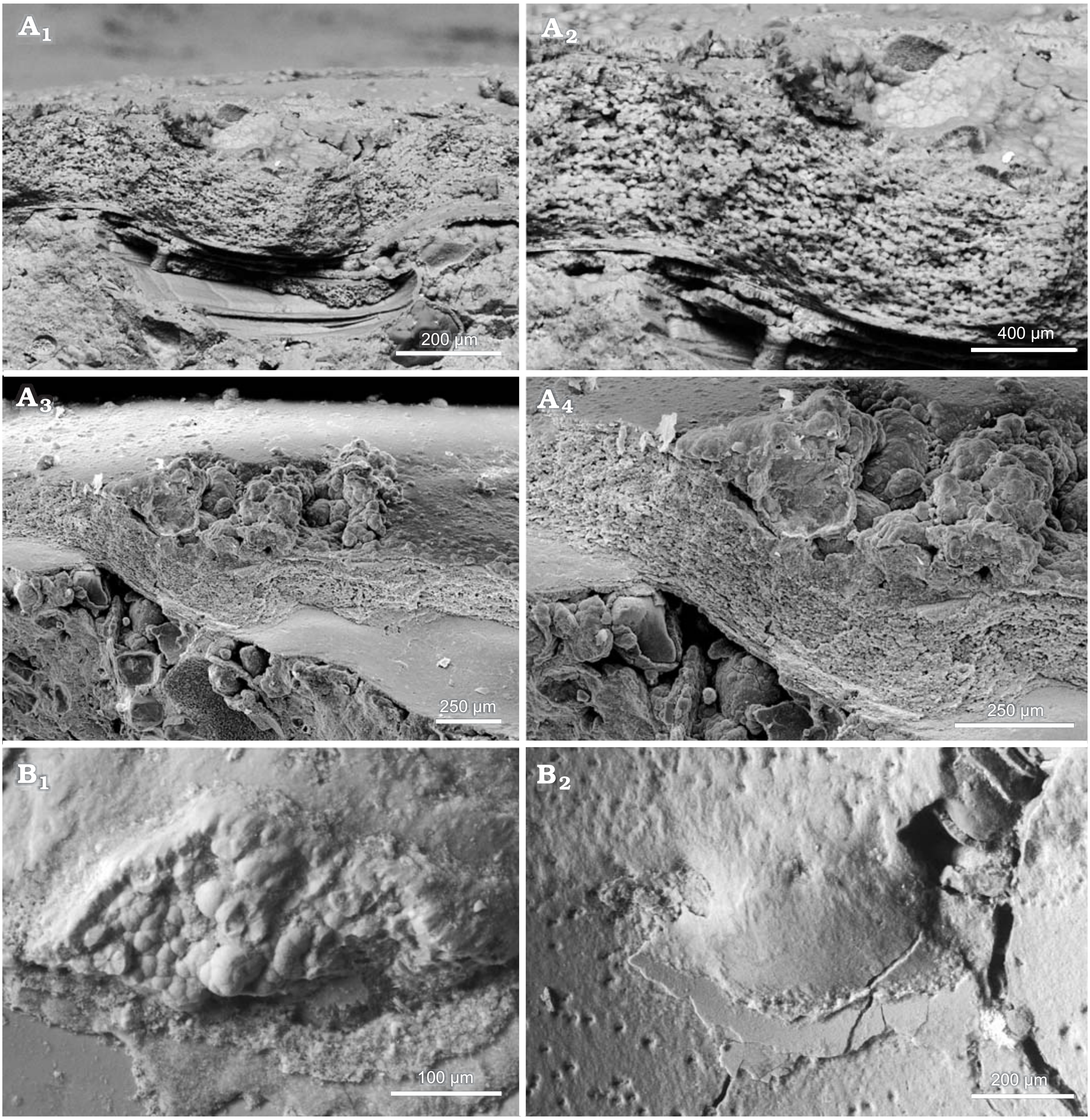

Fig. 11. SEM photographs of the pits on the craspeditid ammonite *Kachpurites fulgens* (Trautschold, 1861) shells from the Late Volgian, *Kachpurites fulgens* Zone, Eganovo (A) and Mnevniki (B) localities, Moscow region, Central Russia. **A**. MSU 118/1. Transverse (A_1, A_2) and longitudinal (A_3, A_4) cross-sections of the shell layers in the pit area. The bending of shell wall inside the pit is clearly visible. **B**. MSU 118/9. The phosphatic mineral inside the pit (B_1) and the tubercle (reflection of the pit) (B_2) located on the dorsal side of the specimen.

malformation of the ammonite shells did not attack them randomly, but lived on the surface of the shell. It explains the duration of the period of formation of pits and the structure of their cross-section. Ammonites formed a soft organic periostracum which is relatively flexible (Checa 1994; Moulton et al. 2015) at the beginning of the shell development stage. The imprints of this periostracum are preserved on the shell surface as growth lines and microsculptural elements (Checa 1994; Moulton et al. 2015). Deformed growth lines related to the pits on specimen MSU 118/1 (Figs. 6C, D, 7A) indicate that the pit formation occurred during the time of shell formation and they were formed on the periostracum. The lack of bite mark traces and mantle damage indicate that pits could have been produced by small animals and their influence on the formed part of the shell most likely was not significant. This as well as the duration of the period of formation of pits supports the influence of epizoans rather than predator attacks. Therefore, this hypothesis is the most plausible explanation of the discussed deformations. Furthermore, this hypothesis is supported by the presence of phosphatic (apatitic) remnants in pits on the surface of the specimen MSU 118/1 (Figs. 5–7), which could have resulted from the decomposition of epizoan soft bodies though it cannot be completely excluded they are remnants of the thickened organic periostracum of the shell.

All the hypotheses related to syn vivo or post mortem influences on the fully-developed solid ammonite shell (hypotheses 1–4) do not explain the deformations under discussion. Since there are no traces of bite marks or bioerosion in the pits, but only deformed growth lines connected with them (Figs. 6C, D, 7A) and a curved shape of the shell wall (Figs. 7C, D, 11A, B), it stands to reason that the pits may have developed on a flexible shell wall. Since the shell was a protective device for ammonites and a base of muscle attachment, therefore it has to be rigid rather than entirely flexible. This is well-known due to the shape of lethal and sublethal injuries (Hengsbach 1996; Keupp 2000, 2012), limpet "home scars" (Akpan et al. 1982; Kase et al. 1994, 1998) and the attachment of epifauna to ammonite shells. However, Checa (1994) showed that the apertures of immature ammonite shells were not fully calcified, i.e., they could have been relatively soft and elastic. Moreover, at the beginning of a new phase of shell development, ammonites formed a soft organic periostracum which isolated the extrapallial fluid from which the calcified shell is precipitated (Checa 1994; Moulton et al. 2015). This organic periostracum is relatively flexible and bears compression wrinkles. These wrinkles were often found imprinted on the ammonite shell surface as microsculptural elements (Checa 1994; Moulton et al. 2015). It can be assumed that discussed pits appeared on a soft uncalcified aperture during the development of a new section of the shell. The hypotheses 5–7 are based on this assumption.

Taking into account all the lines of the reasoning above the hypothesis 7 is the most plausible, i.e., the pits were produced in attachment place of epizoans to the soft newly formed periostracum in the apertural region of the shell. The only exception in this case is a pit on specimen MSU 118/6 (Fig. 8E), which differs from other pits by shape and size and may correspond to the blister pearls (De Baets et al. 2011, 2015), nonetheless the absence of outer shell layers does not allow to substantiate this assumption. Most likely all other pits were formed by epizoan weight and perhaps by their muscular effort on flexible periostracum edge. The possibility of bioerosion (the boring of periostracum) cannot be excluded, but it is not clear how ammonites could have repaired such boreholes. The adapically curved growth lines (Fig. 6C, D) may have resulted from hampering the periostracum growth by the epizoan. It led to distortion of the shell walls and probably in one case to constriction of the shell (Fig. 8B). However, not all pits are associated with curved growth lines. Therefore, it is difficult to say whether epizoans hampered the growth of periostracum purportedly or if it had been an accidental byproduct of attachment to its edge.

The nature of epizoans.—If the studied pits had been formed by epifaunal attachment to the ammonite shells, several questions arise: what was the nature of epizoans which were responsible for forming of these pits? How could they have chosen the places of their location on the shell, whether they accidentally had attached to the newly formed part of the periostracum or not? What was the relationship with their hosts: were they parasites or did they just use the shell as a substrate?

Choice of attachment sites: The epizoans responsible for the formation of pits could have randomly attached to the ammonite shells and only part of them settled the uncalcified edge of the aperture, or, to the contrary they could have purportedly choose the apertural region to settle.

Specimens with pits are very rare (approximately 1.23% of all studied shells and 1.32% of studied *Kachpurites*), however, each ammonite with pits (except only MSU 118/6) bears many of them. If epizoans had been choosing a place of their location randomly, one would expect that there would be many infested ammonites, but each infested shell would display only a few pits (because not all epizoans could have been on the uncalcified apertural edge). The observed pattern is to the contrary: infested ammonites are very rare, but then they bear rather high number of pits on each of them.

Therefore, I favour the hypothesis claiming that the epizoans were able to choose their position on the shell. Moreover, the examination of the best preserved specimen (Figs. 6, 7) suggests that epizoans could have crawled over the surface of the shell. The pits at first glance seem to be arranged randomly on the surface of the body chamber. However, a more detailed inspection reveals all pits on this shell can be divided into three clusters which repeatedly occurred on the shell (Fig. 12A). The first ("ventro-lateral") cluster contains three pits: they appear five times on the shell surface in different positions, but always close to each other. It is worth noting that in the anterior part of the body chamber, two imprints of these three pits are nearly identical (Fig. 12B). It is highly unlikely that this "replication of the cluster" could have arisen accidentally. The second cluster ("mid-lateral") appears on the shell surface four or five times and the last and most indistinct cluster ("dorso-lateral") appears only three or four times (Fig. 12A). Not every epizoan can be traced. If epizoans had accidentally attached themselves to the shell, it is highly unlikely that they would have shared the same pattern of distribution on the surface as their predecessors had done. It is much more likely that epizoans could have periodically crawled over the surface of the shell by more or less parallel trajectories following the periodically formed periostracum edge. The shallow furrows in front of some pits (Fig. 12B) may be the traces that epizoans left in the partially solidified periostracum, nevertheless, these furrows could have been formed by the displacements between periostracum (with epizoans) and newly forming shell.

What was the relationship of epizoans to their hosts? In order to cause a deformation of the periostracum, epizoans must have been located near the edge of the aperture, on its newly formed section. Likely they crawled over the surface of the shell following the periostracum edge. It remains unclear why they were settling the periostracum edge. It seems to be unlikely that they fed on remnants of an ammonite meal—many researchers believe that aptychophoran ammonites fed on small planktic prey (Kruta et al. 2011), with this type of feeding they could not have left scraps of food. Even if large ammonites could have coped with some larger prey, it is less possible for small 2–3 cm *Kachpurites* microconchs. Therefore, this scenario seems to be unlikely.

If the epizoans would be filtering the food particles from the water column during host movement, they would be most likely attached to the ventral side of the ammonite shell and not to the aperture (Andrew et al. 2011). If the epizoans would be filtering the food particles from a stream resulting from ammonite breathing then they would most likely inhabited the sides of the aperture and the umbilical slope because in nautilids and coleoids the water for breathing is pumped from the sides of the head (Bizikov 2002). However, such a pattern of pit distribution is not observed—they are often found on the ventral side—therefore, this assumption appears to be unlikely.

Another possible assumption is that the epizoans by their attachment to the uncalcified part of the aperture formed places to reside (analogously to limpet “home scars”) in which it was easier to anchor and live on the moving ammonite shell. This option does not seem impossible although the author has no data on such examples among modern mollusks. This version can be supported by findings of phosphate minerals inside pits located on the surface of a fully-mineralized shell in MSU 118/1 (Fig. 7) and between shell whorls (Fig. 11C) if they are phosphatized remnants of the epizoan body. However, this adaptation likely implies a long coevolution between epifauna and their hosts: they had to develop during evolution quite complex behavior with the attachment to the soft edge of the periostracum to bend. Nevertheless, similar pits have yet to be found on other ammonites, including *Kachpurites* ancestors (*Laugeites*) and descendants (*Garniericeras*), therefore there is no evidence of coevolution though many excellently preserved ammonoids faunas are known worldwide and no similar malformations were reported to date.

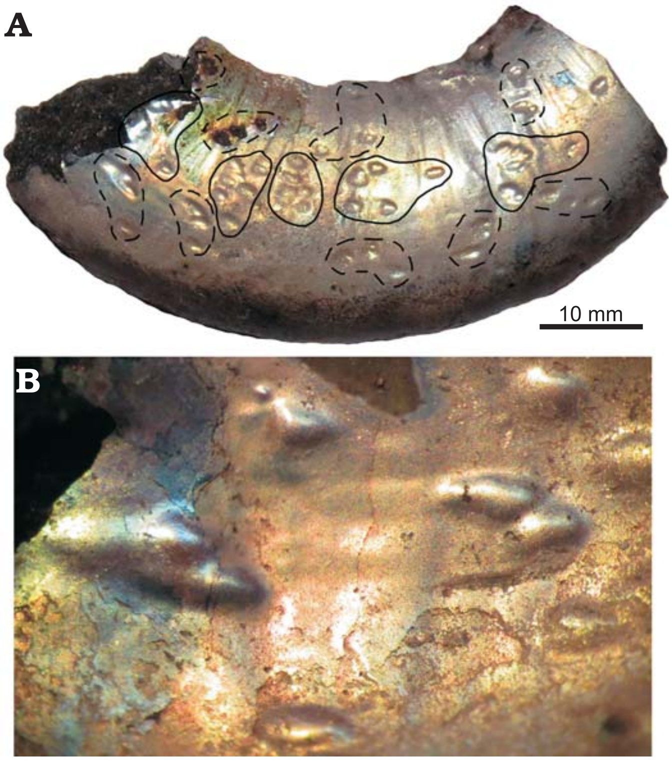

Fig. 12. Clusters of pits on the surface of the craspeditid ammonite *Kachpurites fulgens* (Trautschold, 1861) shell from the Late Volgian, *Kachpurites fulgens* Zone, Eganovo ocality, Moscow region, Central Russia, MSU 118/1. **A**. General view, three clusters which repeatedly occurred on the shell marked by lines: ventro-lateral and dorso-lateral clusters marked by dotted line, mid-lateral cluster marked by solid line. **B**. Two groups of pits on the anterior ventro-lateral portion of the shell. They are very similar to each other and likely were formed by the same epizoans during the subsequent stages of shell growth.

The abnormal growth lines (Fig. 6C, D) associated with the pits are a strong indication that the epizoans not only dented the periostracum due to their weight, but also in some way they hampered the growth of its edge (Fig. 5C, D). Such a situation could have hardly happened if the epizoans would be only passively attached to the periostracum. The growth line malformations together with the signs of presumable growth inhibition of pit-bearing ammonites (small muscle attachment scars, Fig. 8C$_1$; an abnormally deep constriction on the ammonite shell, Fig. 8B) suggest that the epizoans could have fed on newly formed fresh periostracum in the apertural region. In that case they would cause harm to their host and should be considered as parasites.

Low prevalence of pits on ammonites (1.23% shells with pits of all studied ammonoid shells and 1.32% of studied shells of *Kachpurites*) may indirectly confirm the parasitic mode of life of pit-producing epizoans (Keupp 2012) even though the prevalence of parasites in different populations may vary within wide ranges (De Baets et al. 2015).

The shell surface of several *Kachpurites* specimens is covered by a thin phosphatic layer, similar to structures formed during phosphatization of cameral membranes or siphuncle tube (Fig. 12). Although some authors have speculated about the presence of external mantle in some ammonoids (Doguzhaeva and Mutvei 1991, 1993) this assumption seems to be unlikely given the fact that many ammonoids have a black layer in front of the aperture, which is homologous to that of the externally-shelled *Nautilus* (Kulicki et al. 2001; Klug et al. 2004) and have a color pattern on the shell surface (Keupp 2000). Moreover, the presence of relatively large epizoans which were found between

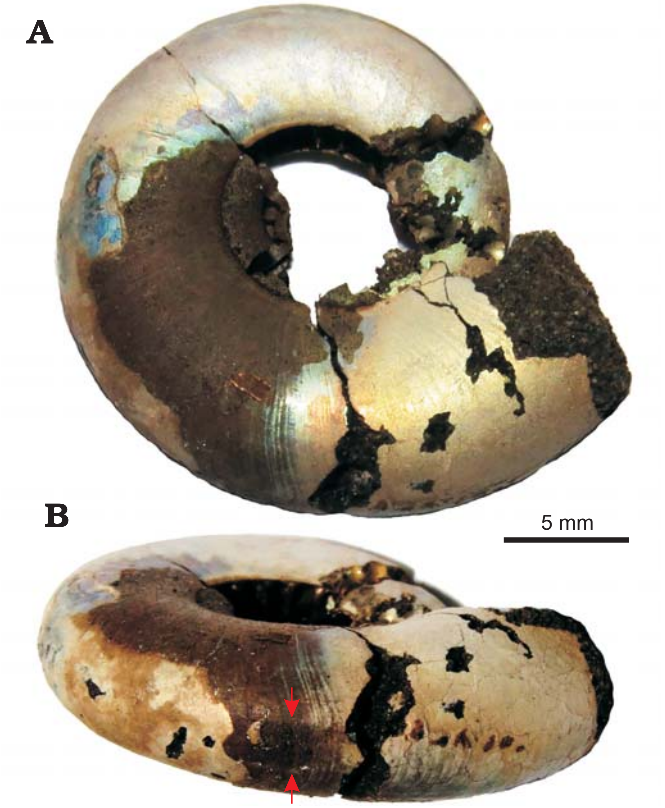

Fig. 13. Phosphatic layer on the surface of the craspeditid ammonite *Kachpurites fulgens* (Trautschold, 1861) shell from the Late Volgian, *K. fulgens* Zone, Eganovo locality, Moscow region, Central Russia. Specimen (MSU 118/17) with fragments of a thin brown phosphate layer on the surface of the shell (presumably remnants of the periostracum) in lateral (**A**) and ventral (**B**) views. A narrow dark band is visible on the venter (arrows).

whorls on *Kachpurites* shells (Fig. 9A, B; see also Mitta et al. 1999; Keupp 2000) excludes the possibility of an internal position of the conch. Therefore, the phosphatic layer on the surface of the *Kachpurites* shells cannot be a remnant of the external mantle. It is more likely that some ammonites had a thick periostracum, similar to that in living *Allonautilus* (see Ward and Saunders 1997). The existence of such a thick periostracum in Cretaceous Scaphitidae was assumed by Landman et al. (2012). It seems very likely that the thin phosphate layer on the surface of some *Kachpurites* shells (Fig. 13) represents the fossilized thick *Allonautilus*-like periostracum. Although the periostracum protects the shell from bioeroders (De Baets et al. 2015), it can be assumed that the newly formed part of this organic layer on the ammonite shell could have attracted parasites. As the newly formed, fresh and softer periostracum was located at the aperture, parasites would have actively follow the edge of the body chamber.

Though I find the hypothesis of feeding on periostracum most plausible explanation for the mode of life of pit producers, the generation of the "home scars" or accidental damage of the periostracum cannot be entirely excluded.

Were these epizoans host-specific? All studied pits were found on the shells of *Kachpurites*. It can be assumed that the epizoans responsible for the formation of these pits were host-specific. However, verification of this assumption appears to be rather difficult. *Kachpurites* make up approximately 80−90% of ammonite shells in *K. fulgens* Zone in all known localities (Rogov and Starodubtseva 2014). From 1218 ammonites from *K. fulgens* Subzone *Kachpurites* make up 92.86%, *Craspedites*, 6.40%, and *Subcraspedites*, only 0.74% (moreover, ammonites of this genus are found only at the bottom of the subzone) (Fig. 4). Pits on *Kachpurites* shells are very rare. If pits on shells of other genera occur with the same frequency, we probably would not be able to find them solely due to their rarity.

It is also difficult to draw conclusions about the stratigraphic distribution of ammonites with pits. Ammonites in the strata above and below the *K. fulgens* Subzone are far less numerous and poorly preserved, it would be very difficult to find the pits on their shells even if they exist.

At the same time the host-specificity cannot be excluded in view of the evolutionary history of *Kachpurites*. This genus appeared at the end of *Epivirgatites nikitini* Chron, evolved from boreal dorsoplanitid genus *Laugeites* (Rogov 2014b) and soon became widespread in the European part of Russia. From the beginning of *Kachpurites fulgens* Chron, *Kachpurites* inhabited the sea in Central Russia from the Spitzbergen in the North to the Saratov region in the South (Rogov 2010; Rogov and Starodubtseva 2014). It was accompanied by other craspeditids (*Craspedites* and *Subcraspedites*), but *Kachpurites* always was the most abundant genus (Fig. 4). Therefore, at the beginning of *Kachpurites fulgens* Chron they were abundant invaders in the Moscow region. Probably, they could contact with new parasites in this new unexplored area. These parasites could have evolved together with previous ammonite inhabitants of this territory (which became extinct at the end of *Epivirgatites nikitini* Chron), or perhaps they infested other animals (e.g., fish or belemnites) and could not widely infest the ammonites because the predecessors of *Kachpurites* were not so abundant.

Identity of the epizoans: Many questions on the nature of these epizoans remain unanswered. Only pits and structureless phosphate nodules remain, there are no hard skeletal parts inside these nodules (Figs. 5B, 6). It remains unclear if these phosphatic minerals are remnants of epizoan bodies or of thickened periostracum, but if the minerals are the result of epizoan decomposition, it is most likely that the animals were entirely soft-bodied or their hard parts were very thin. Their skeletal parts could have been lost or have disappeared during decomposition (e.g., if they were chitinous) and the shape of the pits does not reflect details of the shape of epizoan soft body. The pits can help us only to recognize their size.

It is rather difficult to argue which animals of small size, low fossilization potential, and appropriate lifestyle could produce studied deformations. A possible suggestion are representatives of Copepoda, which match outlined above characteristics. Copepods are known since Carboniferous and many of them are parasites of fishes and crustaceans (Selden et al. 2010). They are the only known parasites of Recent *Nautilus* (Ho 1980; De Baets et al. 2015). Parasitism is typical not only for modern, but also for ancient copepods (Cressey and Patterson 1973; Cressey and Boxshall 1989) albeit parasitic copepods generally live on the soft parts of their hosts. Most of the copepods are minute (near 1 mm in body length) and fragile, hence they have low fossilization potential, their thin chitinous integument could have decomposed rapidly after animal death (Selden et al. 2010). Therefore, if pit-produced epizoans were indeed parasites of ammonites, the copepods seem to be suitable for this role: they are small, mobile, have low fossilization potential and parasitical lifestyle. Theoretically they could have infected ammonites, passing to them from other hosts (e.g., fishes) and could have moved over the surface of the shells. This assumption, however, is highly speculative and requires further collection effort of well preserved specimens and further research.

Conclusions

Different animals often adversely affected ammonite shells: predators often damaged the aperture and the mantle edge, which led to a distortion of the subsequent sections of the shell; bioeroders drilled the shell surface; epizoans which were attached to the shell led to distortion of the shell shape when the ammonite was forced to overgrow them during shell formation. The new type of shell damage described herein, found on the shells of Late Volgian ammonites *Kachpurites fulgens*, was also likely caused by epizoans. Most probably the epizoans responsible for the formation of the studied pits were not attached to a solid part of the ammonite shell, but to the newly formed flexible periostracum edge. They induced distortion of the shape of the flexible periostracum, which led in turn to the formation of the curved parts of the shell wall. The mechanism of their effect on the periostracum is not yet fully understood; either it could be kind of bioerosion or distortion caused by weight and movement of the epizoans.

The nature of these epizoans and their relationship to ammonite hosts remains uncertain. Judging from the size of the pits and their distribution on the shell surface it is plausible to assume that there were small animals, up to 1 mm, possibly capable of crawling along the surface of the shell following periostracum edge. Their relationship with the periostracum edge, damage that they had caused and possible signs of influence on the growth of their ammonoid hosts all suggest that these epizoans could have been parasites. Their prevalence is low (1.23% of studied ammonites) but distortion of the shell in some cases is considerable: it may indicate that they could have been unspecialized or accidental parasites of the ammonites. However, available data do not exclude other possible feeding strategies and relationship with their host.

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