

# STRUCTURE OF THE CALCITIC LAYER OF THE APTYCHUS OF THE AMMONITE GENUS *PELTOCERAS*

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**Abstract:** The aptychi of ammonites combined the functions of lower jaws and protective opercula. They consist of two parts: an inner organic layer and an outer calcitic lamella. In different evolutionary lineages of ammonites, the shape of aptychi, the sculpture of their surface and the microstructure of the calcitic layer vary greatly. However, the structure of the aptychi is not known for all evolutionary lineages of ammonites. Although numerous aptychi have been described for the Jurassic family Aspidoceratidae, almost all of them belong to only one evolutionary branch of this family – the Aspidoceratinae (*sensu lato*). For the second branch – the Peltoceratinae, only one aptychus had been described to date and the structure of its calcitic layer remained unknown. In this article, for the first time, the structure of the aptychus of the Peltoceratinae (upper Callovian *Peltoceras*) is described. The surface of this aptychus is covered with rough ribs and the calcitic part consists of only one layer of dense calcite. The thickness of the aptychus is much greater than that of the aptychi of supposed ancestors of the Peltoceratinae. The increase in the thickness of the aptychi in both the Aspidoceratinae and the Peltoceratinae, contemporaneously with the appearance of spines on their shells, is most likely related to increasing the protective function of the aptychi of these ammonites in the late Callovian.

**Key words:** Aspidoceratidae, Peltoceratinae, *Peltoceras*, aptychi, ammonites, Jurassic.

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## INTRODUCTION

Aptychi are paired symmetrical structures, associated with ammonite shells in Jurassic and Cretaceous beds and up to the base of the Danian stage of the Paleogene (Tanabe *et al.*, 2015; Hoffmann *et al.*, 2021). They consist of outer calcitic and inner organic layers, but both layers are not always preserved together. Originally thought to be opercula (e.g., Schindewolf, 1958), aptychi were correctly interpreted later as the lower jaws of ammonites (Lehmann, 1972). However, according to the widely accepted point of view, aptychi were used by ammonites not only as jaws, but also as protective devices that covered the body chamber from the side of the aperture (Lehmann and Kulicki, 1990). The possibility cannot be excluded that they might have had some additional functions (Parent *et al.*, 2014; Parent and Westermann, 2016). About two dozen different morphotypes of aptychi have been described as formal genera; they differ in shape and surface sculpture and, most importantly, in the microstructure of the calcitic layer (Trauth, 1927–1936; Farinacci *et al.*, 1976; Kruta *et al.*, 2009; Mironenko, 2018). Apparently, in different lineages of ammonites, the functions of the aptychi somewhat varied, in some of them the feeding function was dominant, in others, the protective

one. The structure of the aptychi to a certain extent allows researchers to draw conclusions about the taxonomy of ammonites (Engeser and Keupp, 2002), as well as their palaeoecology and mode of life (see Tanabe *et al.*, 2015).

Among the most famous and best-studied aptychi are those of the macroconchs of the Jurassic family Aspidoceratidae, which are referred to as the formal genus *Laevaptychus* (Trauth, 1930; Schindewolf, 1958; Gąsiorowski, 1960). They are large, wide, and easily identifiable aptychi. They are very abundant in the Kimmeridgian and Tithonian and somewhat rarer in the Oxfordian and upper Callovian beds. The width and length of most laevaptychi correspond to the parameters of the aperture of their host's shells, although in very large shells they are somewhat smaller than the aperture (Mironenko, 2018). Laevaptychi have often been the focus of researchers. They were found in a possibly protective position at the apertural part of ammonite shells, overlapping the opening of the body chamber (Arkell, 1957; Schindewolf, 1958). Laevaptychi with sublethal injuries are also described (Keupp, 2012), and on the inner side of one specimen of this formal genus an imprint of an ammonite radula was found (Keupp *et al.*, 2016).

Laevaptychi reached large sizes, and the largest *Laevaptychus* described to date is 35 cm in length (Zeiss and Leanza, 2010). The calcitic part of *Laevaptychus* consists mainly of a specific thick layer with a sponge-like, porous structure, which is called a tubular or sponge-like layer (Schindewolf, 1958; Farinacci *et al.*, 1976; Kruta *et al.*, 2009). Most likely, this porous structure allowed the ammonites to reduce the weight of large aptychi and the amount of material required for their formation (Schindewolf, 1958). The aptychi of aspidoceratid microconchs are rarer, but also are well studied (Parent *et al.*, 2014; Rogov and Mironenko, 2016; Mironenko, 2018). They do not have a tubular layer and are entirely composed of microporous calcite with a non-uniform density (Mironenko, 2018). This is the only case known to date, in which the aptychi of ammonite sexual dimorphs greatly differ in their microstructure.

However, Aspidoceratidae includes two distinct branches (Fig. 1), usually considered as subfamilies: the Aspidoceratinae and the Peltoceratinae (Miller, 1968; Page, 2008; Énay and Howarth, 2019). Several researchers distinguish among them more separate subfamilies: the Aspidoceratinae, Euaspidoceratinae, Epipeltoceratinae, and Hybonoticeratinae in the first branch and the Peltoceratinae and Gregoryceratinae in the second (see Parent *et al.*, 2020). Aspidoceratids have many significant differences from other perisphinctoid ammonites, so Parent *et al.* (2020) recently proposed to raise the family Aspidoceratidae to the rank of a superfamily Aspidoceratoidea. However, the aspidoceratin and peltoceratin branches also differ from each other. Whereas the discoveries of the aptychi of aspidoceratin group are number in the thousands, possible peltoceratin

aptychi were illustrated only twice (Énay, 1962; Frerichs, 2004). Moreover, in the first case, the aptychus was found in the body chamber of *Epipeltoceras*, which in 1962 was considered as a member of Peltoceratinae, but now it is included in the aspidoceratin group (Aspidoceratinae or Euaspidoceratinae) (Énay and Howarth, 2019; Parent *et al.*, 2020). Thus, to date, only one aptychus of the Peltoceratinae, which was found in the body chamber of a *Peltoceras* sp. Macroconch in France, has been described and depicted (Frerichs, 2004). However, the structure of the calcitic layer of this aptychus is unknown.

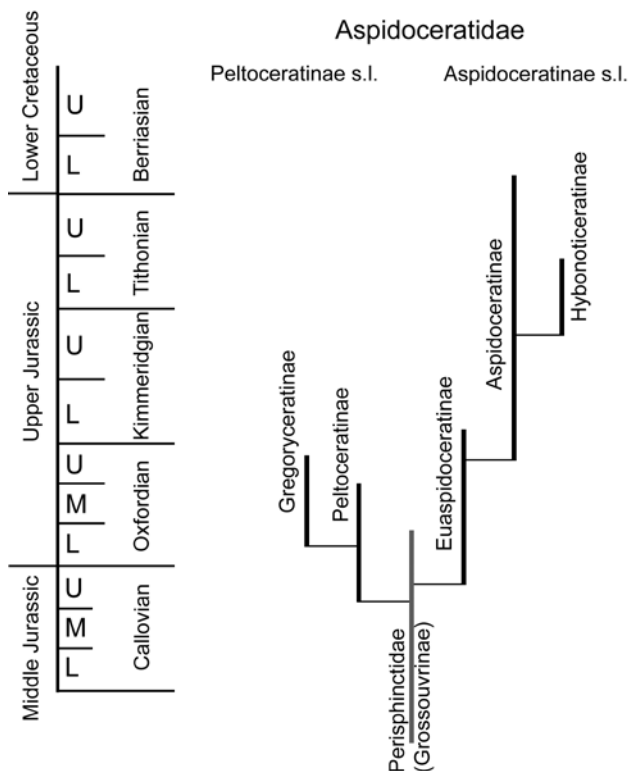
This article describes a new finding of an aptychus in the body chamber of a *Peltoceras* cf. *retrospinatum* (Gérard and Contaut) macroconch from the upper Callovian of Central Russia. In this aptychus, in contrast to the previous specimen, the calcitic layer is well preserved. A study of it showed differences from both aptychi of the Aspidoceratinae and the Perisphinctidae; the latter are the ancestors of aspidoceratids.

## MATERIALS AND METHODS

The aptychus described in this article was found in 2017 in the “Mikhailovcement” quarry in the Ryazan region, Central Russia (54.212885°N, 38.959170°E; see map in Kiselev and Rogov, 2018, fig. 1). Middle to upper Callovian and lower Oxfordian beds, exposed in this quarry, were recently described in detail (Kiselev and Rogov, 2018). The aptychus was found by accident in a fragment of the body chamber (Fig. 2) of a partially flattened *Peltoceras* cf. *retrospinatum* macroconch (Fig. 2) in a concretion of yellowish-grey, oolitic marlstone in the upper Callovian Lamberti Zone (bed 10, according to Kiselev and Rogov, 2018). *Peltoceras retrospinatum* (Gérard and Contaut) was originally described from the terminal horizon of the Athleta Zone, but at the Mikhailovcement locality it also was reported from the basal part of the next ammonite zone, the Lamberti Zone (see Kiselev and Rogov, 2018, p. 96). The diameter of the *Peltoceras* shell, which contained the aptychus, is about 25–30 cm; however, the precise measurement was impossible owing to the incomplete preservation and fragmentation of the concretion. The aptychus is also not completely preserved since most of the body chamber had been destroyed by the time of its discovery (see Fig. 2).

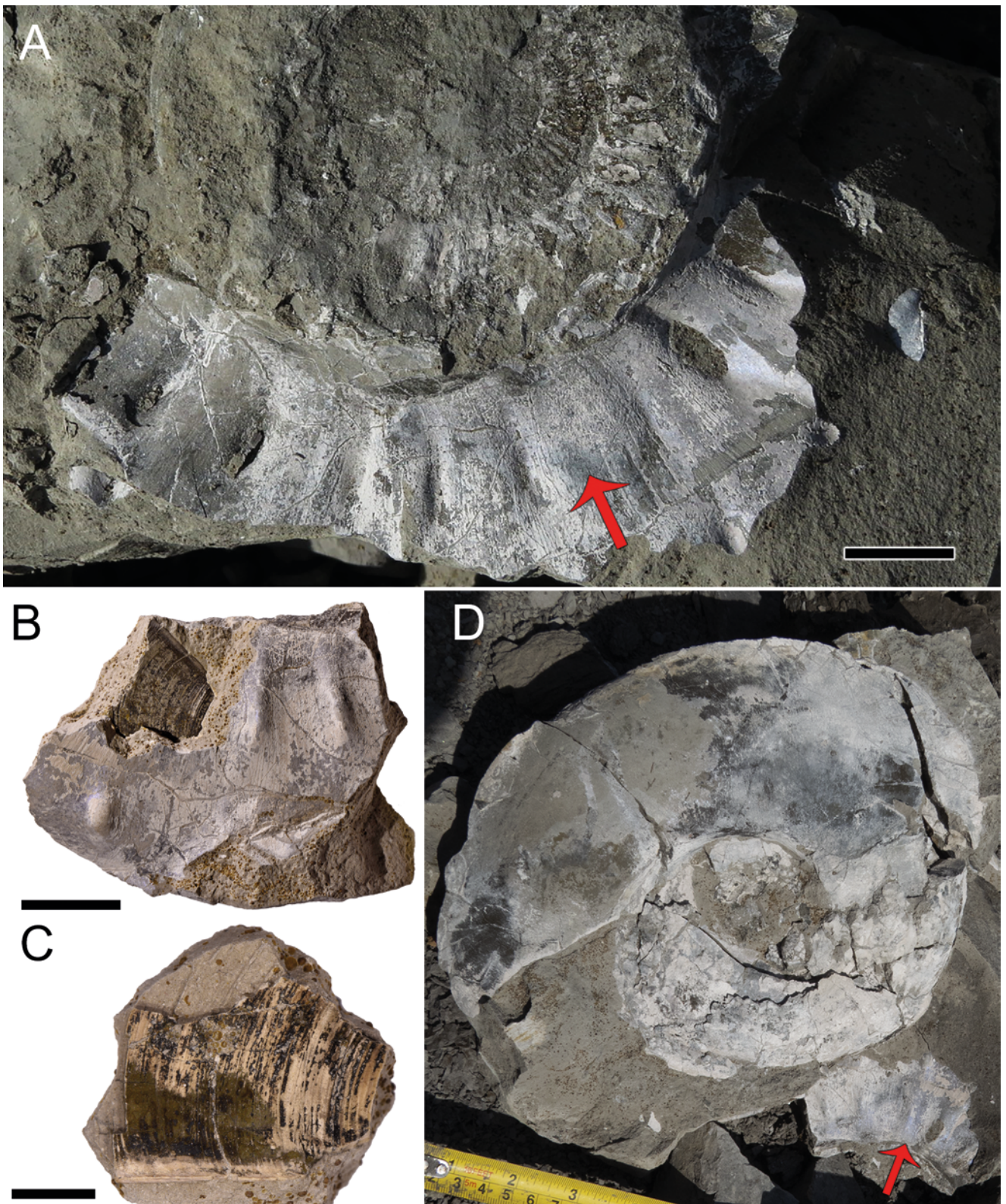
The age of the specimen can be determined precisely. In this locality, Jurassic deposits are mainly represented by clays with rare, relatively small phosphate nodules. These clays are interbedded with only two horizons of large concretions of yellowish-grey, oolitic marlstone (in beds 9 and 10, according to Kiselev and Rogov, 2018). Lithologically, they are very similar to each other, but differ in the fauna of ammonites. The first horizon is located in the upper part of the Athleta Zone and the second in the lower part of the Lamberti Zone. The age of the concretion, in which the *Peltoceras* aptychus was found, is confirmed by ammonites of the genus *Quenstedtoceras*, including large macroconch *Quenstedtoceras* cf. *lamberti* Sowerby, preserved in the same nodule (Fig. 2).

For this study, the aptychus was examined under a scanning electronic microscope SEM TESCAN VEGA III at



**Fig. 1.** Phylogeny of Aspidoceratidae (compiled after Bonnot, 1995; Énay and Howarth, 2019; Parent *et al.*, 2020).





**Fig. 2.** *Peltoceras* with an aptychus and the neighbouring *Quenstedtoceras*. **A.** Flattened central part and imprint of the body chamber of the ammonite *Peltoceras* cf. *retrospinatum*. The arrow marks the position of the fragment containing the aptychus. Please note that this is an imprint, so it is mirrored in relation to the fragment with the aptychus. Scale bar equals 2 cm. **B.** Fragment of the body chamber with the aptychus before preparation. Scale bar equals 2 cm. **C.** Detached fragment of the body chamber with a piece of the aptychus. The inner surface of the aptychus is visible. Scale bar equals 0.5 cm. **D.** Large macroconch *Quenstedtoceras* cf. *lamberti* in the same concretion. The arrow marks a fragment of the *Peltoceras* body chamber, which contains the aptychus.



the Paleontological Institute of the Russian Academy of Science in Moscow. Small fragments of the aptychus were coated with gold and inspected in high-vacuum conditions at 20 kV. Images were generated using both SE and BSE detectors. The specimen studied is housed in the Geological Institute of Russian Academy of Sciences in Moscow, collection GIN MPC 8.

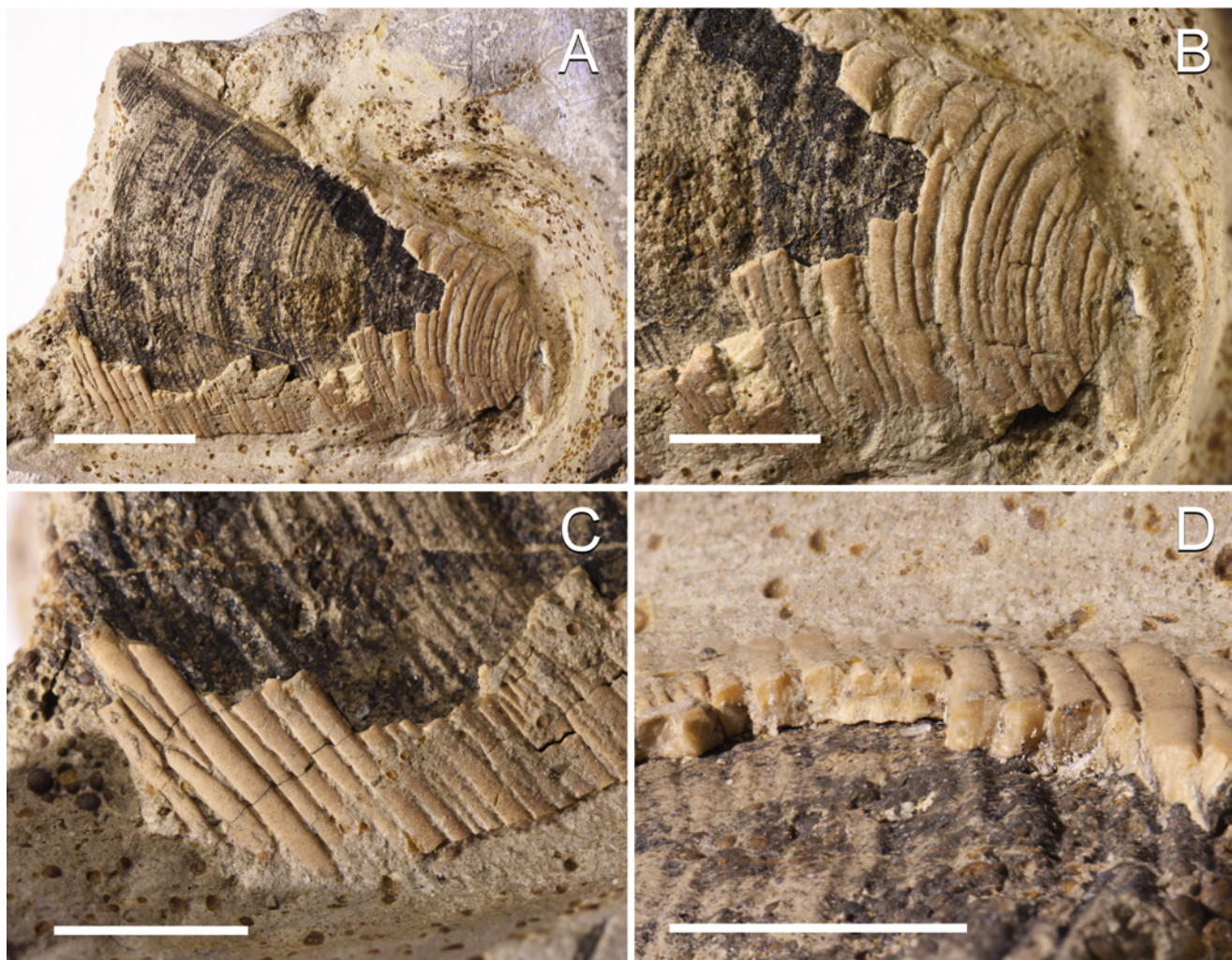
## RESULTS

The length of the preserved part of the aptychus is 5 cm and the maximum width is 3 cm; however, part of the aptychus probably is hidden by the rock. Like the ammonite shell, in which the aptychus was found, the calcitic part of the aptychus is broken with cracks and its individual fragments are displaced relative to each other, apparently as a result of sediment compaction before the formation of the concretion. The calcitic layer of the aptychus and the carbonized organic layer underneath are preserved. The thickness of the calcitic layer in the middle part of the aptychus is 0.8 mm. The surface of the calcitic layer is covered with rough ribs, separated by deep grooves (Figs 3A–C, 4A, B). The ribs merge with each other and branch out, which shows that they are not growth lines, but surface sculpture. SEM

examination of the transverse and longitudinal cross-sections of the aptychus showed that its calcitic part consists of one thick layer of monolithic calcite (Fig. 4C, D). Comparison with the cross-section of the *Praestriaptychus anglicus* (Trauth, 1930) from the same locality, which belonged to ammonites of the genus *Binatisphinctes* shows that although it also consists of a single layer of monolithic calcite (Fig. 4E, F), the *Peltoceras* aptychus is at least five times thicker (Fig. 4C, D). No signs of a tubular layer, which is a characteristic of the aptychi of macroconchs of Aspidoceratinae, were found in the aptychus of *Peltoceras*.

## DISCUSSION

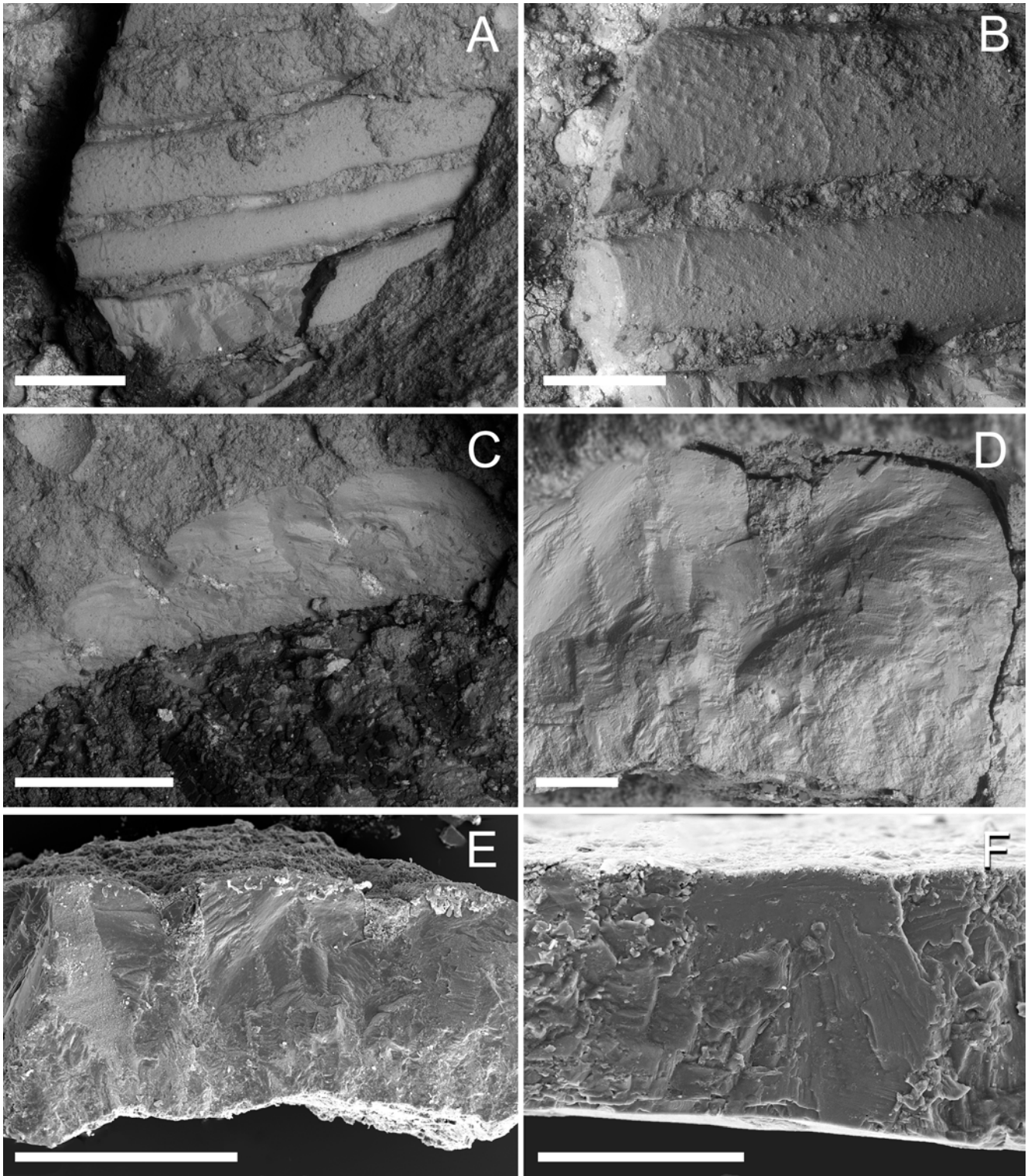
The aptychus of the *Peltoceras* macroconch fundamentally differs from the laevaptychi of macroconchs of the Aspidoceratinae (*sensu lato*) in the structure of its calcitic layer. The *Peltoceras* aptychus consists of one layer of dense calcite, and its surface is covered with prominent ribs. The laevaptychi have an almost smooth surface and consist of two (Kruta *et al.*, 2009) or three layers (Schindewolf, 1958; Farinacci *et al.*, 1976). The difference in the number of layers is possibly related to the type of preservation as



**Fig. 3.** *Peltoceras* aptychus GIN MPC 8/1 and its calcitic layer. **A.** A general view. **B, C.** Ribs on the surface of the aptychus. **D.** Cross-section of the calcitic layer of *Peltoceras* aptychus. Scale bars for A equal 1 cm, and for B–D it is 5 mm.

well as to the fact that the outer lamellar layer, as was shown by Schindewolf (1958), is not a separate item but actually a continuation of the middle tubular layer. This porous, tubular layer makes up most of the volume of *Laevaptychus* (see Schindewolf, 1958, tables 2, 3; Farinacci *et al.*, 1976, pl. 9) and it is completely absent in the aptychus of *Peltoceras*

(Figs 3D, 4C, D). Owing to the aforementioned absence of a tubular layer, the *Peltoceras* aptychus cannot be assigned to *Laevaptychus*. The aptychi of aspidoceratin microconchs, *Mirosphinctes* and *Sutneria*, consist of one or two layers of calcite and do not have a tubular layer. However, their surfaces differ from the ribbed surface of the *Peltoceras*



**Fig. 4.** SEM images of aptychi of *Peltoceras* (GIN MPC 8/1) and *Binatisphinctes* (GIN MPC 8/2). **A, B.** Surface of *Peltoceras* aptychus. **C, D.** cross-section of the *Peltoceras* aptychus. **E.** Cross-section of the aptychus of *Binatisphinctes* for comparison. Scale bars for A and C equal 1 mm, for B it is 500  $\mu\text{m}$ , for D it is 200  $\mu\text{m}$ , for E it is 800  $\mu\text{m}$ , and for F it equals 100  $\mu\text{m}$ . it is 500  $\mu\text{m}$ , for D it is 200  $\mu\text{m}$ , for E it is 0.8 mm, and for F it equals 100  $\mu\text{m}$ .



aptychus; it is either smooth, as in the aptychi of macroconchs, or has wide, shallow ribs (Mironenko, 2018). Moreover, the microstructure of the *Peltoceras* aptychus differs from that of *Mirosphinctes*. In the first case, it is dense, and in the second, rather microporous, with non-uniform density (Mironenko, 2018, fig. 5).

Callovian aptychi of the formal species *Praestriptychus anglicus*, which belong to perisphinctid ammonites of the genus *Binatisphinctes*, the possible ancestors of Peltoceratinae (Page, 1991, 2008), resemble the aptychus of *Peltoceras* (Fig. 4A–D) with their ribbed surface (Trauth, 1930, tab. 5, figs 12, 13) and especially in the microstructure (Fig. 4E, F). However, their thickness is significantly less than that of the *Peltoceras* aptychus and because of this, the depth of the furrows between their ribs is less and the ribs are less prominent. The aptychus of *Peltoceras* also differs from praestriptychi of the Oxfordian perisphinctids, which are very thin and have a smooth surface, but is similar to them in microstructure, represented by dense calcite (Mironenko, 2018). Therefore, although among all types of aptychi, the aptychus of *Peltoceras* is most similar to the *Praestriptychus*, it should not be assigned to this formal genus, owing to significant differences in the thickness and the sculpture of its surface. Perhaps it should be described as a separate formal genus of aptychi, but for this more specimens must be found.

An increase in the thickness of the aptychi in comparison with the ancestral *Praestriptychus* occurred in both Aspidoceratinae and Peltoceratinae concomitantly with the emergence of these taxa, i.e., with the appearance of spines on the shells. The spines on ammonite shells most likely served as protection from predators (Kröger, 2002), and whereas the aptychi were lower jaws, they had several additional functions, including a protective one (see Lehmann and Kulicki, 1990; Parent *et al.*, 2014; Parent and Westermann, 2016). The contemporaneous appearance of spines on the shells and the increase in the thickness of the aptychi leaves no doubt that such changes in the aptychi also were related to increasing of their protective function in both the Aspidoceratinae and the Peltoceratinae.

Among the upper Callovian ammonites at the locality, where the *Peltoceras* aptychus was found, there are numerous ammonite shells with traces of sublethal injuries. Among them, the traces of trauma are most common in *Binatisphinctes* – 16.5% of the total number of these ammonites have sublethal injuries (Mironenko, 2017). This undoubtedly indicates a high level of predator pressure on these ammonites. A high frequency of damage was also noted in *Peltoceras* in the upper Callovian of Normandy, although among *Euaspidoceras* at the same locality there are not so many damaged shells (Keupp and Ilg, 1992). In general, the high frequency of damage in both *Binatisphinctes* and *Peltoceras* may indicate a constant pressure from predators that continued after the emergence of the latter. It should be noted here that in both the aspidoceratins and the peltoceratins, the spines are characteristic for macroconchs, while microconchs and juveniles do not have spines. Therefore, it cannot be ruled out that these ammonites were threatened primarily by some large predators that ignored microconchs and juveniles.

Nevertheless, the increase in thickness of the aptychi in the Aspidoceratinae and the Peltoceratinae occurred in different ways. While the peltoceratins simply increased their thickness without changing the structure of the calcitic part of the aptychus, in the aptychi of the aspidoceratins a fundamentally new tubular layer arose. The porous structure of this layer made it possible to increase the thickness of the aptychus without significantly increasing its weight. In fact, some researchers assumed that large laevaptychi could have served as ballast for lowering the aperture (Gašiorowski, 1960); however, the ballast should not have been too heavy for its owner. The absence of a porous layer in the aptychi of peltoceratins most likely limited thickness growth, since the additional weight of dense calcite affected the buoyancy and orientation of the whole organism; moreover, a lot of calcium carbonate was required for the formation of the aptychus from monolithic calcite. Peltoceratins and aspidoceratins both appeared at the end of the Callovian, but markedly differed in the duration of their existence. The peltoceratins became extinct by the end of the next Oxfordian age, whereas the aspidoceratins existed successfully in the Oxfordian, Kimmeridgian, and Tithonian and became extinct at the very beginning of the Early Cretaceous (Berriasian; see Fig. 1). It is always difficult to draw conclusions about the reasons for the extinction of ancient taxa; however, it cannot be ruled out that the relatively short time of the existence of the peltoceratins in comparison with the aspidoceratins could have been related to the less advanced structure of their aptychi.

In addition, the study of the *Peltoceras* aptychus can help to solve the question of the origin of the two branches of the aspidoceratids. Adult shells of macroconchs of the genera *Peltoceras* and *Euaspidoceras* are very similar to each other, and starting with Waagen (1875), there is an opinion that the Euaspidoceratinae (the first subfamily of aspidoceratin branch) descended directly from the genus *Peltoceras* in the late Callovian. This point of view was supported by many researchers (Spath, 1931; Donovan *et al.*, 1981). However, Callomon (1963) noted that the innermost whorls of the early *Euaspidoceras* are hard to distinguish from those of *Grossouvria* (Perisphinctidae), but they have no resemblance to *Peltoceras*.

Although many representatives of both branches of the aspidoceratids are very similar there is at least one fundamental difference between them. The aspidoceratins (including all subfamilies of this branch) have parabolic notches (or parabolae – see Radtke *et al.*, 2016), which play an important role in the formation of their tubercles and spines (Bonnot, 1995). The same parabolae are typical of most of the genera of the Perisphinctidae, including the Callovian *Binatisphinctes* and *Pseudopeltoceras*, which often are considered as direct ancestors of the peltoceratins (see Page, 1991). Nevertheless, in the Peltoceratinae there are no parabolic notches, their tubercles and spines were formed without the participation of parabolae (Bonnot, 1995). According to the author's knowledge parabolae have been reported as occurring in the Peltoceratinae only twice (Neumayr, 1871; Mangold, 1970). However, in the first case, a parabolae-bearing ammonite later was identified as *Mirosphinctes*, a representative of the Euaspidoceratinae (see Bert, 2004). In the second case, parabolae were

described in *Pseudopeltoceras*, which is currently considered to be an ancestral taxon for Peltoceratinae, but not a part of this subfamily (Énay and Howarth, 2019). *Peltoceras* did not inherit parabolae from its ancestors. The reappearance of parabolae in the Euaspidoceratinae after their disappearance in the Peltoceratinae and the development of a completely different mechanism for the formation of spines and tubercles - in the case of the origin of the first subfamily from the second - appears to be extremely unlikely. This and other differences (such as various types of ribbing on the early whorls) have led several researchers to support a hypothesis proposed by Roman (1938), according to which the aspidoceratids are derived from different, albeit closely related genera of Tethyan perisphinctids and therefore the family Aspidoceratidae is polyphyletic (Callomon, 1963; Bonnot, 1995; Page, 2008).

Regarding the aptychi, Callomon (1963) noted that the aspidoceratins are commonly found at all levels (starting from the Lamberti Zone) with thick aptychi, which are unknown in both the Perisphinctidae and the Peltoceratinae. Discoveries of upper Callovian laevaptychi are rare, but they are known and do not show any differences from later laevaptychi (e.g., Rogov, 2004, pl. 4, fig. 8). The differences in the structure of the *Peltoceras* aptychus described herein from the laevaptychi support the different origins of the two branches of aspidoceratids and the assumption that this family is likely polyphyletic.

The aptychi of *Peltoceras* expand the list of known Jurassic aptychi, which have a simple, single- or two-layered microstructure of the calcitic part. For a long time, the structure of the calcitic part of the Jurassic aptychi was studied using the example of *Laevaptychus*, in which even though the total number of layers is debatable, a complex, porous, tubular layer is always present. Another widespread and well-known formal genus used as an example was *Lamellaptychus* (associated with ammonites of superfamily Haploceratoidea), which has a three-layered structure with a tubular layer (Farinacci *et al.*, 1976). Accordingly, some researchers argued that all Jurassic aptychi had a complex structure with a sponge-like layer, in contrast to the more simply arranged Cretaceous aptychi (see Kruta *et al.*, 2009). However, it recently has been shown that the praestriaptychi of Jurassic perisphinctids and the aptychi of aspidoceratin microconchs are two-layered or even single-layered, and do not have a sponge-like or tubular layer (Mironenko, 2018). This observation is also true for the aptychi of *Peltoceras*.

## CONCLUSIONS

The aptychi of *Peltoceras* macroconchs, like the aptychi of many other ammonites, had a well-developed calcitic layer. The calcitic lamella of their aptychi consists of one thick layer of dense calcite. The outer surface of the calcitic lamella is covered with prominent ribs, separated by deep grooves. The thickness of the aptychus is noticeably greater than the thickness of that in *Praestriaptychus anglicus*, which is characteristic for the possible ancestors of Peltoceratinae. Although the microstructure of the aptychus of *Peltoceras* resembles that of *Praestriaptychus*, it cannot

be assigned to this formal genus owing to significant differences in the thickness and the sculpture of its surface. The spongy tubular layer, characteristic for *Laevaptychus*, belonging to aspidoceratin macroconchs, is absent in the *Peltoceras* aptychus, which means that it cannot be assigned to this formal genus. These differences also support the hypothesis that the Aspidoceratinae and the Peltoceratinae independently diverged from different perisphinctid ancestors. The increase in the thickness of the aptychi in both these groups, contemporaneously with the appearance of spines on their shells, most likely was related to the increase in the protective function of the aptychi of these ammonites in the late Callovian.

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