

# Middle and Late Callovian Aptychi (Ammonoidea) of the Russian Plate

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**Abstract**—All known records of Middle and Late Callovian aptychi from the Russian Plate are revised. Aptychi first figured in the 19th century by S.N. Nikitin and I.I. Lahusen are refigured and described. The re-examination of the holotype *Praestriptychus kostromensis* Trauth, 1930, originally identified as "Aptychus des *Cosmoceras galilaei* Nikitin," showed that it is an imprint of a bivalve shell (Astartidae). Aptychi figured by Lahusen (1883) and specimens from my collection are assigned to the genera *Praestriptychus* and *Kosmogranulaptychus* gen. nov. Relationships between the so-called smooth aptychi of the Middle Jurassic and ammonite taxa are discussed. A phylogenetic scheme for the genera *Praestriptychus*, *Laevaptychus*, *Kosmogranulaptychus*, and *Granulaptychus*, based on the associated occurrences of aptychi and ammonites, in the context of ammonite phylogeny is proposed. A new genus, *Kosmogranulaptychus* (with the type species *K. calloviensis* (Trauth)), and two new species, *Praestriptychus ryanensis* and *Kosmogranulaptychus lahuseni*, are described.

**Key words:** aptychi, revision, Callovian, Russian Plate.

## INTRODUCTION

Aptychi are paired structures composed of calcitic and organic layers developed to a varying extent. At present, aptychi are considered to be jaw elements of ammonoids, or, less commonly, ammonoid opercula. Although aptychi are known for most families of Callovian ammonoids, they are usually rarely found and poorly studied. Aptychi are usually found outside ammonoid shells, hence, their classification has required an artificial system.

The first data on the occurrence of aptychi from the Callovian of the Russian Plate appeared at the end of the 19th century. Two pairs of aptychi assigned to *Aptychus hecticus* were figured and described by Lahusen (1883). Later, Trauth (1927, 1930) assigned these species to two new genera, *Cornaptychus* and *Praestriptychus*. Gasiorowski (1962) suggested that these aptychi belonged to either *Praestriptychus* or *Granulaptychus*. Soon after the publication of Lahusen's paper, Nikitin (1885a, 1885b) published on the Lower Callovian aptychi from the Kostroma Region. Fortunately, Nikitin's and Lahusen's original material has been preserved at the Mining Institute Museum in St. Petersburg. Until recently, further finds of aptychi from the Callovian of the Russian Plate have not been described or recorded. Only recently, Rogov and Gulyaev (2003) published on Lower Callovian aptychi, while Middle Callovian aptychi were mentioned in the abstract of the unpublished PhD thesis of M.A. Rogov (2001).

On the Russian Plate, Middle Callovian aptychi are recorded from several outcrops in the Ryazan Region,

while Upper Callovian aptychi are found in the vicinity of Saratov (Fig. 1). Unfortunately, the section from which Lahusen's original material was collected (vicinity of the town of Skopin, Ryazan Region) no longer exists. The Middle Callovian part of the section in the quarry of the Mikhailovtsement Plant (Mikhailovskii District of the Ryazan Region) where I collected aptychi is described below (Fig. 2a).

The eroded surface of the yellow oolitic marl of the Middle Callovian *obductum* Subzone or (in the southern part of the quarry) the ?Lower Callovian silt is overlain by the following sequence:

(1) *coronatum* Zone, *obductum* Subzone, *crassum* faunal horizon, recognized by Kiselev (2001):

Bed 1. Orange, sometimes brownish, oolitic (oolites are relatively rare) silt, containing quartz pebbles (up to 1cm in diameter) and, rarely, small (up to 5 cm) phosphorite nodules. The bed contains numerous ammonites *Kosmoceras crassum* Tint., *K. castor* (Rein.), *K. pollucinum* Teiss., *Erymnoceras* spp., *Binatisphinctes* sp. juv., *Pseudocadoceras* cf. *laminatum* Buckm., *Zieteniceras* sp. nov., *Brightia* (*Brightia*) sp. nov., *B. (B.)* cf. *brightii* (Pratt), *Lunuloceras fallax* (Zeiss), *L. orbigny* (Tsynt.), *Rossienceras acuticosta* (Tsynt.), *R. balkarense* (Lominadze), and *Putealicerias virile* (Zeiss). The bed is 0.3-0.7 m thick.

(2) *coronatum* Zone, *grossouvrei* Subzone, *posterior* faunal horizon.<sup>1</sup>

<sup>1</sup>The presence of the *grossouvrei* and *posterior* faunal horizons, originally recognized in England, in the *grossouvrei* Subzone of the Russian Plate was independently established by Kiselev (2001) and Rogov (2001) based on different sections.

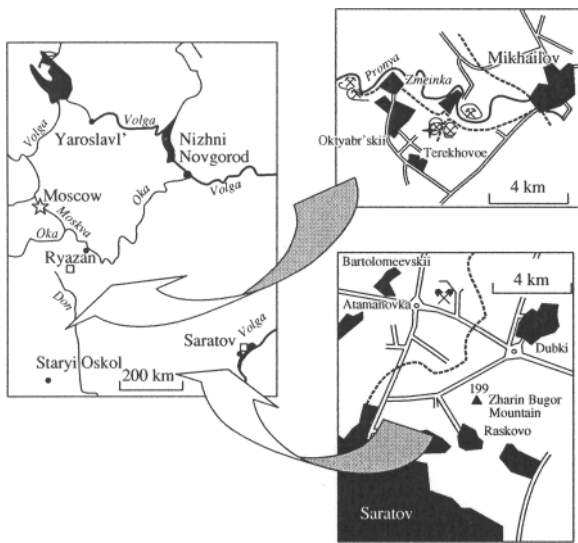


Fig. 1. Map, showing the sections studied.

Bed 2. Clayey, gray, bedded silt, with rare small (up to 5 cm in diameter) phosphorite nodules. Ammonites: *Kosmoceras posterior* Brink., *K. pollucinum* Teiss., *K. clavifer* Tint., *K. bigoti* Douv., *Cadoceras* sp. indet., *Binatisphinctes rossicus* (Siem.), *Erymnoceras coronatum* (Brug.), *Lunuloceras* cf. *lonsdalii* (Pratt), *L. fallax*

(Zeiss), *L. orbignyi* (Tsytt), *Brightia* (B.) sp. nov., *B. (B.) brightii* (Pratt), *Zieteniceras* sp. nov., *Rossieniceras rossense* (Teiss.), and *R. cf. multicostatum* (Tsytt.). *Kosmogranulaptychus* cf. *lahuseni* Rogov, sp. nov. was found 15 cm above the base of the bed in the living chamber of *Kosmoceras* sp. indet. The bed is 0.4-0.5 m thick.

(3) *coronatum* Zone, *grossouvrei* Subzone, *grossouvrei* faunal horizon.

Bed 3. Clayey silt similar to that in Bed 2, upward in the section replaced by silty clay. Ammonites: *Kosmoceras grossouvrei* Douv., *K. pollux* (Rein.), *K. pollucinum* Teiss., *K. cf. aculeatum* (Eichw.), *Pseudocadoceras* sp., *Novocadoceras* cf. *diffusum* Kiselev, *Cadoceras allae* Kiselev, *Binatisphinctes rossicus* (Siem.), *B. fluctuosus* Buckm., *Lunuloceras lonsdalii* (Pratt), ?*L. subinvolutum* (Bon.), *L. orbignyi* (Tsytt.), *L. cf. michailowense* (Zeiss), *Brightia* (B.) sp. nov., *Rossieniceras pseudocracoviense* (Tsytt.), and *Putealicerias mangoldi* Lominadze. *Praestriaptychus anglicus* (Trauth) was found together with numerous *Binatisphinctes rossicus* and *B. fluctuosus* about 20-30 cm above the base of the bed. Two such aptychi were also found loose in the talus. The bed is 1.4 m thick.

The overlying Callovian beds do not contain aptychi.

In the vicinity of Saratov, the Upper Callovian aptychi were found in a small quarry near the village of

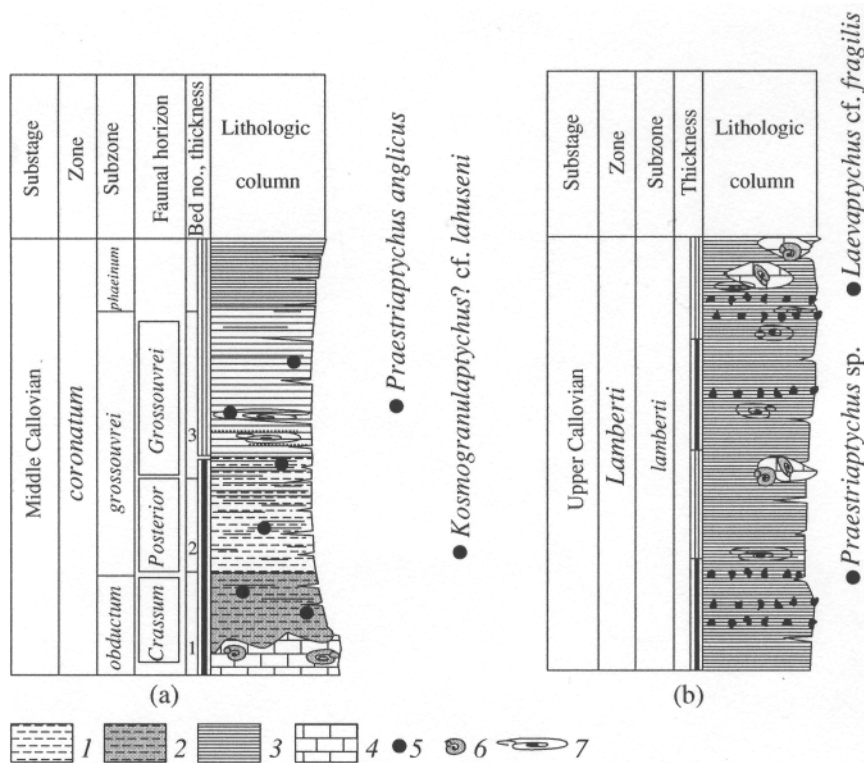


Fig. 2. Stratigraphic distribution of Middle and Upper Callovian aptychi: (a) quarry of the Mikhailovtsement Plant and (b) quarry near the village of Dubki. (1, 2) silt: (1) light gray and (2) brownish; (3) clay; (4) marl; (5) phosphorite nodules; and (6, 7) ammonites: (6) in nodules and marl beds and (7) in clay and silt.

Dubki (Fig. 2b). A collection of ammonites from this outcrop has not been fully examined.

Terminology used in the description of aptychi follows that in Khalilov (1978), Kozlova and Arkadiev (2003), and Rogov and Gulyaev (2003) (Fig. 3).

The material described is housed at the Paleontological Institute of the Russian Academy of Sciences (PIN), collection no. 4986 and St. Petersburg State Mining Institute Museum (SPGGI), collection nos. 50 and 60.

#### SYSTEMATIC PALEONTOLOGY Genus *Praestriaptychus* Trauth, 1927

##### *Praestriaptychus anglicus* Trauth, 1930

Plate 4, figs. 2 and 3

*Aptychus*: Quenstedt, 1949, p. 316, pl. 22, fig. 31. *Praestriaptychus anglicus*: Trauth, 1930, p. 384, pl. 5, figs. 12 and 13.

**H o l o t y p e.** Not established. The type series comes from the Middle-Upper Callovian of England (Oxfordian Clay Formation, Peterborough and Stewartby Members) (Cox *et al.*, 1992). According to Trauth (1930), the specimen displayed in pi. 5, fig. 13, is housed at the Geological-Paleontological Institute of Göttingen University (Geologisches-Palaontologisches Institut, Universität Göttingen, Germany).

**Description.** The valves are medium-sized and rounded triangular. In some specimens, a small furrow extends along the symphysis. The angle between the symphysis and frontal margin is approximately 90°. The valves are composed of two layers similar in thickness (external calcitic and internal organic layers). The inner and outer surfaces of the valve possess fine densely spaced growth lines.

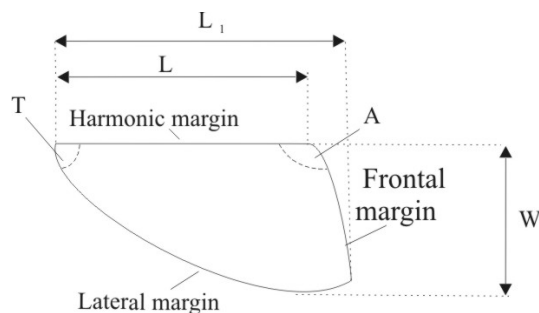
**Dimensions** in mm, ratios in % and angles in deg:

Specimen PIN, no.	L	L <sub>1</sub>	W	L/L <sub>1</sub>	W/L	A	T
4986/1	31.2	30.4	19.1	97.4	61	81	38
4986/2	27.7	28.4	16.1	102.7	58.3	86	56

**Comparison.** The comparison with *P. ryasanensis* sp. nov. is given after the description of the latter species.

**Remarks.** The aptychus that most likely belongs to this species was figured by Page (1991, 1994, text-fig. 4.1) from the *coronatum* Zone of England. Page (1991, pi. 24, fig. 6; 1994, pi. 24, fig. 6) following Cox (1988, pi. 18, fig. 1) figured almost identical aptychi in the body chamber of *Binatisphinctes comptoni* (Pratt.). A similar aptychus, which cannot be identified to species because of its poor preservation, was found by me in the Dubki quarry near Saratov in the *lamberti* Zone (Upper Callovian) (Pl. 4, fig. 7).

**Occurrence.** Middle Callovian, *coronatum* Zone, *grossouvrei* and *phaeinum* Subzones of England, Germany, and the Russian Plate.



**Fig. 3.** Terminology used in descriptions of aptychi and standard measurements.

**Material.** Two specimens from the quarry of the Mikhailovtsement Plant.

##### *Praestriaptychus ryasanensis* Rogov, sp. nov.

Plate 4, fig. 1

*Aptychus hectici*: Lahusen, 1883, pp. 76 and 90, pl. 11, fig. 21 (non fig. 20 = *Kosmogranulaptychus? lahuseni* sp. nov.).

*Cornaptychus* L 7: Trauth, 1930, p. 353, pi. 3, fig. 15.

**Etymology.** After the locality in the Ryazan Region.

**Holotype.** SPGGI, no. 427/60; Ryazan Region, Skopinskii District, Chulkovo; Middle Callovian, *coronatum* Zone.

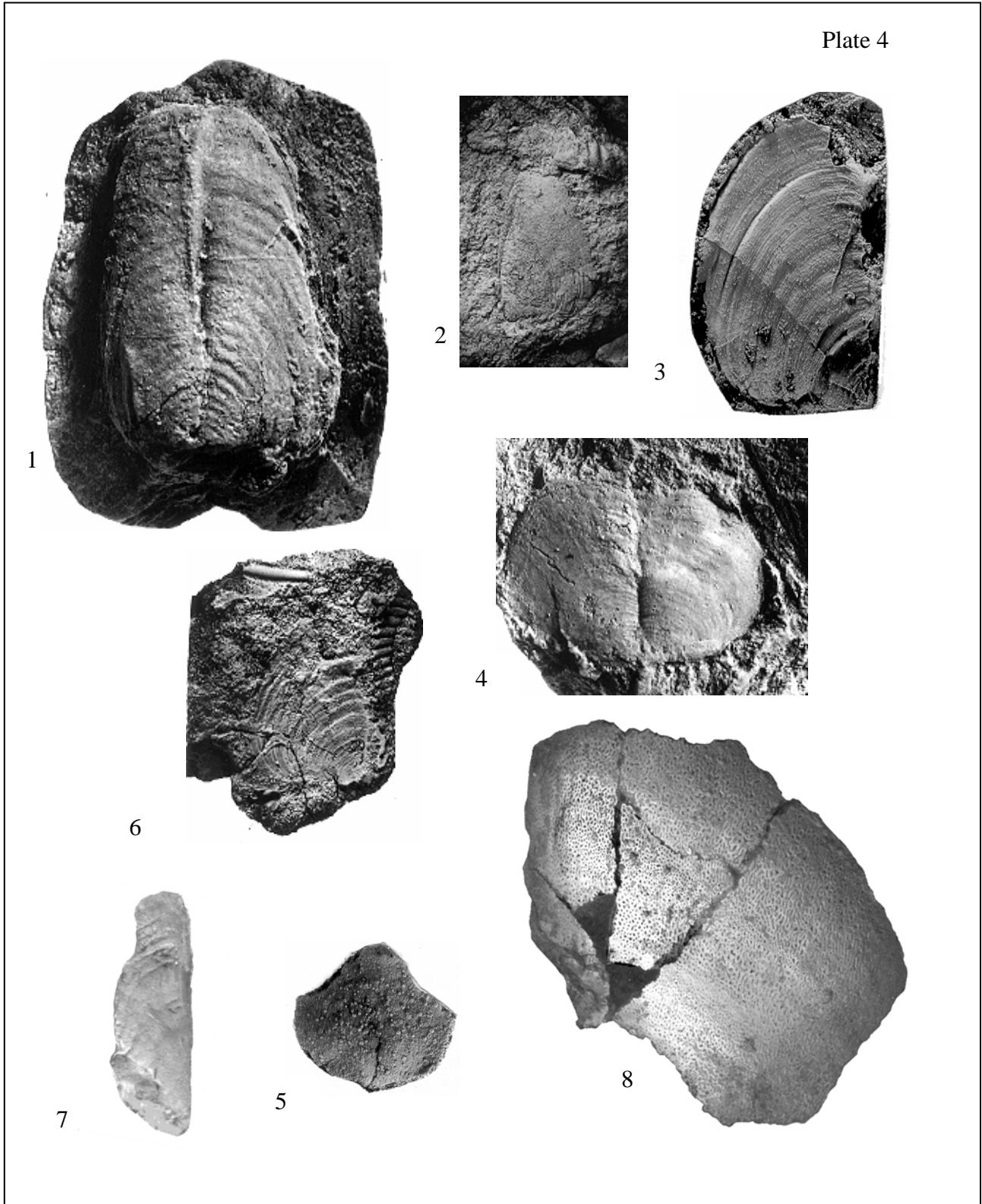
**Description.** The valves are relatively large, rounded-triangular, with the length considerably exceeding the width. The external calcitic layer is not preserved. The holotype is an imprint of the inner surface of the aptychus, which is covered by wide and relatively widely spaced growth lines. A depression runs along the symphysis, which is especially noticeable near the terminal angle.

**Dimensions** in mm, ratios in % and angles in deg:

Specimen PIN, no.	L	L <sub>1</sub>	W	L/L <sub>1</sub>	W/L	A	T
Holotype SPGGI no. 427/60	30.7	30.4	10.6	99.02	34.5	80	90

**Comparison.** The combination of elongated valves with relatively widely spaced and wide growth lines observed in this species is not typical of other Callovian aptychi. Although growth lines of some *P. anglicus*, are also widely spaced and wide (Trauth, 1930, pi. 5, fig. 12), the new species is readily diagnosed by its considerably narrower valves. The new species is distinguished from Lower Callovian *P. koenigi* Rogov (Rogov and Gulyaev, 2003) by the wider and more widely spaced growth lines.

**Remarks.** The narrow valves of *P. ryasanensis* are similar to those of *Cornaptychus hectici* (Quenstedt, 1849, pl. 22, fig. 29; 1886-1887, pl. 82, figs. 51-56, 59, 60; Trauth, 1930, pl. 3, figs. 4-9), a species of the same



age. The new species differs in that in early ontogeny (valve less than 1 cm long) its valves are wider than in *Cornaptychus*. The valve shape in *P. ryanensis* is most similar to that of aptychi belonging to the subfamilies Proplanulitinae and Grossouvriinae. Apparently, these aptychi also belonged to the Perisphinctidae.

Material. Holotype.

**Genus *Kosmogranulaptychus* Rogov, gen. nov.**

**Etymology.** A combination of *Kosmoceras* and *Granulaptychus*.

**Type species.** *Granulaptychus calloviensis* Trauth, 1930; Middle-Upper Callovian (Ornatenthon) of southern Germany (Württemberg).

## Explanation of Plate 4

**Fig. 1.** *Praestriptychus ryanensis* sp. nov.; holotype SPGGI, no. 427/60, x2; Chulkovo; *coronatum* Zone (collected by I.I. Lahusen).

**Figs. 2 and 3.** *Praestriptychus anglicus* (Trauth, 1930): (2) specimen PIN, no. 4986/1, x1; quarry of the Mikhailovtsement Plant, talus; *coronatum* Zone, *grossouvrei* Subzone (collected by M.A. Rogov); (3) specimen PIN, no. 4986/2, x2; quarry of the Mikhailovtsement Plant; *coronatum* Zone, *grossouvrei* Subzone, *grossouvrei* faunal horizon (collected by M.A. Rogov).

**Fig. 4.** *Kosmogranulaptychus? lahuseni* sp. nov.; holotype SPGGI, no. 426/60, x2; Chulkovo; *coronatum* Zone; (collected by I.I. Lahusen).

**Fig. 5.** *Kosmogranulaptychus? cf. lahuseni* sp. nov.; specimen PIN, no. 4986/5, x2; quarry of the Mikhailovtsement Plant; *coronatum* Zone; *grossouvrei* Subzone, *posterior* faunal horizon (collected by M.A. Rogov).

**Fig. 6.** Astartidae indet. (= "*Praestriptychus kostromensis* Trauth"); specimen SPGGI, no. 40/50; bank of the Unzha River near the village of Vysokovo; *calloviense* Zone (collected by S.N. Nikitin).

**Fig. 7.** *Praestriptychus* sp.; specimen PIN, no. 4986/3, x2; quarry near the village of Dubki; Upper Callovian, *lamberti* Zone, *lamberti* Subzone, *lamberti* faunal horizon.

**Fig. 8.** *Laevaptychus cf. fragilis* Trauth, 1930; PIN, no. 4986/6, x2, quarry near the village of Dubki; *lamberti* Zone, *paucicostatum* faunal horizon.

**Diagnosis.** Aptychi consisting of external calcitic layer of medium thickness and inner organic layer. Valves broad, as wide as long. Terminal angle usually slightly less than 90°. General valve outline rounded. Surface of calcitic layer covered by even rows of small tubercles following growth lines. Growth lines discernible on inner surface of calcitic layer usually fine and densely spaced.

**Species composition.** Four species: *K. call-oviensis* (Trauth, 1930); *K. intermedius* (Trauth, 1930); *K. spinogranulosus* (Trauth, 1930) from the Middle-Upper Callovian of South Germany; and *K. ? lahuseni* sp. nov. from the Middle Callovian of the Russian Plate.

**Comparison.** This genus is distinguished from *Granulaptychus* Trauth, 1927 and *Strigogranulaptychus* Schweigert, 2000 by the less regular arrangement of tubercles on the external (calcitic) side. In addition, it differs from *Granulaptychus* in the less elongated valves.

**Remarks.** Apparently, these aptychi belong to ammonites from the family Kosmoceratidae (superfamily *Stephanocerataceae*). This is supported by a unique find of *K. calloviensis* in the living chamber of the Late Callovian *Kosmoceras* (Schweigert, 2000, text-fig. 1). At the same time, the morphologically similar genera *Strigogranulaptychus* and *Granulaptychus* are related to the Perisphinctaceae. This is an indication of the repeated and independent appearance of tubercular ornamentation in aptychi belonging to ammonites considerably different morphologically and with different paleobiogeographic background. The functional significance of the tubercles remains uncertain. It seems significant that ammonites belonging to the Perisphinctaceae, clearly closely related to each other and possessing tubercular aptychi, were found together with *Praestriptychus* lacking tubercles. For instance, the Bajocian-Bathonian boundary beds in Germany contain both *Garantiana* [M] with *Granulaptychus* and *Strenoceras* (with *Praestriptychus*), often considered to be their microconchs (Dietl, 1983, text-fig. 5). A similar situation is observed in perisphinctids from the

Kimmeridgian-Tithonian boundary beds. Within one subfamily Lithacoceratinae, some genera (*Lithacoceras* and *Silicisphinctes*) possess *Praestriptychus*, whereas other genera (*Euvirgalithacoceras* and *Subplanites*) are associated with *Strigogranulaptychus* (Schweigert, 1998, 2000).

*Kosmogranulaptychus? lahuseni* Rogov, sp. nov.

Plate 4, fig. 4

*Aptychus hectici*: Lahusen, 1883, pp. 76 and 90, pl. 11, fig. 20 (non fig. 21 = *Praestriptychus ryanensis* sp. nov.).

*Praestriptychus* ? f. 4: Trauth, 1930, p. 386, pl. 5, fig. 11.

**Etymology.** In honor of the paleontologist and stratigrapher I.I. Lahusen.

**Holotype.** SPGGI, no. 426/60; Ryazan Region, Skopinskii District, Chulkovo; Middle Callovian, *coronatum* Zone.

**Description.** The valves are medium-sized, wide, rounded, with a length only slightly exceeding the width. The external calcitic layer is not preserved. Fine growth lines are discernible on the inner layer.

**Dimensions** in mm, ratios in % and angles in deg:

Specimen no.	L	L <sub>1</sub>	W	L/L <sub>1</sub>	W/L	A	T
Holotype	15.3	15.3	11.7	100	76.4	90	90
SPGGI no. 426/60							

**Comparison.** This species differs from the similar species *K. calloviensis* in the less conspicuous growth lines and wider valves. Compared to the new species, *K. intermedius* and *K. spinogranulosus* have wider and more widely spaced growth lines on the inner surface of the valve.

**Remarks.** The aptychi *Praestriptychus* (*Stephanocerataceae*) described from *Normannites* (Westermann, 1954, pl. 32), *Erycitoides* (Westermann, 1964, pl. 62, fig. 7, pl. 73, fig. 12), and *Quenstedtoceras* (Lehman, 1972, pl. 10, fig. 3) most closely resemble the new species. I found a similar but poorly preserved specimen, which can be determined only as *K. cf. lahuseni*,

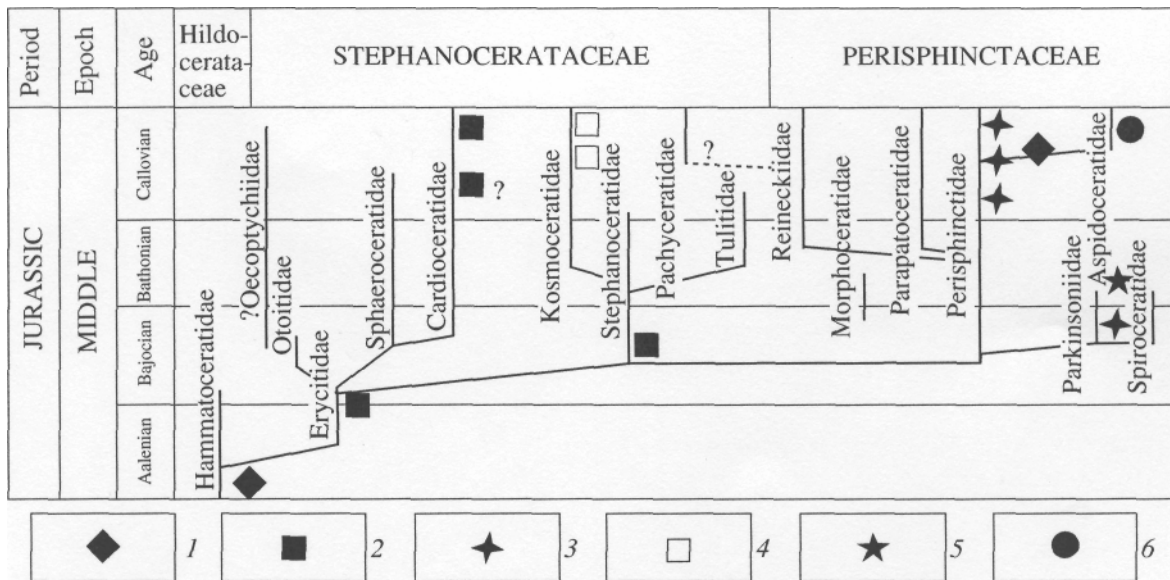


Fig. 4. Development of aptychi from the suborder Perisphinctina in the Middle Jurassic related to ammonite phylogeny. Phylogeny of ammonites after Besnossov and Mikhailova (1991), modified: (1) *Cornaptychus*, (2) *Praestriaptychus* with wide valves, (3) *Praestriaptychus* with narrow valves, (4) *Kosmogranulaptychus*, (5) *Granulaptychus*, and (6) *Laevaptychus*.

Pl. 4, fig. 5), in the body chamber of *Kosmoceras* sp. from the posterior faunal horizon (*grossouvrei* Subzone, *coronatum* Zone) in the Mikhailovtsement quarry. This suggests that *K. ? lahuseni* also belongs to *Kosmoceras*. Lahusen (1883, p. 76) suggested that these aptychi belong to hectioceratins: "I believe that they both belong to the genus *Harpoceras*."

Material. Holotype.

#### DISCUSSION

Let us consider the taxonomic position of so-called *Praestriaptychus kostromensis* Trauth, 1930. Nikitin (1885a, 1885b) described "Aptychus des *Cosmoceras galilaei*" from the Lower Callovian of the Kostroma Region (village of Vysokovo, near the Unzha River). It was found in the sandy beds, which is not typical for aptychi, but it was very important because this aptychus was believed to be associated with the Kosmocerotidae. Later, based on Nikitin's figures and descriptions, Trauth (1930, p. 386, pl. 5, figs. 17, 18) established a species *Praestriaptychus kostromensis*. The study of Nikitin's type specimen, which is housed at the museum of SPGGI (Pl. 4, fig. 6), showed that some characters (delineated beak and intercalating ribs) distinguish this specimen from all known aptychi. Although poor preservation (incomplete imprint) precludes positive identification, it most likely belongs to a bivalve of the family Astartidae.

Morphologically similar aptychi are not always associated with certain ammonite groups. For instance, the clearly unrelated genera *Lamellaptychus* and *Rugaptychus*, which are separated by a considerable geochronological gap, have similar sequences of different

ornamentation types changing over time. At the same time, different aptychi are sometimes associated with closely related ammonite genera. For instance, Middle Jurassic *Lissoceras* is associated with *Lamellaptychus* and, to a lesser extent, *Cornaptychus* (Sei and Kalacheva, unpublished report), whereas *Haploceras* and the apparently Late Jurassic *Lissoceras* are associated with *Punctaptychus* (Drushchits and Doguzhaeva, 1981, pl. 43, fig. 5).

Gasiorowski (1962) recognized two major groups of Jurassic aptychi: (1) ribbed aptychi, including narrow *Lamellaptychus*, *Cornaptychus*, *Laeviamellaptychus*, and *Punctaptychus*; and (2) smooth aptychi, which are usually considered to include wider and more weakly ornamented *Praestriaptychus* and *Laevaptychus*.

Smooth Middle Jurassic aptychi (*Praestriaptychus* and *Laevaptychus*) and *Granulaptychus* and *Kosmogranulaptychus* are characteristic of the suborder Perisphinctina. In many families of this suborder, aptychi are found in the living chamber of ammonites. Therefore, the most recent phylogenetic reconstructions for Middle Jurassic perisphinctins, at least, at family level, can be put in correspondence with the data on aptychi from ammonoids of these families; this provides an independent test of the extent to which Middle Jurassic *Laevaptychus*, *Praestriaptychus*, *Granulaptychus*, and *Kosmogranulaptychus* are a natural group.

The most recently published phylogenetic reconstruction for Jurassic ammonoids was proposed by Besnossov and Mikhailova (1991) based on the ontogenetic-phylogenetic approach. In the present paper it is accepted virtually unmodified, except the family Ocoptychiidae is considered to be a descendant of an unknown group, based on recent evidence of the

appearance of *Oecoptychus* in the Bajocian (Schweigert and Dietze, 1998). Hence, the hypothesis that the Oecoptychiidae evolved from the Bathonian Tullitidae (Besnossov and Mikhailova, 1991) is unsupported. In addition, taking new data into consideration, the geochronological ranges of some families were changed. Following Meledina (1994), the Cardioceratidae are considered to have evolved from the Sphaeroceratidae. The Macrocephalitinae are assigned to the Sphaeroceratidae (Gulyaev, 1999).

New data suggest that the distribution of the so-called smooth Middle Jurassic aptychi *Praestriptychus* and *Laevaptychus* in the ammonite families primarily indicates phylogenetic relationships rather than parallel evolution. For instance, wide representatives of *Praestriptychus* have only been found in association with members of the Stephanocerataceae,<sup>2</sup> whereas the narrower *Praestriptychus* and, possibly, some *Cornaptychus* belong to the Perisphinctaceae. However, while *Praestriptychus* are known to belong only to the Perisphinctinae, *Cornaptychus* also occur in the Ammonitina (Hildocerataceae) (Friebold, 1964; Lehman, 1972; Hirano *et al.*, 1990) and Haploceratina (Sonniniaceae) (Morton, 1973). *Laevaptychus* is a rare example of a case when a certain aptychus genus is associated with only one family (Aspidoceratidae), although it is possible that the earliest occurrences of *Laevaptychus* are associated with the ancestors of the Aspidoceratidae. In the Russian Platform, *Laevaptychus* appears at the end of the Callovian, in the *paucicostatum* faunal horizon, also yielding considerable numbers of early *Euaspidoceras* (Pl. 4, fig. 8). In Middle Jurassic *Praestriptychus*, the valve shape was apparently a very conservative character, almost independent of the ammonite shell shape. In the future, this situation may enable the use of aptychi for checking phylogenetic reconstructions made on the basis of other criteria (sutural ontogeny, ornamentation, etc.).

Middle Jurassic *Granulaptychus* and *Kosmogranulaptychus* are different in that they are morphologically similar while belonging to different superfamilies. Interestingly, independent from their superfamilial affinities, tubercular *Granulaptychus*, *Spinogranulaptychus*, and *Kosmogranulaptychus* are wider than *Praestriptychus* from the same beds. For instance, among Upper Kimmeridgian *Strigogranulaptychus* associated with some Lithacoceratinae, there are specimens with valves in which width exceeds length (*S. trescorrensis*, see Trauth, 1937, pl. 11, figs. 13-16). The narrowest *Praestriptychus*, which are similar in their main dimensions to *Cornaptychus*, appeared at the end of the Middle Jurassic in *Proplanulites* (Rogov and Gulyaev, 2003) and most likely are not directly related to the similar Upper Jurassic aptychi.

<sup>2</sup> There are records in the literature on the occurrence of aptychi in the Macrocephalitinae (Sphaeroceratidae). However, these finds were neither described nor figured (Bardhan *et al.*, 1993).

## CONCLUSIONS

Until now, only aptychi with relatively wide valves and weak ornamentation (*Praestriptychus*, *Granulaptychus*, *Strigogranulaptychus*, *Kosmogranulaptychus*, and *Laevaptychus*) were thought to be associated to the suborder Perisphinctina. If aptychi are considered to be a part of the ammonite jaw apparatus, their unvarying morphology in a group with a very diverse shell morphology could indicate similar feeding strategies in such different ammonites as *Quenstedtoceras*, *Erycites*, *Normannites*, and *Lithacoceras*, while finds of narrower aptychi in *Proplanulites* would indicate feeding adaptations different from other perisphinctins (note that the problem remains if aptychi are considered to be ammonite opercula). However, in modern coleoids, the jaws are all similar despite different modes of life (K.N. Nesis, personal communication). However, the appearance of tubercular aptychi with wide valves in different groups of the Perisphinctina in different times remains unresolved. Unfortunately, available data are insufficient to formulate a positive conclusion about the relationship of aptychi of a certain shape and Perisphinctina with a characteristic whorl section. It is possible that some aptychi assigned to *Cornaptychus* and *Laevilamellaptychus* could also belong to the Perisphinctina.

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