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Middle Jurassic ammonoid jaws (anaptychi and rhynchaptychi) from Dagestan, North Caucasus, Russia

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A R T I C L E I N F O

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A B S T R A C T

The Middle and Upper Jurassic stage of evolution of the anaptychus-type ammonoid jaw apparatus is relatively poorly known due to a small number of findings and uncertainty of their taxonomic position. All previously found anaptychi of this age are preserved either in flattened and dissolved shells or separately from ammonoid conchs. Rhynchaptychus-type jaws were still hitherto unknown from Jurassic deposits. In this paper we describe three-dimensionally preserved ammonoid lower jaws from the Bajocian/Bathonian boundary (Middle Jurassic) beds of Dagestan, Russia. These findings demonstrate a wide variety of their shape and structure. One specimen, consisting only of organic matter which is considered as anaptychus *sensu stricto*, is located *in situ* in the body chamber of *Lytoceras* (*Dinolytoceras*) *zhivagoi* (Besnosov). Three specimens which likely belonged to any Phylloceratiadae (*Adabofoloceras*, *Holcophylloceras*, or *Pseudophylloceras* which are presented in the ammonoid assemblage) contain prominent calcareous conchorhynchs, and the outer organic lamellae of these jaws were initially covered with a thin calcareous layer. The last lower jaw, probably from *Nannolytoceras*, has also a small calcareous conchorhynch in its tip despite a lack of coating. These findings are the first direct evidence of the existence of rhynchaptychus-type lower jaws in the Middle Jurassic. A variety in the shape and structure of the studied lower jaws indicates a variation in the mode of life and feeding behavior of Middle Jurassic ammonoids.

1. Introduction

The ammonoid jaw apparatus has been and still is the focus of a great deal of research for more than a century (see Tanabe et al., 2015 for review). Despite this fact, there are still a lot of open questions regarding the evolution and structure of ammonoid jaws. Ammonoids had a well-developed jaw apparatus, which, like in most other cephalopods, consisted of a pair of mandibles (upper and lower) and the radula enclosed between them. Each jaw consists of two lamellae: outer and inner, whose size and shape considerably varies among different ammonoid taxa. Ammonoid jaws also differ in chemical composition: they may consist only of organic matter or bear additional calcareous elements. Currently, researchers recognize five variants of ammonoid jaw apparatuses: normal, anaptychus, aptychus, rhynchaptychus and intermediate types (see Tanabe et al., 2015) which differ in shape and composition of the jaws. The recently described phyllaptychus type can also be added to this list (Mitta and Schweigert, 2016).

In general, the evolution of ammonoid mandibles is thoroughly known. The oldest type of ammonoid jaws is called the normal-type, which belonged to Paleozoic and Triassic ammonoids. This relatively conservative type of jaws remained virtually unchanged from the end of the Devonian to the end of the Triassic, it is characterized by upper and lower mandibles of a similar size (Tanabe et al., 2015). At the beginning of the Jurassic, the structure of the ammonoid upper jaw slightly changed, thus the anaptychus type appeared (Tanabe et al., 2015). However, the lower jaw of the anaptychus-type does not differ from the lower mandible of the ancestral normal-type, so the term “anaptychus” in a broad sense is often applied to the lower jaws for both anaptychus and normal types (Zakharov and Lominadze, 1983; Dagys et al., 1989). The anaptychi *sensu stricto* consisted exclusively of organic matter (Arkell, 1957), but in several of the Lower Jurassic ammonite taxa (Arietitidae, Eoderoceratidae), the outer surface of the anaptychus is coated with a thin layer of calcite (Cope and Sole, 2000; Keupp, 2000). Tanabe et al. (2012, 2015) suggested that all anaptychi may have had a calcareous coating, but in many cases it could have dissolved during diagenesis or it could have been secondarily exfoliated during preparation.

Whereas in the Toarcian (Early Jurassic) in Ammonitina a new aptychus-type of ammonoid mandibles appeared (Engeser and Keupp, 2002; Tanabe et al., 2015), which is characterized by a bivalved

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structure of the outer lamella of the lower jaw, whose external surface is covered with paired calcitic plates (aptychi *sensu stricto*), the anaptychus-type of jaws persisted in the Jurassic Phylloceratina and Lytoceratina.

However, the Jurassic stage of evolution of anaptychi is very poorly known. Findings of the mandibles of Jurassic Phylloceratina and Lytoceratina are very scarce and were reported either from completely flattened ammonoid shells with a dissolved aragonite layer (Schmidt, 1928; Hauff, 1953), or were found separately from the conchs (Quilty, 1970; Lehmann, 1980; Westermann et al., 1999; Schweigert et al., 2016). Such peculiarities of preservation make it difficult to determine with certainty the ammonoid taxa to which these anaptychi belonged. From the Middle Jurassic, only two anaptychus-like specimens have been reported to date (Quilty, 1970; Westermann et al., 1999), whereas in the first case one cannot be sure that the depicted specimen is a part of jaw apparatuses, in the second case the anaptychus was found separately from ammonoid shells.

Late Cretaceous Phylloceratina and Lytoceratina are characterized by the rhynchaptychus-type of jaws (Tanabe et al., 2013, 2015; Takeda et al., 2016). The rhynchaptychus lower jaw is very similar to the jaws of normal and anaptychus types, but its surface is covered with a calcareous layer. Both upper and lower jaws of the rhynchaptychus type have calcareous rostral tips (Tanabe and Landman, 2002; Tanabe et al., 2015). These calcitic structures are very similar to rhyncholites and conchorhynchs in jaws of modern nautilids and it is likely that part of Mesozoic rhyncholites belonged to ammonoids (Tanabe et al., 1980). Until now, findings of jaws of the rhynchaptychus-type are known only from the Late Cretaceous of Japan. Several Jurassic anaptychi, which probably belonged to Lytoceratina, have prominent notches in their rostra (Lehmann, 1980; Westermann et al., 1999), which gave ground for the assumption that they should be assigned to rhynchaptychus types of jaws (Tanabe et al., 2015). However, proven rhynchaptychi have not yet been found in strata older than the Late Cretaceous.

To understand how the jaw apparatus of ammonoids worked and what prey they hunted, the construction of their mandibles is usually compared with the jaw apparatus of modern cephalopods. The normal-type jaws of ammonoids resemble the jaws of modern nautilids and coleoids. However, there are some differences. Ammonoid mandibles of the normal-type, according to most researchers, neither had calcareous elements, which are present in the tips of the jaws of *Nautilus*, nor sharp edges which are present in coleoid jaws (Zakharov, 1974; Dagys and Dagys, 1975; Dagys and Weitschat, 1988; Landman and Grebneff, 2006). Based on a fairly large upper jaw and lack of a pronounced cutting edge, Dagys and Weitschat (1988) assumed that the main function of the jaw apparatus of a normal type was not for cutting but for crushing prey. Calcareous coating appeared on the surface of some Lower Jurassic anaptychus-type lower jaws likely for strengthening the jaws and for more effective crushing of prey or for protecting mandibles from resisting prey. Injuries which were observed on the lower jaws of modern *Nautilus* show that the mandibles can be injured by too hard or actively resisting prey (Kruta and Landman, 2008).

The aptychus type of jaws which appeared at the end of the Early Jurassic is the most unusual among ammonoid jaws and it is very difficult to compare them with mandibles of modern cephalopods. Bivalved lower jaws of this type, which are covered with paired calcitic plates, most likely were used not only as a jaw, but also as a protective opercula (Lehmann and Kulicki, 1990). In addition, it could have other functions (Parent and Westermann, 2016). It is likely that the complication of the radula, which became multi-toothed (multicuspidate) in the Early Jurassic, reduced the value of the feeding function of the lower jaw and opened the way for its modification (Keupp et al., 2016). Since aptychi most likely were ineffective for cutting and retaining large prey, most researchers suggest that ammonoids with aptychus-type jaws were microphagous or planktonophagous (see review in Tanabe et al., 2015).

The rhynchaptychus-type jaws are the most similar in structure to the jaws of modern nautilids among all ammonoid jaws (Tanabe et al., 1980, 2015). Like the *Nautilus* jaws, the rhynchaptychus-type ammonoid jaws have powerful calcareous rostral tips and a calcareous covering of the lower jaw. Ammonoids with rhynchaptychi undoubtedly could have crushed hard shells of well-protected prey, as nautiluses do. The appearance of the rhynchaptychus type, apparently, allowed ammonoids to significantly expand the array of their prey and it is important to understand when this happened.

In this paper, we present five three-dimensionally preserved ammonoid lower jaws from the Bajocian/Bathonian boundary (Middle Jurassic) of the mountainous region of Dagestan, Russia. These findings shed light on the evolution of ammonoid jaws during the Jurassic as well as on the shape and structure of lower jaws of the Jurassic Phylloceratina and Lytoceratina. Four of these specimens have calcareous conchorhynchs. This fact indicates that they should be considered as rhynchaptychus-type jaws, which, therefore, appeared at least in the Middle Jurassic.

1.1. Terminology

Some terms which are used herein for the description of ammonoid jaws and their elements need clarification. In this publication we are talking about two types of ammonoid jaws: anaptychus and rhynchaptychus. The difference between them is that the jaws of the anaptychus type consist entirely of organic matter, while the jaws of the rhynchaptychus type contain calcareous elements. The upper and lower jaws of modern *Nautilus* also contain calcitic elements, which are called the rhyncholite and conchorhynch respectively (Saunders et al., 1978; Tanabe et al., 2015). Both rhyncholites and conchorhynchs are several times smaller than the jaws which contain these elements (see Saunders et al., 1978: text-fig.1; Kostak et al., 2010:text-fig. 8). Originally the terms “rhyncholite” and “conchorhynch” were used to refer to isolated calcitic elements from Mesozoic and Cenozoic deposits (Teichert et al., 1964; Klug, 2001; Kostak et al., 2010). Since the relation of such jaw elements to specific cephalopod taxa is difficult to determine in the case of the absence of a shell and organic parts of the jaw, a parataxonomic classification (*e.g.* Hadrocheilus, Akidocheilus, *etc.*) is used for their description. Tanabe et al. (1980) have proven that calcareous elements are present not only in nautiloid jaws, but also in the rhynchaptychus-type jaws of some Cretaceous ammonoids. Therefore, some isolated Mesozoic rhyncholites and conchorhynchs likely belonged to ammonoid jaws (Tanabe et al., 1980, 2015). In this paper we use the terms “rhyncholite” and “conchorhynch” to refer to calcareous elements of upper and lower ammonoid jaws respectively.

2. Material and methods

2.1. Localities

Ammonoid jaws described in this paper come from the Middle Member of the Tsudakhar Formation of the central part of Mountainous Dagestan. This Member belongs to the middle and upper parts of the Upper Bajocian Parkinsoni Zone and the lowermost part of the Lower Bathonian Zigzag Zone (Besnosov, 1967; Besnosov and Mitta, 1998). It is characterized by approximately 200-m-thick dark shales (mudstones) with numerous horizons of siderite concretions which quite often show signs of underwater erosion and condensation. These deposits were formed in vast prodelta conditions at the marginal marine basin of the active northern continental edge of Tethys (Gavrilov, 2005).

Ammonoid jaws have been found in two localities (Fig. 1). One of them is situated near Khurukra village in the Laksky District of Dagestan. The Bajocian-Bathonian section, a description and subdivision as well as the ammonites, belemnites and foraminifera of this locality have been published recently (Gulyaev et al., 2015; Glinskikh et al., 2016). Three specimens of ammonoid lower jaws were found by amateur paleontologist Vadim V. Kitain in the concretions of bed 15 which has a

Fig. 1. Localities of the Middle Jurassic anaptychi in the central part of the Dagestan Mountain region (marked by asterisks): 1 - Khurukra N 42.149°, E 47.134°, A 1700 m; 2 - Gunib N 42.402°, E 46.980°, A 970 m.

thickness of 3.6 m and belongs to the Densicosta Subzone of the Parkinsoni Zone (see Gulyaev et al., 2015). This level contains a rich well-preserved ammonoid assemblage of phylloceratins, lytoceratins and parkinsoniids. The first two groups are numerically predominant. They are represented by *Calliphylloceras demidoffi* (Rousseau), *Adabofoloceras abichi* (Uhlig), *A. subobtusum* (Kudernatsch), *Pseudophylloceras kudernatschi* (Hauer), *Lytoceras* (*Dinolytoceras*) *zhivagoi* (Besnosov), *Nannolytoceras* aff. *tripartitum* (Raspail) (Fig. 2). Parkinsoniidae are not so numerous, however, among them, the Zone and Subzone index-species are present (Fig. 2).

The second locality is situated near the Gunib settlement in the same named district of Dagestan. Two specimens of lower jaws were found by D.B. Gulyaev in the concretion horizon of the upper part of the Middle Tsudakhar Member. These concretions contain multiple small shells and fragments of ammonoid conchs. There are different numerous phylloceratins (*Holcophylloceras*, *Adabofoloceras*, *Calliphylloceras*), infrequent lytoceratins (*Lytoceras*, *Nannolytoceras*) and relatively abundant ammonitins (*Parkinsonia* sp. ind. [M = macroconch], *Cadomites* ex gr. *deslongchampsi* (d'Orbigny) [M], *Polyplectites* sp. [m = microconch] (*cf.* "*psilacanthus* (Wermbter)" *sensu* Pavia et al., 2008), *Oxycerites*? sp. juv. (ex gr. *plicatella* Gemmellaro) [M], *Paroecotraustes* ex gr. *formosus* Arkell [m], *Oecotraustes bomfordi* Arkell [m].The most abundant ammonoid in this complex is *Adabofoloceras abichi*. This ammonoid assemblage is assigned to the Bajocian/Bathonian boundary (see Besnosov and Mitta, 1993; Pavia et al., 2008). However, it is still not clear whether this is the uppermost Parkinsoni Zone or the lowermost Zigzag Zone.

2.2. Methods

The anaptychi were investigated using a binocular microscope and scanning electron microscope TESCAN VEGA with a BSE detector at the Paleontological Institute of the Russian Academy of Sciences in Moscow. Data on elemental composition of ammonoid jaws were obtained using Energy dispersive X ray Analysis (EDX) on the SEM-coupled INCA Energy Dispersive X-ray Spectroscopy Detector.

The Jurassic specimens are housed at Moscow State University Museum, Russia, with the collection number MSU 124, one Triassic specimen is housed in Geological Institute of Russian Academy of Sciences.

2.3. Description of specimens

Terminology of the lower jaw description (Fig. 3) is partially based on Tanabe et al., 2013: Fig. 1.

2.3.1. Specimen MSU 124/1

Specimen MSU 124/1 (Fig. 4) from the Khurukra locality is a large anaptychus which is located in the anterior part of the body chamber of *Lytoceras* (*Dinolytoceras*) *zhivagoi*. The shell is not fully preserved, but its aperture is intact and is 38 mm in maximum diameter. The specimen is preserved in two parts: the anaptychus in the body chamber (MSU 124/1-1) and an imprint of its left wing in a separate fragment of the concretion (MSU 124/1-2).

Measurements: AH - 15 mm, L - 18 mm, DL - 19 mm, W – 26 mm, *a* – 80°. The anterior height was probably slightly larger, since the posterior part of the anaptychus is not fully preserved due to its proximity to the edge of the concretion. The anaptychus is fully organic and has no traces of calcareous elements neither on the specimen nor on its imprint. Its outer lamella has a notch in the anterior part, in which an organic protuberance of the inner lamella is located (Fig. 5). This arrow-shaped projection has a sharp tip and resembles a conchorhynch, but formed from organic matter. There are thickened areas formed by protrusions of the inner organic lamella along the anterior part of the specimen on both sides of the rostrum.

2.3.2. Specimen MSU 124/2

The specimen MSU *124/2* (Fig. 6) from the Khurukra locality is a middle-sized lower jaw with a prominent rostrum. The thickness of the organic outer lamella sufficiently increases towards the rostrum from 10 to 15 μm in the posterior part of the jaw to 300 μm near the tip. The surface of the outer lamella is covered with a reticulate pattern, formed by closely spaced growth lines and thin longitudinal lines, but on the most part of the specimen the organic layer is missing. The inner lamella is not visible in this specimen.

In the anterior part of the jaw on the surface of the outer organic lamella, the thin calcareous layer is preserved. Its thickness is 5–7 μm, the surface is covered with tiny regularly spaced growth lines, the distance between increases towards the posterior part of the specimen, but the thickness of this layer seems to be constant. In the anterior part of the tip, a slightly damaged conchorhynch is visible (Fig. 7).

Measurements: AH – 14 mm, L - 14 mm, DL- 16 mm, W – 16 mm, *a* – 50°.

2.3.3. Specimen MSU 124/3

Specimen MSU 124/3 (Fig. 8) from the Khurukra locality is the left wing of the lower jaw. The right wing is not preserved either due to either the location of the specimen on the edge of the concretion or due to probable destruction before the burial. The specimen (MSU 124/3-1) and its imprint (MSU 124/3-2) are preserved.

Measurements: AH – 7 mm, L – 8 mm, DL - 10 mm, but the ventral edge of the specimen is not fully preserved, therefore, it could have been larger. At the edge of the concretion, thin and short inner lamella is visible under the outer lamella. Both lamellae are very thin and their thickness is nearly constant throughout the length of the specimen. The outer lamella bears clearly visible shallow ribs. There is a partially preserved calcareous structure (conchorhynch) at the rostrum of this specimen.

2.3.4. Specimen MSU 124/4

Specimen MSU 124/4 (Fig. 9) from the Gunib locality is a middle-sized lower jaw with a prominent rostrum. The surface of the outer lamella shows a reticulate pattern, formed by closely spaced growth lines and thin longitudinal lines, but on the most part of the specimen the organic layer is missing. There is a notch in the apical part of the

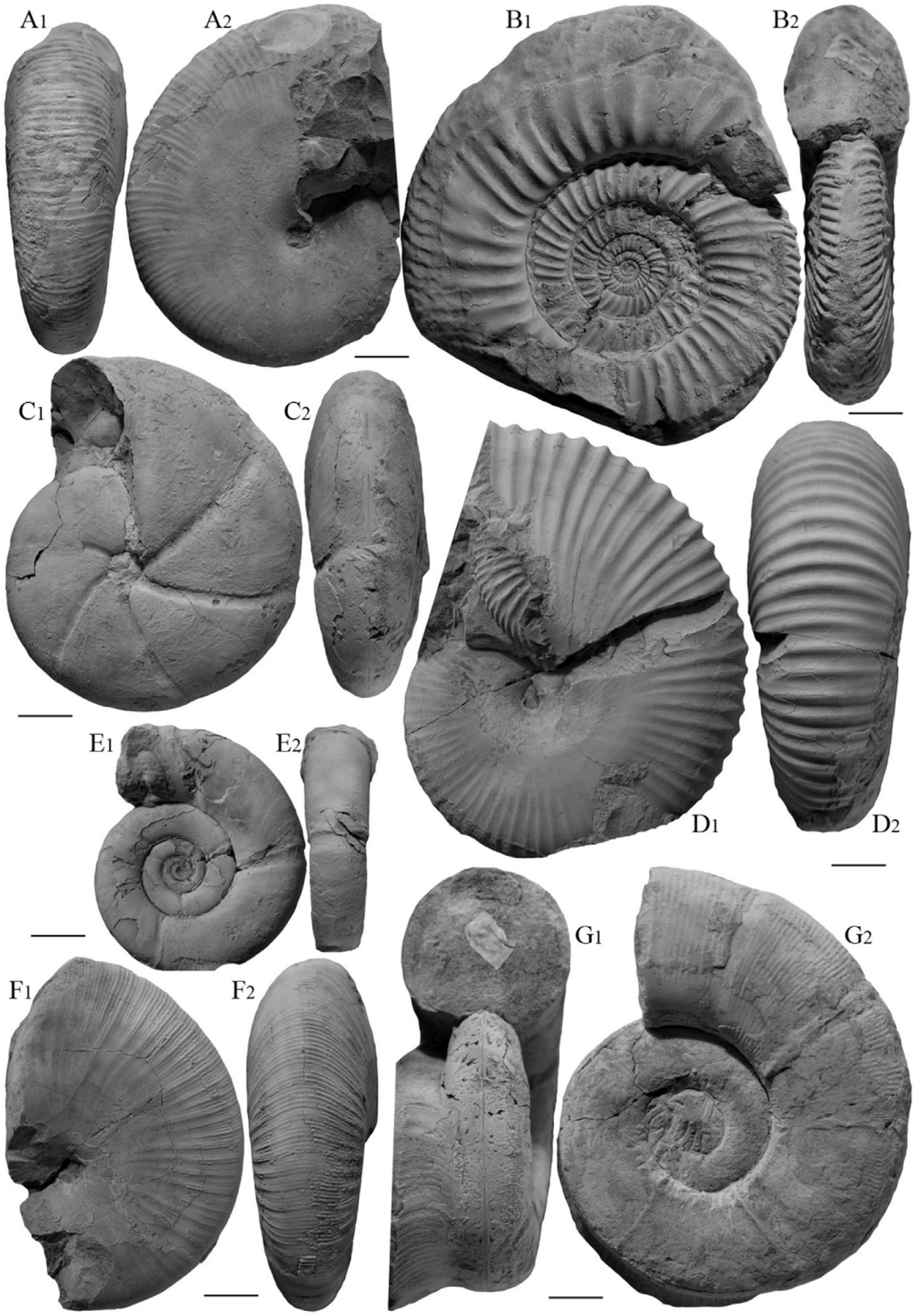

Fig. 2. Ammonoid assemblage from the Khurukra locality. A - *Adabofoloceras subobtusum* (Kudernatsch); B - *Parkinsonia parkinsoni* (Sowerby); C - *Calliphylloceras demidoffi* (Rousseau); D - *Adabofoloceras abichi* (Uhlig); E - *Nannolytoceras* aff. *tripartitum* (Raspail); F - *Pseudophylloceras kudernatschi* (Hauer); G - *Lytoceras* (*Dinolytoceras*) *zhivagoi* (Besnosov). Scale bars 1 cm.

specimen, which contains a calcareous conchorhynch (Fig. 10). The thickness of the outer organic lamella increases by the sides of the conchorhynch, but in the most part of the specimen this lamella seems to be constantly thin. There are remnants of a thin calcareous layer in several places on the surface of the organic lamella (Fig. 10), similar to the calcareous layer in specimen MSU 124/2.

Measurements: AH – 10 mm, L - 12 mm, DL- 13 mm, W – 15 mm, *a* – 60°.

2.3.5. Specimen MSU 124/5

Specimen MSU 124/5 (Fig. 11) from the Gunib locality is a small-sized partially preserved lower jaw with a prominent rostrum. The central anterior part of the jaw together with a part of the left wing are preserved (MSU 124/5-1). Additionally, a full imprint of this wing is located in a separate fragment of a concretion (MSU 124/5-2). The outer organic lamella is thin and in several places it is covered with remnants of calcareous layer. There is a notch in the apical part of the specimen, which contains a sharp conchorhynch (Fig. 12). The thin inner lamella runs along both sides of this conchorhynch.

Measurements: AH – 6 mm, L - 10 mm, DL- 11 mm, other parameters cannot be measured due to incomplete preservation.

EDX microanalysis of specimens MSU 124/2 and MSU 124/4 (Fig. 13, Table 1) confirms that the jaws are located in sideritic concretions and their outer layers and conchorinchs consist of calcareous mineral.

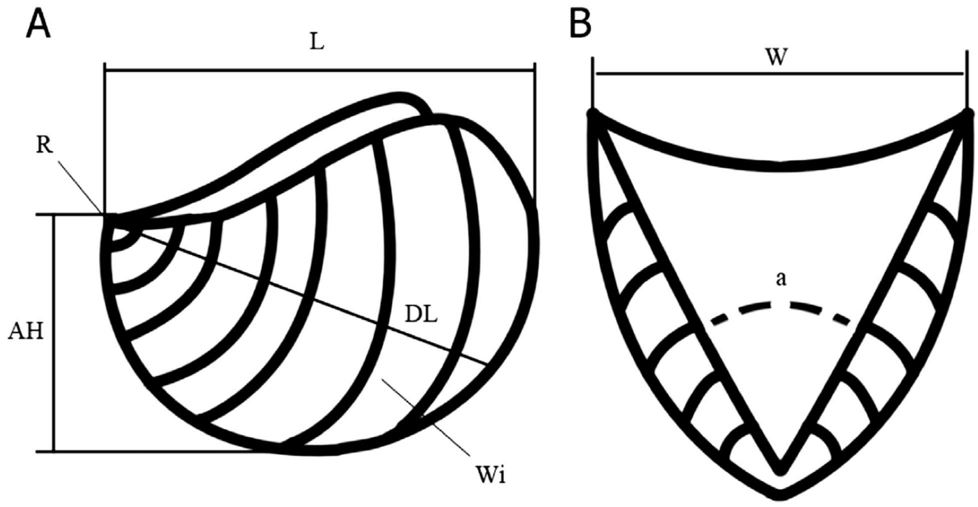

Fig. 3. Terminology of anaptychi description. A – lareral view; B – dorsal view. Wi – wing, R – rostrum or tip, AH – anterior height, L – length of the wing, DL- diagonal length, W – width (distance between posterior parts of wings), a – angle between wings.

Fig. 4. A lower jaw (anaptychus) of *Lytoceras* (*Dinolytoceras*) *zhivagoi* from the Khurukra locality. A, B, D, E – specimen MSU 124/1-1, C - MSU 124/1-2. A – right view of the anaptychus with a body chamber wall (anterior part of the body chamber on top); B – view of the right and central parts of the anaptychus; C - an imprint of a left wing of the anaptychus; D – ventral view of the anaptychus with an arrow-shaped area of organic conchorhynch-like structure; E – left view of the anaptychus. OCR – organic conchorhynch-like structure. Scale bars 1 cm.

3. Discussion

3.1. Determination of the taxa which jaws belonged to

Specimen MSU 124/1 has no calcareous elements and should be classified as anaptychus *sensu stricto* (Arkell, 1957). It was found *in situ* in the anterior part of the body chamber of *Lytoceras* (*Dinolytoceras*) *zhivagoi*. The width of the jaw (the maximum distance between the apical parts of the wings) is 26 mm, this value is approximately 70% of the diameter of the *Lytoceras* aperture (38 mm). The length of each wing of the anaptychus is 19 mm, therefore, the jaw in a flattened position would be 38 mm in width, this value entirely coincides with the diameter of the aperture. Although the findings of allochthonous jaws in ammonoid chambers are known (*e.g.* Bachmayer, 1963, see discussion in Engeser and Keupp, 2002), judging by its size this anaptychus most likely belongs to the ammonite in whose body chamber it was found. Therefore, the specimen MSU 124/1 should be consider as a lower jaw of *Lytoceras* (*Dinolytoceras*) *zhivagoi*.

Three of the studied specimens (MSU 124/2, MSU 124/4, MSU 124/5) are similar to each other in terms of a compact shape and the absence of coarse ribs, instead of these ribs the surface of their outer lamellae bears a fine reticular pattern. All three specimens have calcareous conchorhynchs (Figs. 7, 10, 12) and a very thin calcareous layer with densely arranged growth lines on the outer surface. This layer is better preserved in the specimen from the Khurukra locality (MSU 124/2), but its remnants are also visible on the surface of both mandibles from

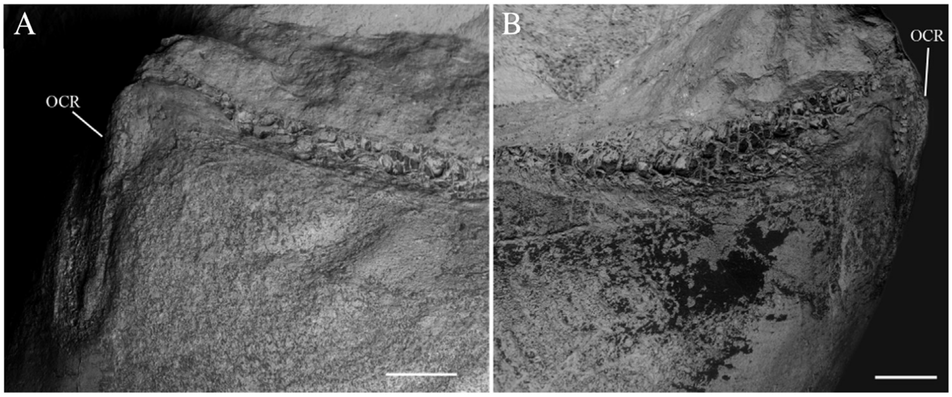

Fig. 5. SEM images of *Lytoceras* anaptychus (MSU 124/1-1). A – left view; B – right view. OCR – organic conchorhynch-like structure, formed by protuberance of the inner lamella of the jaw. Scale bars 1 mm.

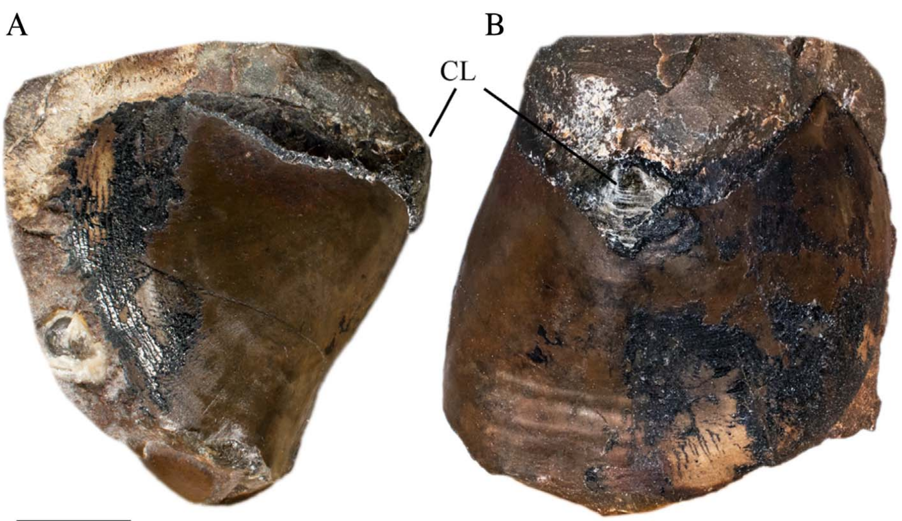

Fig. 6. A lower jaw MSU 124/2 from the Khurukra locality. A – right view; B – ventral view. CL – preserved part of the calcareous layer on the surface of the jaw. Scale bars 5 mm.

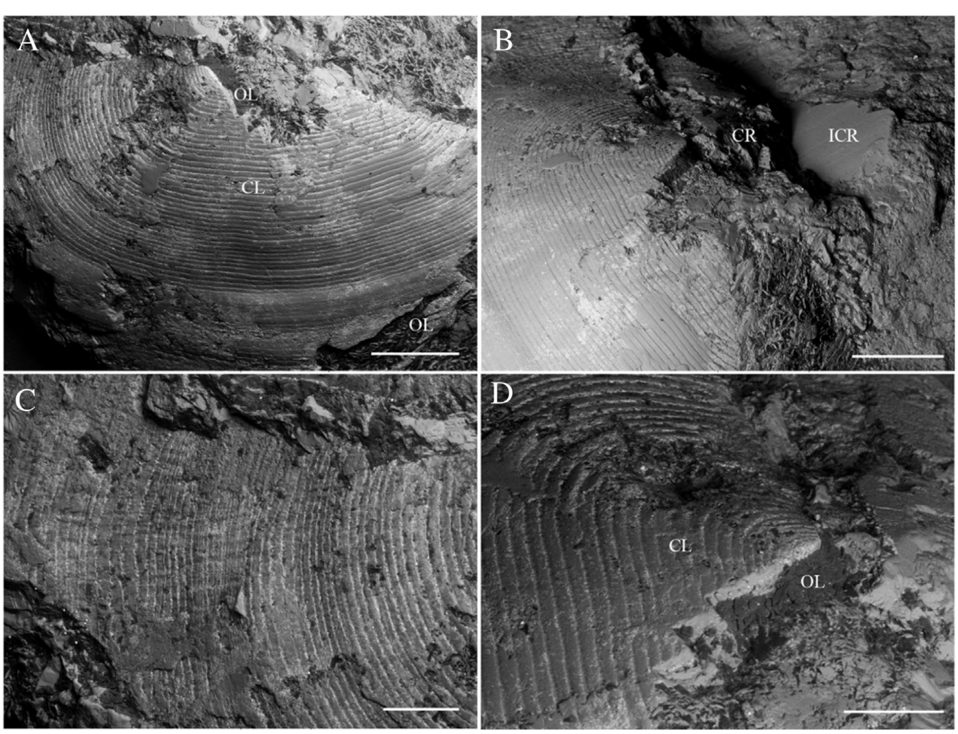

Fig. 7. SEM images of the lower jaw (specimen MSU 124/2). A – view of the center of the anterior part of the jaw. Scale bar 500 μm; B – a tip of the jaw with an imprint of the conchorhynch. Scale bar 500 μm; C - view of the outer calcareous layer in the anterior part of the left wing of the jaw. Scale bar 200 μm; D – lateral view of the anterior part of the jaw which demonstrates the thickness of the calcareous layer. The specimen on D is rotated 90° relative to A. Scale bar 200 μm. CR - calcareous conchorhynch, ICR – imprint of the conchorhynch, CL – calcareous layer, OL – organic layer.

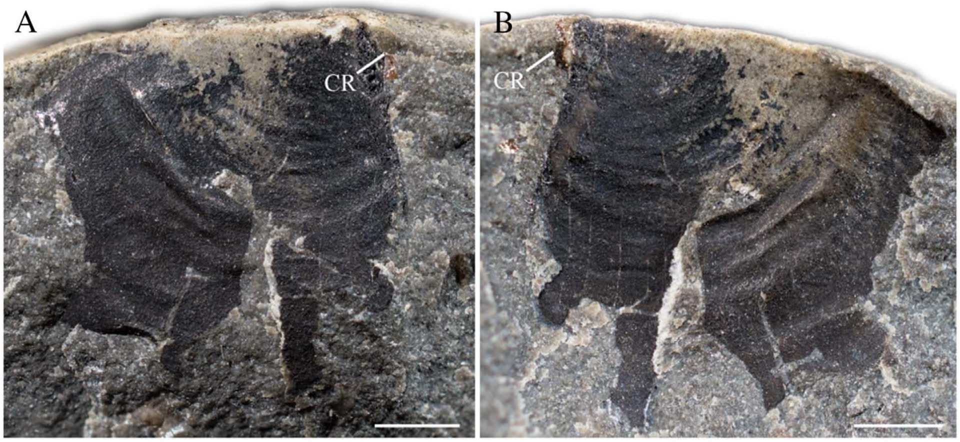

Fig. 8. A fragment of a lower jaw (specimen MSU 124/3) from the Khurukra locality. A – a wing of the jaw (MSU 124/3-1); B - an imprint of the jaw (MSU 124/3-2). Scale bars 2 mm. CR – a fragment of the conchorhynch.

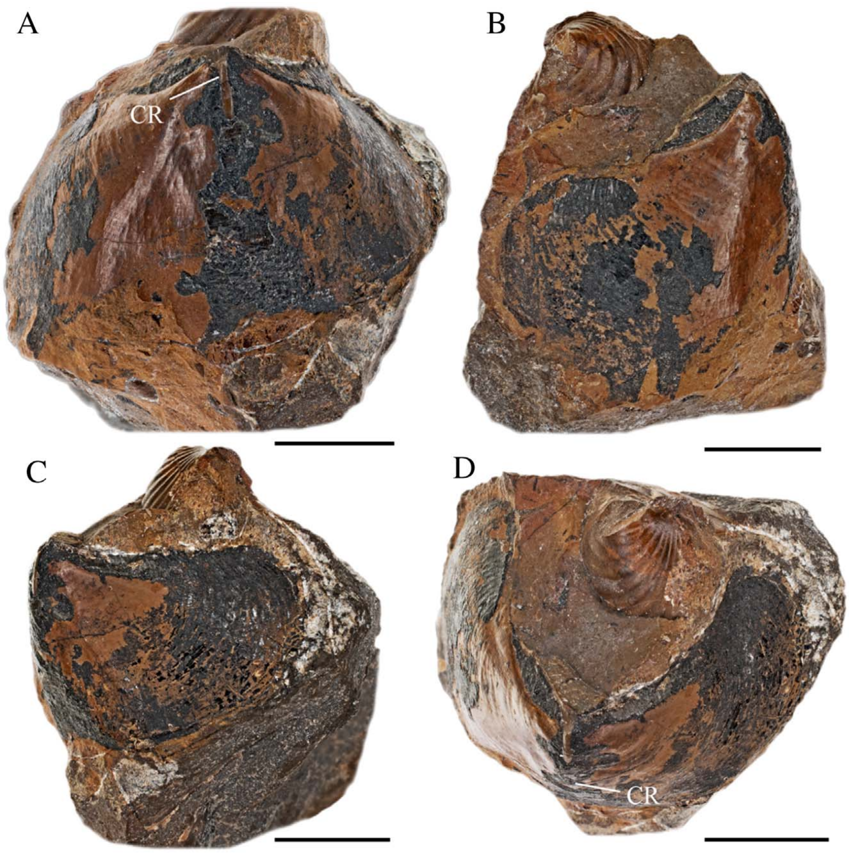

Fig. 9. A lower jaw (rhynchaptychus), specimen MSU 124/4, from the Gunib locality. A – ventral view; B – right view; C – left view; D – frontal view. Scale bars 5 mm. CR - calcareous conchorhynch.

Gunib (MSU 124/4, MSU 124/5). Due to the presence of conchorhynchs, these lower jaws should be classified as rhynchaptychi.

These specimens markedly differ from the anaptychus of *Lytoceras* and obviously belonged to other ammonoid taxa. Only two genera of Lytoceratina occur together with the jaws in Middle Jurassic deposits of Khurukra and Gunib: *Lytoceras* and *Nannolytoceras*. However, *Nannolytoceras* are small-sized ammonoids, the maximum size of the aperture of their shells is smaller than the width of specimen MSU 124/2. Moreover, in the Gunib locality lytoceratins are extremely rare.

The Ammonitina in studied localities is represented only by aptychophoran taxa (see Engeser and Keupp, 2002), characterized by thin aptychi which usually belong to the form genus *Praestriaptychus* (Lehmann, 1978; Engeser and Keupp, 2002). Therefore, the rhynchaptychi with an external calcareous layer are not jaws of Lytoceratina or Ammonitina, they could only belong to Phylloceratina.

There are shells of several phylloceratin genera found together with the studied lower jaws: *Calliphylloceras*, *Adabofoloceras* and *Pseudophylloceras* in Khurukra and *Adabofoloceras*, *Holcophylloceras*, *and Calliphylloceras* in Gunib (arranged according to frequency of occurrence). *Calliphylloceras* is present in both localities, however, an unusual bivalved specimen of the lower jaw ("phyllaptychus") was recently described from the body chamber of the Upper Bajocian *Calliphylloceras* from the Niortense Zone (two ammonite Zones below specimens studied herein) (Mitta and Schweigert, 2016). Although it cannot be excluded that different species of *Calliphylloceras* could have had different jaw apparatuses, due to the discovery of phyllaptychus, it seems unlikely that rhynchaptychi are lower jaws of *Calliphylloceras*. Most likely the rhynchaptychi with a reticulate pattern of the outer organic lamella and calcareous conchorhynchs are lower jaws of *Adabofoloceras*, *Holcophylloceras*, or *Pseudophylloceras*. Since *Adabofoloceras abichi* is the

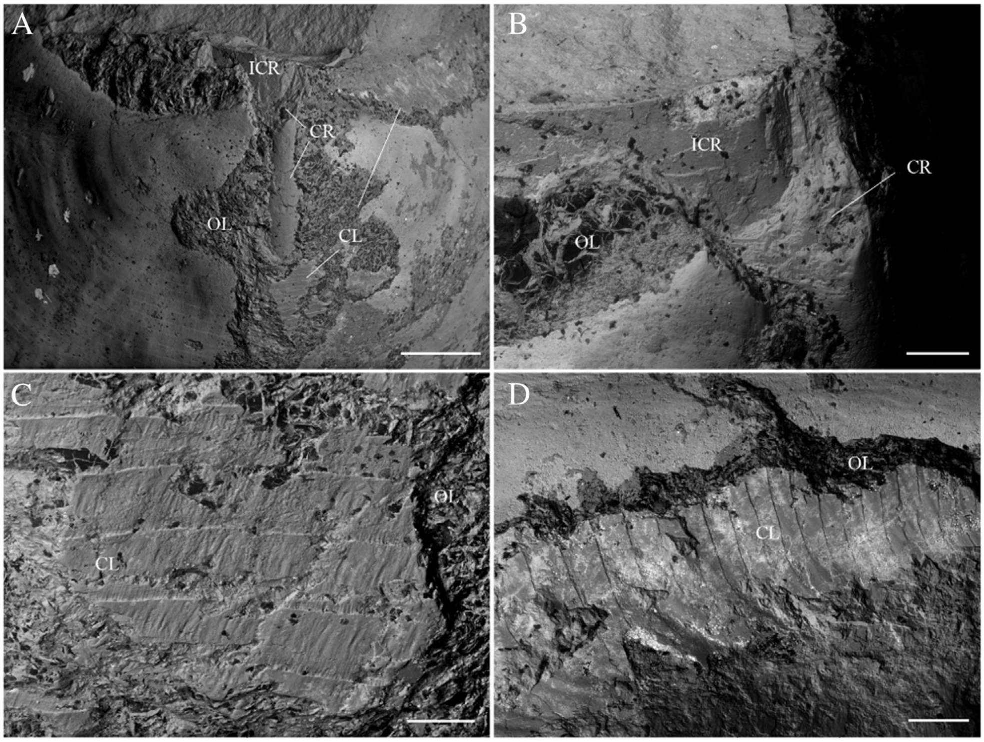

Fig. 10. SEM images of the lower jaw (specimen MSU 124/4). A, B – view of the tip of the jaw; C, D – fragments of the outer calcareous layer. CR - conchorhynch, ICR – imprint of the conchorhynch, CL – calcareous layer, OL – organic layer. Scale bars: A – 1 mm; B - 250 μm; C - 200 μm; D – 300 μm.

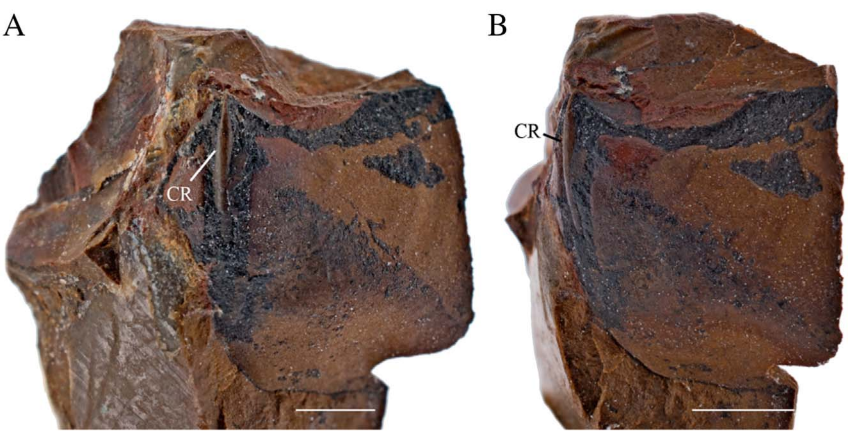

Fig. 11. A lower jaw (rhynchaptychus), specimen MSU 124/5-1 from the Gunib locality. A – ventral view; B – left view. CR - calcareous conchorhynch. Scale bars 2.5 mm.

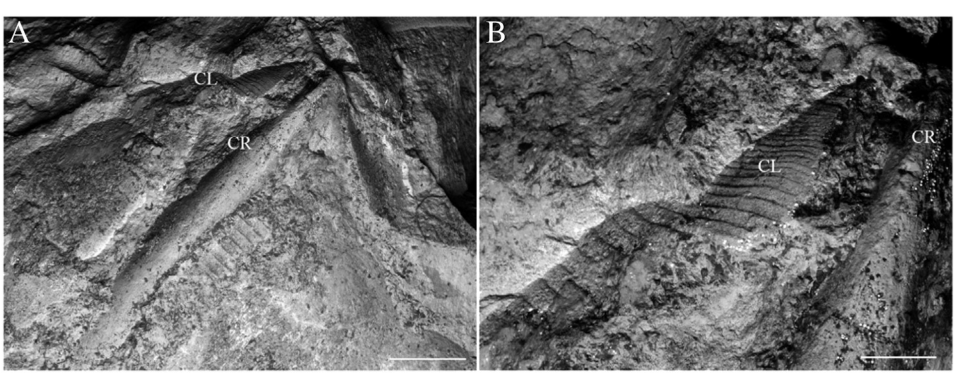

Fig. 12. SEM images of an anterior part of the specimen MSU 124/5-1. Scale bars: A – 0.5 mm; B – 200 μm. CR - calcareous conchorhynch, CL – outer calcareous layer.

most abundant species in Gunib locality, it looks possible that both specimens from Gunib (MSU 124/4 and MSU 124/5) are lower jaws of this species of Phylloceratina.

Determination of taxonomical affinity of the fifth specimen (MSU 124/3) is complicated by its poor preservation. Despite the presence of a small conchorhynch, this lower jaw fragment is not similar to jaws of phylloceratins: its surface, ornamented with shallow ribs without a calcareous coating, resembles the ribbed surface of *Lytoceras* anaptychus (MSU 124/1). The small size of this rhynchaptychus and its similarity with the anaptychus of *Lytoceras* gave ground for the assumption that this is a lytoceratin mandible, probably a lower jaw of *Nannolytoceras*, as only two lytoceratin genera were found in studied

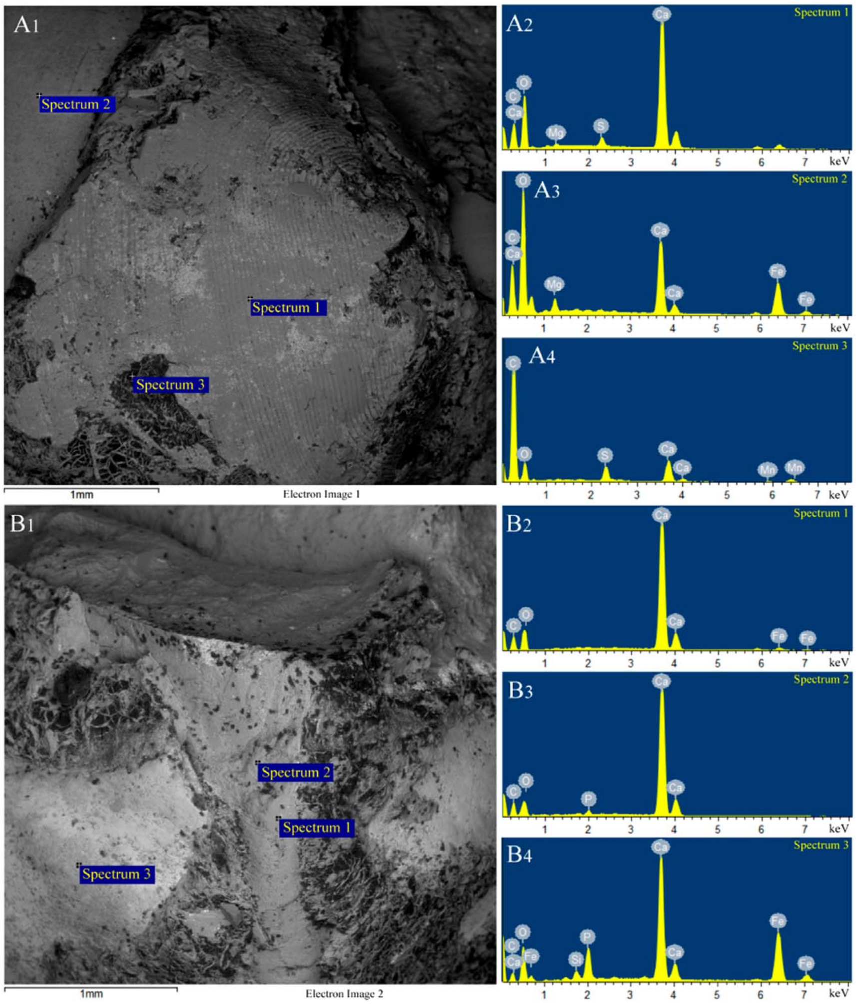

Fig. 13. EDX data of elemental composition of ammonoid jaws and surrounding rock. A – specimen MSU 124/2: A1 – general view, A2 - spectrum 1, the outer calcareous layer, A3 - spectrum 2, the surface of the internal mould of the jaw, A4 - spectrum 3, the outer organic lamella; B - specimen MSU 124/4: B1 – general view, B2 - spectrum 1, surface of the conchorhynch, B3 -spectrum 2, broken part of the conchorhynch, B4 – spectrum 3, rock between jaw lamellae. See also Table 1.

ammonoid assemblages. However, due to poor preservation of the jaw this assumption remains speculative, it cannot be excluded that this jaw belongs to one of phylloceratin taxa, so new findings are needed for verification of this assumption.

3.2. Conchorhynchs, their predecessors and the appearance of rhynchaptychus-type lower jaws

The present study of five ammonoid lower mandibles from the Bajocian-Bathonian of Dagestan demonstrates that as early as the Middle Jurassic, rhynchaptychi with calcareous conchorhynchs already existed along with the jaws of the anaptychus type. The anaptychus of *Lytoceras* (*Dinolytoceras*) *zhivagoi* also has an arrow-shaped conchorhynch-like structure in its tip, formed by the protuberance of an inner lamella, but consisting only of organic matter (Fig. 14). This anaptychus shows an unexpected similarity to the Upper Cretaceous lower jaws which are considered as belonging to *Placenticeras* (Landman et al., 2006). Lower mandibles of *Placenticeras* have arrow-shaped organic protuberance in the tips, formed by the protrusion of the inner lamella of the jaw (Landman et al., 2006, Figs. 15, 18, 20). *Placenticeras* jaws were referred to as an aptychus type, whereas not all of them have a clearly visible symphysis on the ventral side.

Pronounced organic inner lamella of *Lytoceras* anaptychus likely played a similar role as conchorhynchs in rhynchaptychus-type jaws of the Phylloceratina and Cretaceous Lytoceratina. It can be assumed that such organic protuberances were predecessors of conchorhynchs, since both these structures shared the same shape and location and differ only in the presence or absence of a calcareous layer. The calcification of the inner surface of the protuberance of inner organic lamella could have reinforced the biting function of the lower jaws and turned anaptychus into rhynchaptychus.

The presence of both anaptychi and rhynchaptychi in Middle Jurassic ammonoids may indicate that calcification of the lower jaw could have occured repeatedly and at various times in different ammonoid taxa. The possibility that within the Mesozoic Ammonoidea, the calcification of the lower jaw occurred several times in connection with a hard-shelled feeding specialization, was previously assumed by Engeser and Keupp (2002). Keupp (2000) suggested that anaptychi of some Triassic ammonoids could also have had a calcareous coating. Based on that, Parent and Westermann (2016) assumed that the calcification of jaws of Jurassic ammonoids could have been related with the reactivation of the secretory function, which appeared in the Triassic. However, the presence of calcified lower jaws in Triassic ammonoids looks doubtful. Dagys and Dagys (1975) argued that the anaptychi of the Triassic ammonoids initially were completely organic, whereas a great deal of secondary calcite is present in the concretions which contain anaptychi. Other studies of Triassic ammonoid jaws also did not mention any calcareous elements (Zakharov, 1974; Dagys and Weitschat, 1988; Landman and Grebneff, 2006). Tanabe et al. (2015) also argued that normal-type jaws to which Triassic ammonoid mandibles belong do not have any calcareous coating or tips. Triassic anaptychi from the Cape Tsvetkov (North Siberia) which are available for the authors, also have no calcareous elements, but have secondary white calcite which fills the cracks in their lamellae (Fig. 15). If a crack were along the surface of a jaw, then such calcite would be similar to the original coating.

Table 1
Elemental composition of the jaws and surrounding rock.

	Chemical element	Weight %	Atomic %
Specimen MSU 124/2 (from the Khurukra locality)			
Spectrum 1, outer calcareous layer (Fig. 13 A2)	C	14.30	21.93
	O	55.46	63.86
	Mg	0.55	0.41
	S	1.26	0.72
	Ca	28.44	13.07
Spectrum 2, surface of the internal mould of the jaw (Fig. 13 A3)	C	20.30	29.67
	O	55.24	60.61
	Mg	1.83	1.32
	Ca	10.19	4.49
	Fe	12.44	3.91
Spectrum 3, outer organic lamella (Fig. 13 A4)	C	68.09	76.78
	O	24.14	20.44
	S	2.28	0.96
	Ca	5.18	1.75
	Mn	0.31	0.08
Specimen MSU 124/4 (from the Gunib locality)			
Spectrum 1, surface of the conchorhynch (Fig. 13 B2)	C	10.50	17.96
	O	47.32	60.75
	Ca	39.99	20.49
	Fe	2.18	0.80
Spectrum 2, broken part of the conchorhynch (Fig. 13 B3)	C	11.17	19.91
	O	40.52	54.23
	P	0.38	0.27
	Ca	47.93	25.60
Spectrum 3, rock between jaw lamellae (Fig. 13 B4)	C	8.54	17.43
	O	32.60	49.96
	Si	1.39	1.22
	P	5.17	4.09
	Ca	25.15	15.38
	Fe	27.16	11.92

These data were obtained using Energy dispersive X-ray Analysis (EDX). See also Fig. 13.

Therefore, the presence of calcareous elements in Triassic anaptychi having been inherited by Jurassic ammonoids, cannot be considered as a proven fact. Most likely the calcareous layer on the surface of aptychi in the Early Jurassic family Hildoceratidae and anaptychi of several Arietitidae and Eoderoceratidae (Cope and Sole, 2000) and calcareous elements of the lower jaws of Middle Jurassic Phylloceratina (and probably Lytoceratina) appeared independently and were not inherited from Triassic ancestors.

Moreover, the rhynchaptychus-type jaws in different ammonoid taxa contain calcareous elements, consisting of different polymorphs of calcium carbonate: the outer calcareous layer on the lower jaw of *Anagaudryceras* is made of aragonite (Tanabe et al., 2012, 2015), whereas the calcified tip of the upper jaw and the outer calcareous layer of the lower jaw in *Hypophylloceras* both consist of calcite (Tanabe et al., 2013, 2015). This fact also may be evidence in favor of multiple appearances of calcareous jaw elements in different evolutionary lineages of ammonoids.

The previously described Toarcian and Bathonian lower jaws likely belonged to Lytoceratina which have prominent notches in their tips (Lehmann, 1980; Westermann et al., 1999). These notches gave the basis for the assumption about the initial presence of calcareous conchorhynchs in these areas (Tanabe et al., 2015). However, among the jaws of *Placenticeras*, specimens with diagenetically shattered inner lamella were also found and demonstrate nearly identical notches in their anterior parts (Landman et al., 2006, Figs. 3, 9). Due to this fact and to the simultaneous presence of both anaptychi and rhynchaptychi in Middle Jurassic deposits, if only the outer lamella with a notch is preserved without an inner lamella, it seems impossible to determine whether the calcareous or organic structure had been originally located in the tip of a lower jaw.

3.3. Possible mode of life of ammonoids with studied jaws

The structure and shape of the Middle Jurassic ammonoid lower jaws together with the shell shape of taxa to which the mandibles belong, help us to reach hypotheses about ammonoid lifestyles. *Lytoceras* had a wide and fully organic anaptychus without any calcareous elements, which coincided with a highly evolute shell with a reticulate surface ornament and large flares (Hoffmann, 2010). Most likely these lytoceratins fed on soft-bodied prey, but probably large-sized, since the sharp tip of the organic conchorhynch-like structure could have been used for cutting gentle prey tissues. Most likely the prey was very sluggish since the *Lytoceras* shell shape and flares prevented them from swimming fast.

Phylloceratins had discoconic, moderately ribbed streamlined shells, the lower jaws of these ammonoids had prominent calcareous conchorhynchs together with a calcareous covering on the outer surface. A combination of a streamlined shell with a reinforced lower jaw indicates the ability to feed on fast and well-protected prey.

The lower jaw, which probably belongs to *Nannolytoceras* (specimen MSU 124/3) is very similar to *Lytoceras* anaptychus, but differs by the presence of a small calcareous conchorhynch. In contrast to the *Lytoceras* shell, the *Nannolytoceras* has a smooth surface with very short flattened flares (Beznosov, 1958; Hoffmann, 2010). It could be assumed that *Nannolytoceras* fed on small, but protected prey, whereas it should be noted that the association of this lower jaw with *Nannolytoceras* is only tentative.

It also should be noted that the preservation of conchorhynchs in the specimens studied herein is not excellent and the shape of their tips still unclear: it is difficult to determine whether they are toothed, like *Nautilus* conchorhynchs or if they have sharp points. The upper jaws of studied ammonoids are also still unknown. Due to these limitations our assumptions about the feeding behavior of studied ammonoids are quite speculative.

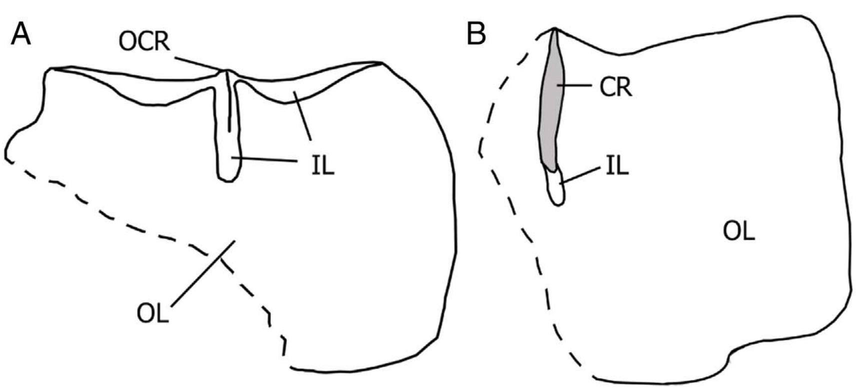

Fig. 14. Schematic structure of the studied jaws. A. anaptychus-type jaw, based on specimen MSU 124/1-1. B. rhynchaptychus-type jaw, based on specimen MSU 124/5-1. Abbreviations: OL - outer lamella, IL - inner lamella, CR - calcareous conchorhynch, OCR - organic conchorhynch-like structure = projection of the inner lamella. A dotted line indicates not preserved or hidden parts of jaws.

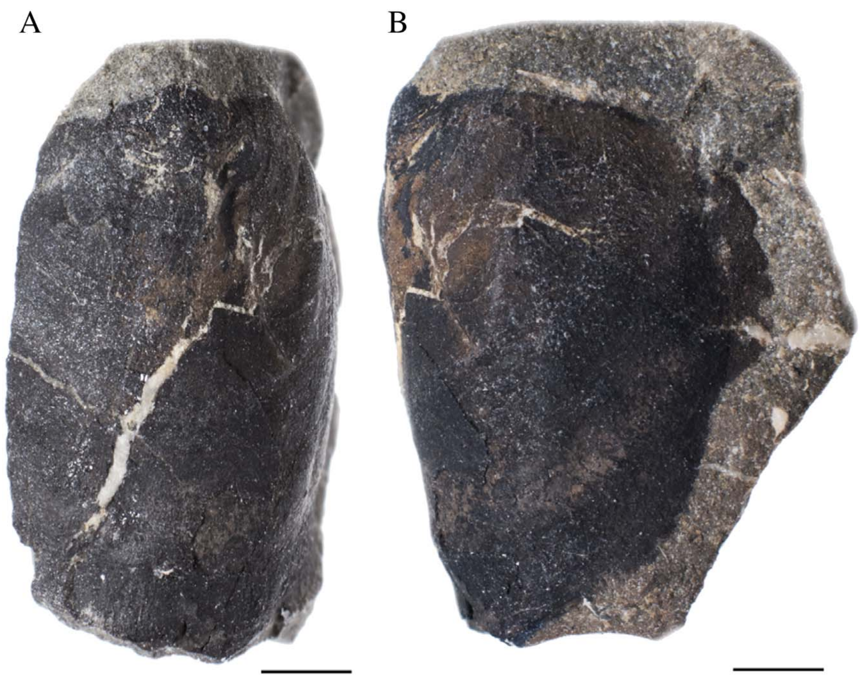

Fig. 15. A lower jaw of Middle Triassic (Anisian) ammonoid from the Cape Tsvetkov (North Siberia, Russia), specimen No. MC-Tr 2. A – ventral view, note the crack infilled with calcite in the central part of the jaw; B – lateral view. Scale bars 2 mm.

4. Conclusions

The study of five three-dimensionally preserved ammonoid lower jaws from Dagestan revealed that the rhynchaptychus-type of jaw apparatus appeared at least in the Upper Bajocian (Middle Jurassic) and co-existed with the anaptychus type. Ammonoids, which inhabited the Northern part of the Mediterranean-Caucasian realm (Page, 2008), demonstrate a substantial variability of the lower jaw structure: *Lytoceras* (*Dinolytoceras*) *zhivagoi* had a wide and fully organic anaptychus (*sensu stricto*) without any calcareous elements, whereas representatives of Phylloceratina (*Adabofoloceras*, *Holcophylloceras*, or *Pseudophylloceras*) had rhynchaptychi with a prominent conchorhynch, a reticulate pattern of the surface of the outer organic lamella and a thin finely calcareous striated coating. Another ammonoid taxon (probably *Nannolytoceras*, but a phylloceratin affiliation cannot be excluded) had rhynchaptychus-type lower jaws with a small-sized conchorhynch, but without a calcareous coating.

A wide variation of lower jaws of the Middle Jurassic ammonoids evidences that ammonoid ability for the formation of calcareous jaw elements was highly developed and the presence of such elements likely depended on environmental conditions and lifestyle rather than taxonomical affinity. It is also possible that the organic conchorhynch-like structure which is located in the rostrum of the *Lytoceras* anaptyhus (formed by protuberance of the inner lamella) could have been a predecessor of calcareous conchorhynchs. At the same time, the outer organic lamellae of anaptychi and rhynchaptychi are very similar and if only this part of the jaw is preserved with a notch in its tip, it is impossible to determine whether a calcareous conchorhynch or an organic protuberance of the inner lamella had been initially located in the rostrum of such a jaw.

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