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

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ABSTRACT

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