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Cretaceous Research xxx (xxxx) xxx

Contents lists available at ScienceDirect

Cretaceous Research

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Unusual findings of cephalopod jaws in the Mesozoic shallow water sandy facies

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A R T I C L E I N F O

Article history:
Received 5 June 2023
Received in revised form
17 August 2023
Accepted in revised form 22 August 2023
Available online xxx

Keywords:
Cephalopoda
Cephalopod jaws
Coleoidea
Octobrachia
Jaw apparatus
Cretaceous
Sandy facies

A B S T R A C T

Jaws of fossil cephalopods, originally composed mainly of organic matter, are rare findings. They are sometimes can be found in nodules, in body chambers of their hosts (ammonoids and nautiloids), and in the fine-grained deposits, including Konservat-Lagerstätten. Findings of fossil coleoid jaws, which were completely organic and devoid of mineralized elements, are especially rare. Here, for the first time, numerous specimens of three-dimensional phosphatized cephalopod jaws, preserved in the extremely shallow-water coastal sandy facies of the Upper Jurassic (Volgian), Lower (Albian) and Upper Cretaceous (Cenomanian, Turonian, and Campanian), all of which have so far been widely considered only as a source of vertebrate fossils, are described. Both upper and lower cephalopod jaws were found, whereas lower jaw elements are more common. Most of the jaws were referred to as belonging to coleoids, judging by their shape and the ratio of the sizes of their outer and inner lamellae. The overall shape and rounded front tips of the lower jaws, as well as the relatively straight, not curved shape of the upper jaws suggest that they belonged to octobrachian coleoids. One of the jaws most likely belongs to a nautilid specimen. Some coleoid jaws from the Upper Cretaceous are relatively large, suggesting the large body size of their owners. It should be noted that elements of the jaw apparatus are the only remnants of cephalopods at most localities with coastal sandy facies. The study of these jaws sheds light on the diversity of cephalopods in coastal ecosystems of the Cretaceous time.

1. Introduction

Findings of the jaws of cephalopod mollusks are known starting from the first half of the Paleozoic: from the Devonian (Klug et al., 2016) or even from the Silurian, if we consider *Aptychopsis* and similar structures as primitive jaws (Mironenko, 2020). The jaws of cephalopods are especially numerous in Mesozoic marine deposits. One of the main sources of fossil cephalopod jaws are fine-grained clays, black shale, and limestones, including Konservat-Lagerstätten, which also yield exceptionally well-preserved fossils with soft tissue remains. These layers were formed mostly at relatively large depths in low-energy, often hypoxic or anoxic conditions, which ensured a good preservation of the organic jaw tissues. These layers may contain various jaws of ammonoids (Keupp, 2007; Klug et al., 2012; Schweigert et al. 2016), jaws of nautilids with calcitic tips (Klug et al., 2021a), as well as initially fully organic jaws of various coleoid cephalopods (Klug et al., 2005, 2010a, 2010b, 2020a). Findings *in situ*, i.e. directly in the shells or fossilized bodies of cephalopods, are especially important, despite the fact that in coleoids, remnants of head tissues often prevent detailed study of the jaw apparatus (e.g. Klug et al., 2021b). Another important source of finds of cephalopod jaws is various concretions, in which elements of the jaw apparatus are often buried together with accumulations of shells of their hosts, primarily ammonoids (Landman et al., 2006, 2015; Keupp and Mitta, 2013; Tanabe et al., 2015a; Mironenko and Mitta, 2023). The jaws of coleoids can also be preserved in concretions (Dzik, 1986; Tanabe et al., 2008, 2015b, 2017; Tanabe and Hikida, 2010; Tanabe 2012; Keupp and Mitta, 2013). Preservation within the nodules and concretions which are cemented with phosphate or carbonate cement, generally ensures good three-dimensional appearance of the jaw elements. The body chambers of ammonoid and nautilid shells filled with fossilized sediment, in which the jaws can often be found *in situ* (see Tanabe et al., 2015a for review) can also be considered special cases of nodules as well as rare findings of fossilized stomach content of marine reptiles containing cephalopod jaw remains (Sato and Tanabe, 1998).

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https://doi.org/10.1016/j.cretres.2023.105687

However, fine-grained layered deposits and various concretions are not the only sources of cephalopod jaw specimens. This article is devoted to new findings of phosphatized cephalopod jaws (mostly of coleoid affinity), which come from extremely shallow coastal sandy Mesozoic (mostly Upper Cretaceous) deposits which previously had served only as a source of findings of bones and teeth of marine vertebrates. Such a type of preservation of cephalopod jaws is described for the first time and new findings shed light on the diversity of coleoids in coastal ecosystems of the Late Cretaceous.

2. Localities

Phosphatized cephalopod jaws were found at six localities, most of which are located in the European part of Russia on the Russian platform, and one is in the far north within the Asian part of Russia (Fig. 1A).

2.1. Kapotnya (Chagino)

This is the only Jurassic locality to date in which phosphatized cephalopod jaws have been found. This locality is known for more than a century and quite popular among amateur collectors. It represents the high left bank of the Moscow River in the territory of the city of Moscow, in the Kapotnya district. The locality was described at the end of the 19th century as Chagino, by the name of the village nearby (Nikitin, 1890) (Fig. 1B, loc. 1). The layers of the Upper Jurassic (upper Kimmeridgian and middle Volgian) deposits are exposed there, represented mainly by clays, with interlayers of sand with phosphorite nodules. The jaw was found in a thin layer of a dark sand, rich in shark teeth and phosphorite nodules, belonging to the Upper Jurassic (middle Volgian) *Dorsoplanites panderi* ammonite zone (layer JCr a^1 according to Nikitin, 1890).

2.2. Malogolubinsky

This natural outcrop is located 65 km northwest of Volgograd in the Volgograd region (Fig. 1B, loc. 2). The area is represented by high slopes of hills, composed of sandy rocks, partially eroded due to a natural erosion process. The jaws of cephalopods were found in a thin (about 20 cm in thickness) layer of coarse-grained sand containing numerous phosphorite concretions. These concretions contain remains of vertebrates, mainly teeth of sharks, whose age was determined as Albian (personal communication with Yarkov A.A., Volga branch of the Volgograd State University).

2.3. Malyy Prolom

Malyy Prolom quarry is located north-east of the eponymous village in Shatsky district of the Ryazan region, 6 km north-west of the town Shatsk, and approximately 170 km to the south-east of Ryazan City (Fig. 1B, loc. 3). The Upper Cretaceous deposits in the Malyy Prolom are attributed to the Yakhroma and Dmitrov Formations of a local stratigraphic scale (Solonin et al., 2021a, 2021b). All jaws of cephalopods from this locality come from a relatively thin (10–50 cm thick) sandy layer saturated with phosphorite concretions and numerous remnants of vertebrates, such as bones and teeth of fish and marine reptiles, and pterosaurs (Fig. 2). Recently, researchers attributed this fossileferous layer to the middle-upper Santonian Dmitrov Formation based on the fragments of inoceramid bivalves and radiolarians (Solonin et al., 2021a, 2021b). However, the researchers have pointed out that the ornithocheirid pterosaur teeth from the Dmitrov Formation are most likely derived from the underlying Cenomanian Yakhroma Formation: “This implies that the pterosaur teeth described here are reworked and most likely of Cenomanian age, given that no ornithocheirid teeth have yet been reported from strata younger than Cenomanian from anywhere in the world.” (Solonin et al., 2021a, p. 2). Since most of the vertebrate fauna from this locality is also typical for the Cenomanian deposits (Sidorenko, 1971), cephalopod jaws should also be considered of Cenomanian age.

2.4. Fedorovka

This locality is a natural outcrop near Fedorovka village on the bank of the river Inokovka, 70 km east of Tambov in the Tambov region (Fig. 1B, loc. 4). According to the author's knowledge, it still has not been described in the literature, but popular among amateur paleontologists. The locality is situated on the high bank of the river, and specimen collection is mainly carried out in the scree of the slope. Because of this, it is sometimes difficult to establish a relation between a finding and a specific layer. Upper Cretaceous rocks here, as in the Malyy Prolom locality, are represented by sands with interlayers of phosphate nodules. Judging by the fauna of vertebrates (teeth of sharks and marine reptiles), the deposits are predominantly Cenomanian in age, but an admixture of Santonian fossils is also possible. The different ages of the findings are confirmed by the various types of preservation and color differences of the specimens from this locality.

2.5. Yangoda river

The section on the Yangoda River is the northernmost locality from which the jaws described here were collected. The locality is a natural outcrop located near the mouth of the Syruta-Bigai stream, 170 km north of the city of Norilsk in the Taimyrsky Dolgano-Nenetsky district of the Krasnoyarsk region in Siberia (Fig. 1C, loc. 5). A single but large cephalopod jaw was found in layer VII (according to Zakharov et al. 1989). In this layer, bivalve inoceramid shells and fragments of ammonites were found, but belemnites are absent. This layer is dated to the upper Turonian (Zakharov et al. 1989).

2.6. Beloe Ozero

The locality “Beloe Ozero“ is situated in the Lysogorsky district of the Saratov region, 78 km south-west of Saratov City, 2 km east of Beloe Ozero village (Fig. 1B, loc. 6). The locality is a natural outcrop on the right side of the Golyi ravine, which stretches for several kilometers from the village of Beloe Ozero (Averianov and Arkhangelsky, 2021; Ebersole et al., 2022; Grigoriev et al. 2022). The Upper Cretaceous deposits at Beloe Ozero are attributed to the Rybushka Formation of a local stratigraphic scale, which is correlated to the lower Campanian. Cephalopod jaws from this locality were found in layer 2 according to Averianov and Arkhangelsky (2021). This layer is a relatively thin (20 cm) sandy-phosphorite horizon which contains numerous phosphorite nodules and remnants of marine vertebrates (bones and teeth of fish and marine reptiles) and rare pterosaur bones (Averianov and Arkhangelsky, 2021; Ebersole et al., 2022). Cephalopods are represented here by rare finds of belemnites *Belemnellocamax mammillatus* and *Belemnitella mucronata*, and ammonites *Hoplitoplacenticeras* sp. and *Baculites* sp.

3. Description of specimens

In the description of the examined jaw specimens, this paper uses the terms of the modern coleoid jaw apparatus proposed by Clarke (1962: fig. 1; 1986: fig. 4; see Fig. 3).

Fig. 1. Map of the localities. A. Map of Russia. B. Map of the central and southern parts of the Russian platform and the Volga region. Localities: 1 — Kapotnya (55°38′52.6″N, 37°47′12.7″E); 2 — Malogolubinsky (48°54′22.4″N, 43°35′48.6″E); 3 — Malyy Prolom (54°04′10.9″N, 41°41′31.1″E); 4 — Fedorovka (52°35′44.4″N, 42°27′59.7″E); 6— Beloe Ozero (51°14′36.9″N, 45°02′19.4″E). C. Map of the Krasniyarsk region, 5 — Yangoda locality (70°53′17.7″N, 88°33′00.7″E).

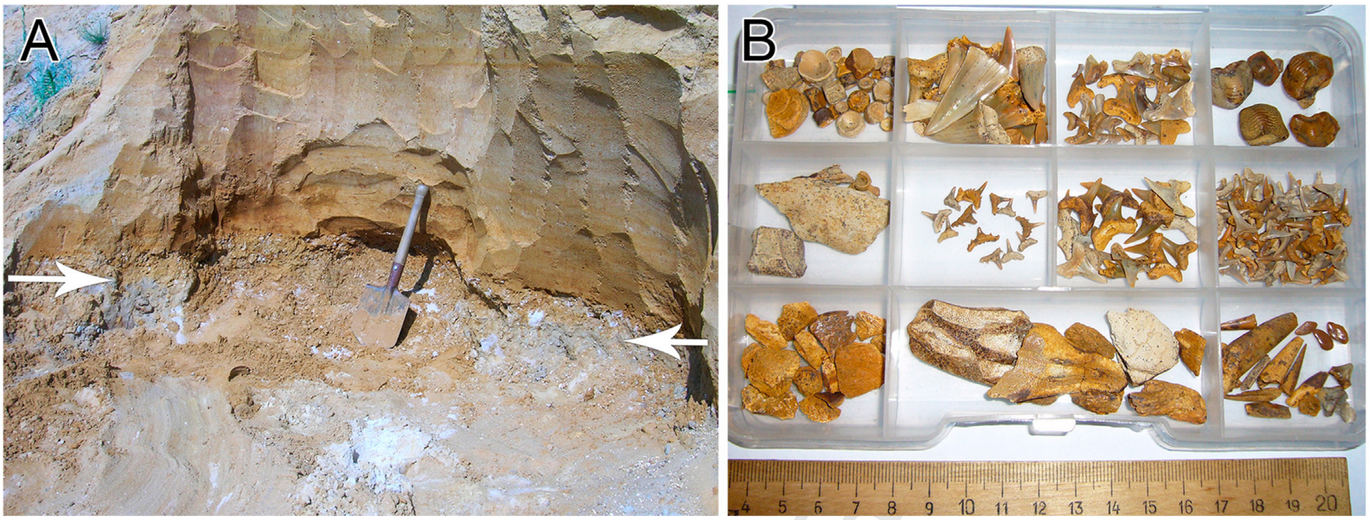

Fig. 2. Malyy Prolom outcrop and typical fossils from this locality. A. Sandy deposits in Malyy Prolom locality and thin horizon which contain numerous phosphotized fossils (marked with arrows). B. The most typical fossils from this horizon: bones of fish and reptiles and teeth of the Elasmobranchian fish of the Cenomanian age. Photos are provided by Alexander Lebedev (Moscow).

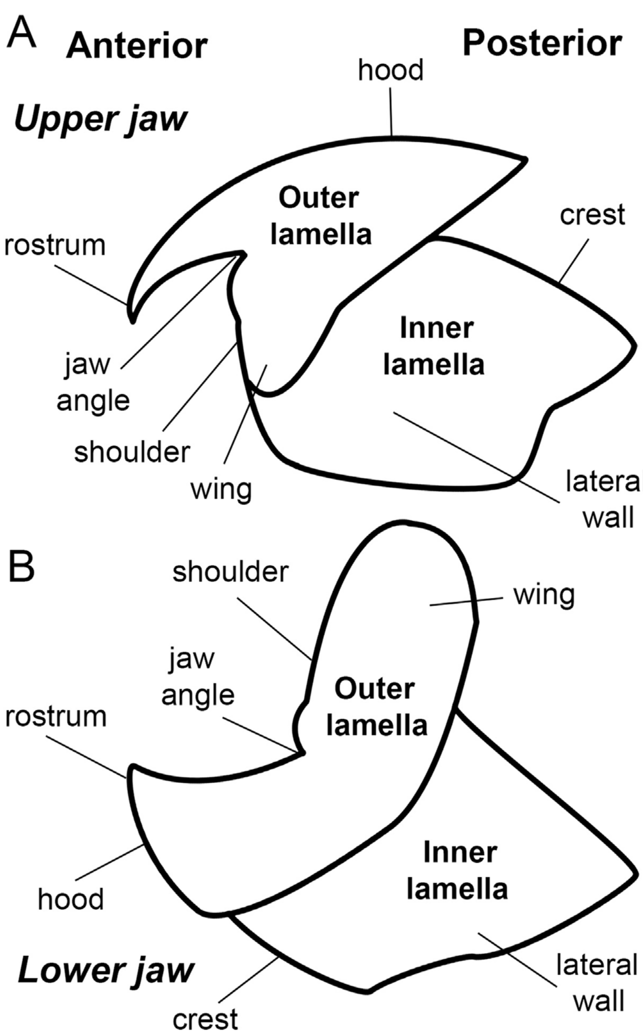

Fig. 3. The jaws of coleoid cephalopods. Schematic drawing of the upper and lower jaws of coleoid cephalopod (lateral view). Based on Clarke (1962): fig. 1. A – upper jaw, B – lower jaw.

All cephalopod jaws from shallow water sandy deposits described herein are phosphatized (see EDX data in supplement 1). They are more or less eroded: the anterior tips (rostra) of some specimens are missing, and the rear parts of both lamellae are not preserved in most of them. This makes it difficult to assess their original dimensions. However, many specimens are preserved quite well.

All specimens described herein, regardless of the type of preservation, can be divided into three groups or types.

The first and most numerous group includes specimens with a strongly concave inner side (originally facing towards the oral cavity and radula) and posteroventrally elongated lateral walls (Figs. 4–6). The angle between the lateral walls vary among the specimens examined, the rostral tip of the jaw is pointed or rounded, the outer side (if it is not eroded) is convex. In some specimens, a wider outer lamella forming the wings and a narrower and longer inner lamella with preserved crest and lateral walls are clearly visible (Figs. 4B, 5A, 6B). In several specimens, the rear parts of the lamellae were eroded or broken off before burial, but the strong concavity of their inner surface indicates that they belong to the same type. Judging by the general shape, the convex outer side and elongated wings of the outer lamellae, the specimens of the first type (Figs. 4–6) most likely are the lower jaws of cephalopods.

The second group includes specimens with an almost flat, very slightly concave inner surface (Fig. 7). In well-preserved specimens of this type (Fig. 7A is the most representative), the rostrum is always sharply pointed, and the outer surface is less convex than in specimens of the first type. The posterior ends of both inner and outer lamellae of such specimens are eroded approximately at the same distance from the anterior point. These findings most likely represent the anterior parts of the upper jaws of cephalopods.

The third group, the smallest one, includes three specimens (Fig. 8) which have a slightly raised middle part of the inner side. All of them are very strongly eroded. The noticeably convex outer side of these specimens suggests that initially they, most likely, were identical to the specimens of the first group, but their lateral walls along the edges of the inner side were worn away by sand or dissolved. The specimens of the second group (upper jaws) are more pointed and elongated, and even after erosion they can hardly obtain such a shape as is characteristic of the third group.

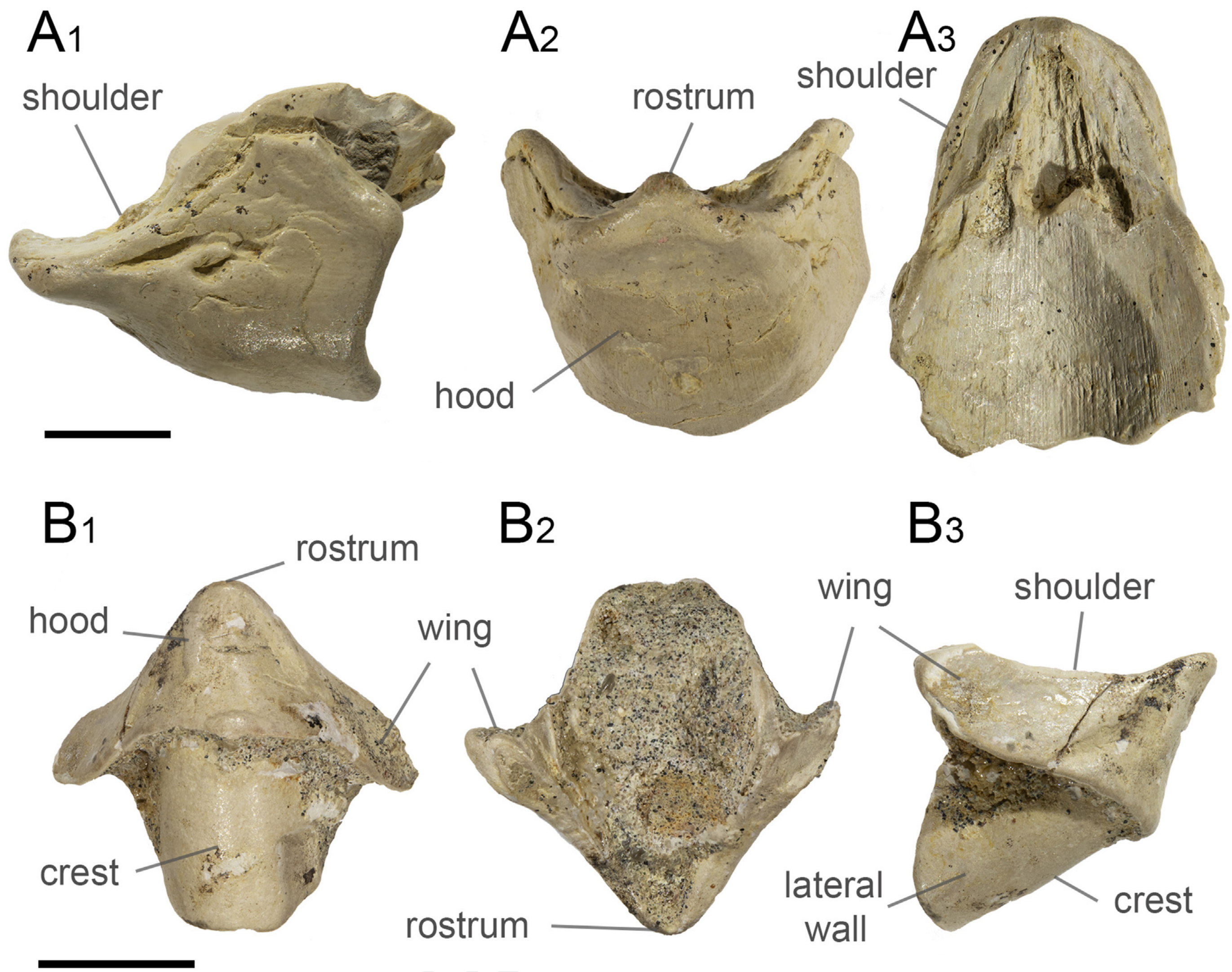

Fig. 4. Cephalopod lower jaws from Malyy Prolom (Cenomanian). A. specimen PIN 5877/1, nautilid lower jaw, A1 – lateral view; A2 – anterior view, A3 – dorsal view. B. Specimen PIN 5877/2, coleoid lower jaw, B1 – ventral view, B2 – dorsal view, B3 – lateral view (tip of the jaw on the right). Scale bars are 5 mm.

Therefore, most likely these specimens (Fig. 8) also represent the remnants of the lower jaws, but poorly preserved due to dissolution or sand abrasion.

The length of the smallest specimen is 9 mm, the largest one is 30 mm. Detailed descriptions and measurements of the specimens are given in Supplement 2. The described and figured specimens are housed at the Palaeontological Institute of Russian Academy of Science (PIN RAS), Moscow, Russia, collection number PIN 5877.

4. Discussion

4.1. General identification of the taxonomic affiliation of the jaws

A precise clarification of the hosts of the cephalopod jaws examined herein is a somewhat complicated task. During the Late Cretaceous, three subclasses of Cephalopoda existed: Ammonoidea, Nautiloidea (with only one order Nautilida) and Coleoidea and all of them had well-developed jaw apparatuses.

Ammonoids boasted the most diverse jaws among cephalopods of that time: in the Cretaceous they had three different types of jaw apparatus: aptychus type (Engeser and Keupp, 2002; Tanabe et al., 2015a for review), anaptychus (Schweigert et al., 2016; Klug et al., 2020a) and rhynchaptychus (Tanabe et al., 2015a; Mironenko and Gulyaev, 2018; Mironenko and Rogov, 2018) types. Rare findings of internal moulds of ammonite shells are known from the Cenomanian deposits in the Maly Prolom, from which most jaw specimens came, and from Campanian deposits of the Beloe Ozero. Ammonite shells from Maly Prolom belong to the genus *Schloenbachia*, from Beloe Ozero – to the genera *Hoplitoplacenticeras* and *Baculites*. All these ammonite genera belong to suborder Ammonitina, which had aptychus-type jaws (Engeser and Keupp, 2002; Tanabe et al. 2015a). However, the lower jaws described herein clearly differ from the lower jaws of the aptychus-type, which consisted of two symmetrical valves (Engeser and Keupp, 2002; Tanabe et al., 2015a). The upper jaws also differ from the aptychus-type upper mandibles (Keupp and Mitta, 2013; Mitta and Mironenko, 2021), although the latter are not yet well known. Representatives of the ammonoid suborders Lytoceratina and Phylloceratina, which possessed two other types of ammonoid jaw apparatuses (anaptychus and rhynchaptychus types), avoided epeiric sea and their shells have never been found in marine sediments of Central Russia. Therefore, these ammonoids cannot be considered as hosts of the jaws from most localities. In the north of Siberia, where one specimen (Fig. 8C) originates from,

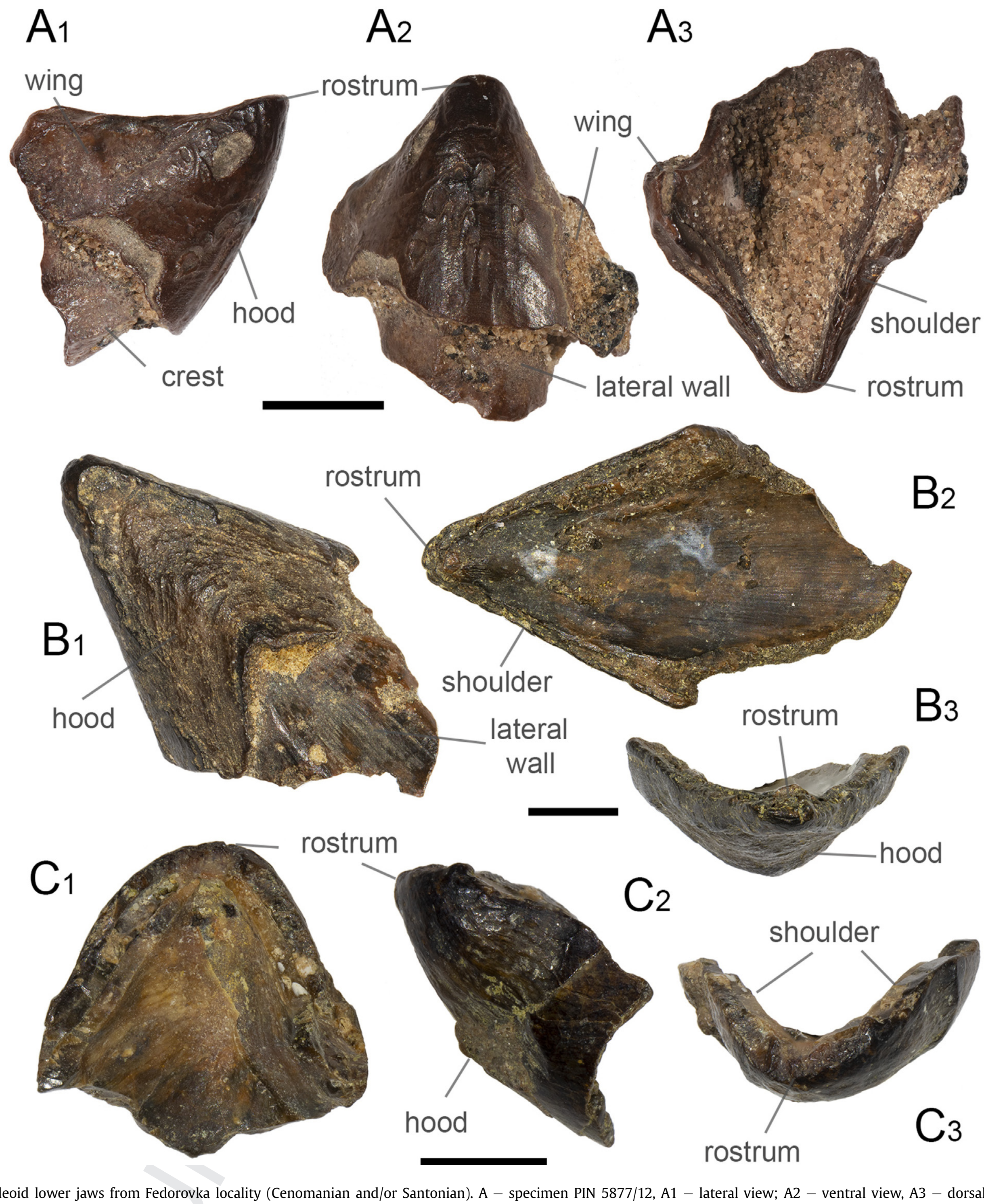

Fig. 5. Coleoid lower jaws from Fedorovka locality (Cenomanian and/or Santonian). A – specimen PIN 5877/12, A1 – lateral view; A2 – ventral view, A3 – dorsal view; B – specimen PIN 5877/11, B1 – ventral view, B2 – dorsal view, B3 – anterior view; C – specimen PIN 5877/10, C1 – ventral view, C2 – lateral view, C3 – anterior view. Scale bars are 5 mm.

phylloceratins of the genus *Boreophylloceras* are known from the Lower Cretaceous deposits, but they are absent in the Upper Cretaceous and directly in the Turonian. Therefore, all ammonoids should be excluded from the list of potential hosts for the jaw specimens described herein.

The jaws of two other groups of cephalopods – Nautilida and Coleoidea – usually can be easily distinguished by the proportions of the outer and inner lamellae. In nautilids, the outer lamella of the lower jaw is always larger and longer than the inner one, while in coleoids, on the contrary, the outer lamella of the lower jaw is short, while the inner one is large and wide (Saunders et al., 1978). Additionally, the lower jaws of nautilids have a much wider and more rounded anterior margin (see Saunders et al., 1978: pl. 9). Moreover, the jaws of coleoids are completely organic, whereas the jaws of nautilids have calcitic elements – a conchorhynch in the lower jaw and a rhyncholite in the upper one (Saunders et al., 1978;

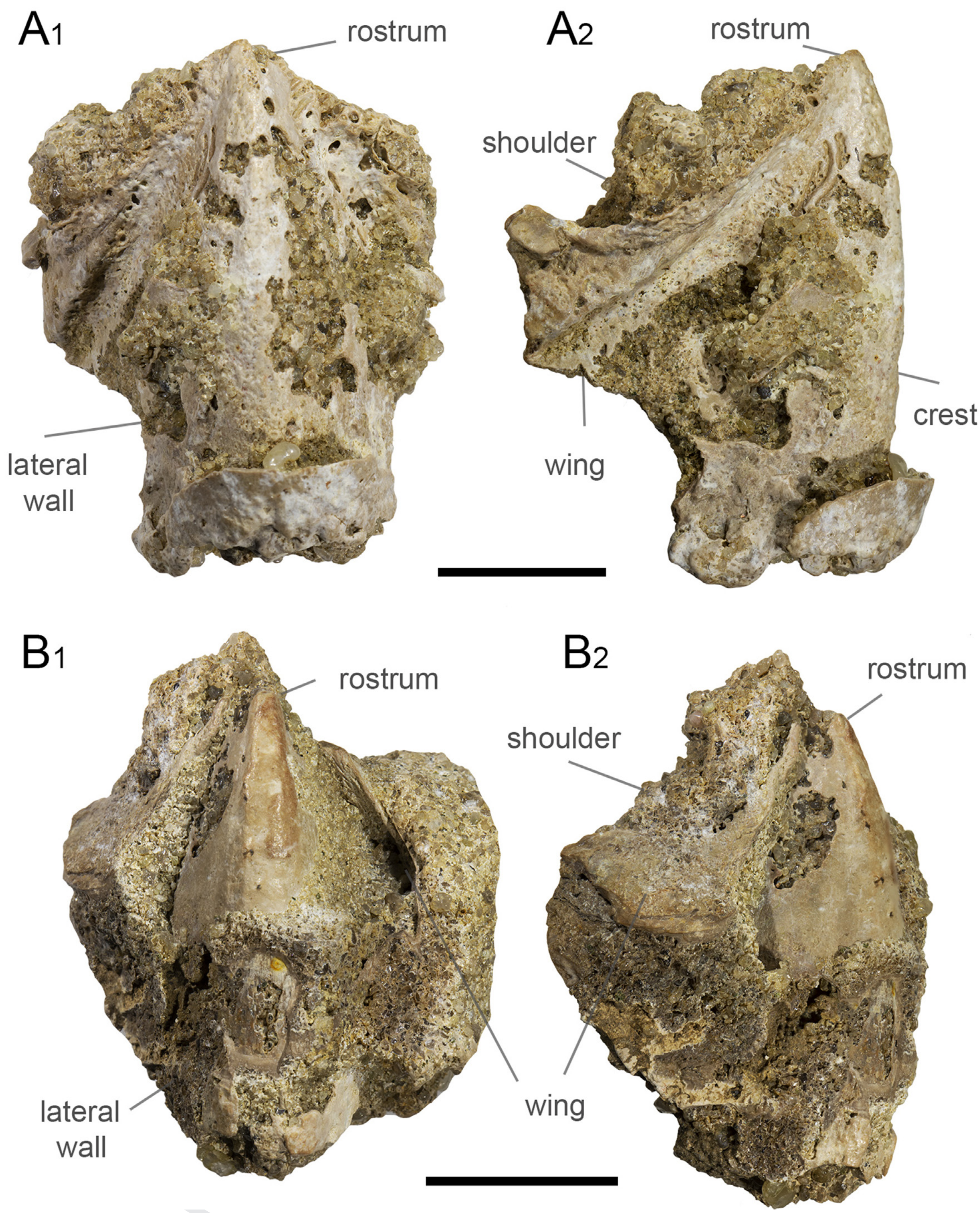

Fig. 6. Coleoid lower jaws from Malogolubinsky locality (Albian). A — specimen PIN 5877/19, A1 — ventral view; A2 — lateral view; B — specimen PIN 5877/20, B1 — ventral view, B2 — lateral view. Scale bars are 1 cm.

Klug, 2001; Klug et al., 2021a). The structure of the upper jaws of coleoids and nautilids in general is similar, but they can be easily distinguished by the presence of a calcitic tip — a rhyncholite — in the anterior part of nautilid jaws.

Unfortunately, the incomplete preservation of the posterior part of the lower jaws from sandy deposits (see Figs. 4A, 5B,C, 8) makes it somewhat difficult to recognize the original proportions of both lamellae of many specimens. However, one specimen, the lower jaw PIN 5877/1 (Fig. 4A) has almost equal length of both lamellae and a very wide anterior margin, considerably wider and more rounded than the rest of the specimens. Such proportions are not typical for coleoid jaws. In addition, the dorso-ventral compression of its anterior part resembles the imprint of a calcitic covering (see Tanabe et al., 2015a: F ig. 10.3) which could have been located in this area, but was destroyed or dissolved after the death of the mollusk. Therefore, it seems most likely that the specimen PIN 5877/1 (Fig. 4A) is a lower jaw of a nautilid.

Other lower jaw specimens, on the contrary, show clear characteristics of the coleoid lower jaws (Figs. 4B, 5, 6). Their outer lamellae are clearly shorter than the inner ones, and this is not related with the incomplete preservation of these specimens. Their general shape is also quite consistent with the shape of the coleoid

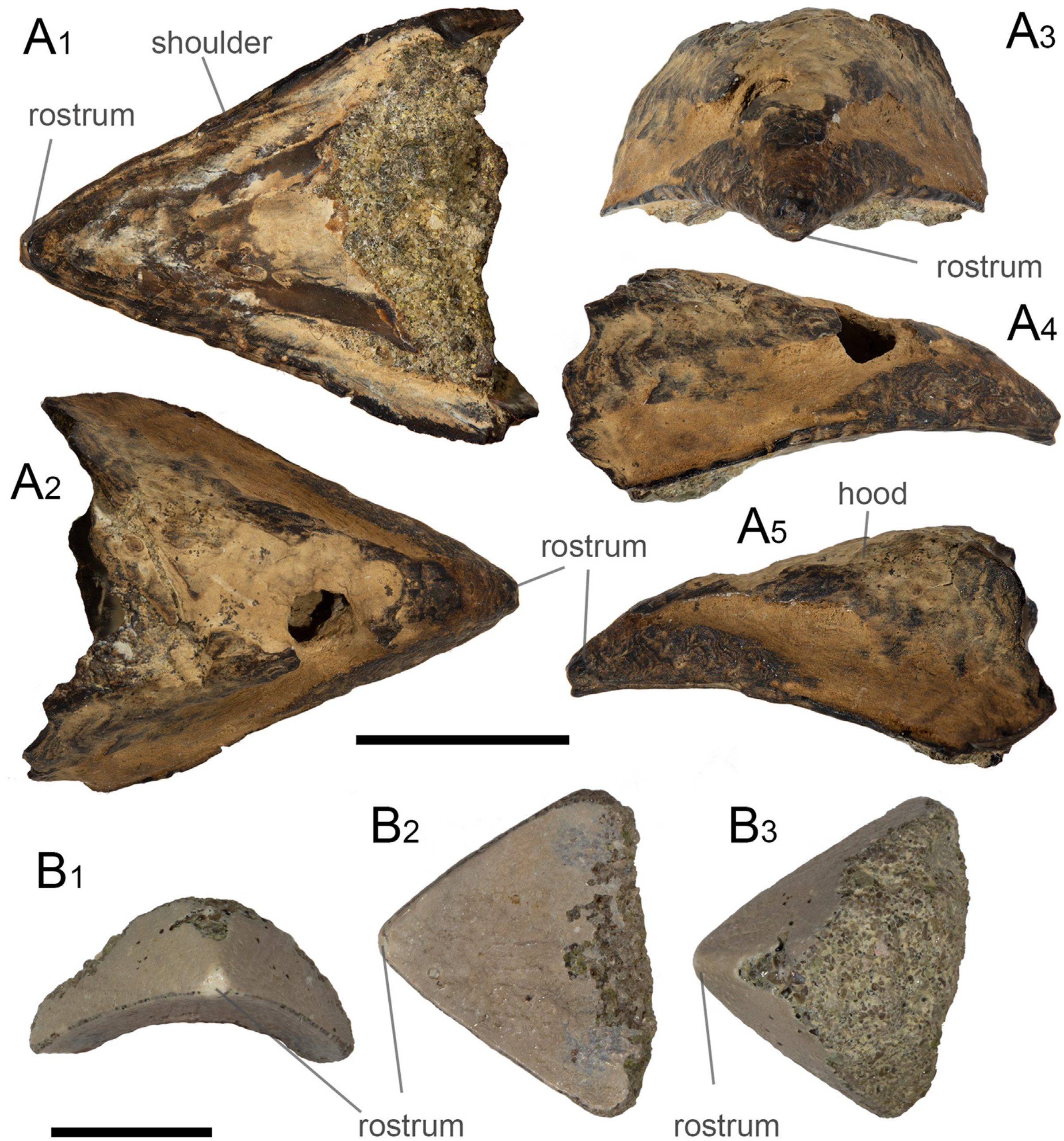

Fig. 7. Coleoid upper jaws. A – specimen PIN 5877/13 from Fedorovka locality (Cenomanian or Santonian), A1 – ventral view; A2 – dorsal view, A3 – anterior view, A4 and A5 – lateral views. Scale bar – 1 cm. B – specimen PIN 5877/7 from Malyy Prolom (Cenomanian), B1 – anterior view, B2 – ventral view, B3 – dorsal view. Scale bar – 5 mm.

lower jaws (see Fig. 3B). Upper jaws (Fig. 7), do not have any traces of calcitic rhyncholites. Rhyncholites are robust structures deeply embedded in the jaw, and they cannot collapse without leaving a trace. Therefore, these upper jaws also belong to coleoids. The poorly preserved specimens, whose proportions and original shape are difficult to recognize (Fig. 8), clearly show similarities with the jaws discussed above, so most likely they also belong to the coleoid cephalopods.

4.2. Overview of the jaws of fossil coleoids

It is worth discussing which of the diverse coleoid taxa could have been the hosts of these jaws. Among the Coleoidea in the Late Cretaceous, as in modern seas, there were two main evolutionary branches: octobrachians and decabrachians. The jaws in these groups are similar, but can be distinguished. The lower jaws of modern decabrachians have a more pointed anterior tip (rostrum), and when viewed from above or below, the lateral walls of the anterior part of the jaw form an acute angle (Tanabe 2012: fig. 3). Fossil decabrachian jaws have the same pointed anterior rostra (Tanabe et al., 2015b: fig. 7). The same is true for the decabrachian upper jaws: they have elongated pointed rostra (Tanabe et al., 2006: fig. 1; Klug et al., 2020b: fig. 2d). The jaws of octobrachians, in general, have a shorter rostrum with a rounded tip. The only exception is the modern *Vampyroteuthis infernalis*, which also has a pointed anterior part of the lower jaw, however, its lower jaws are

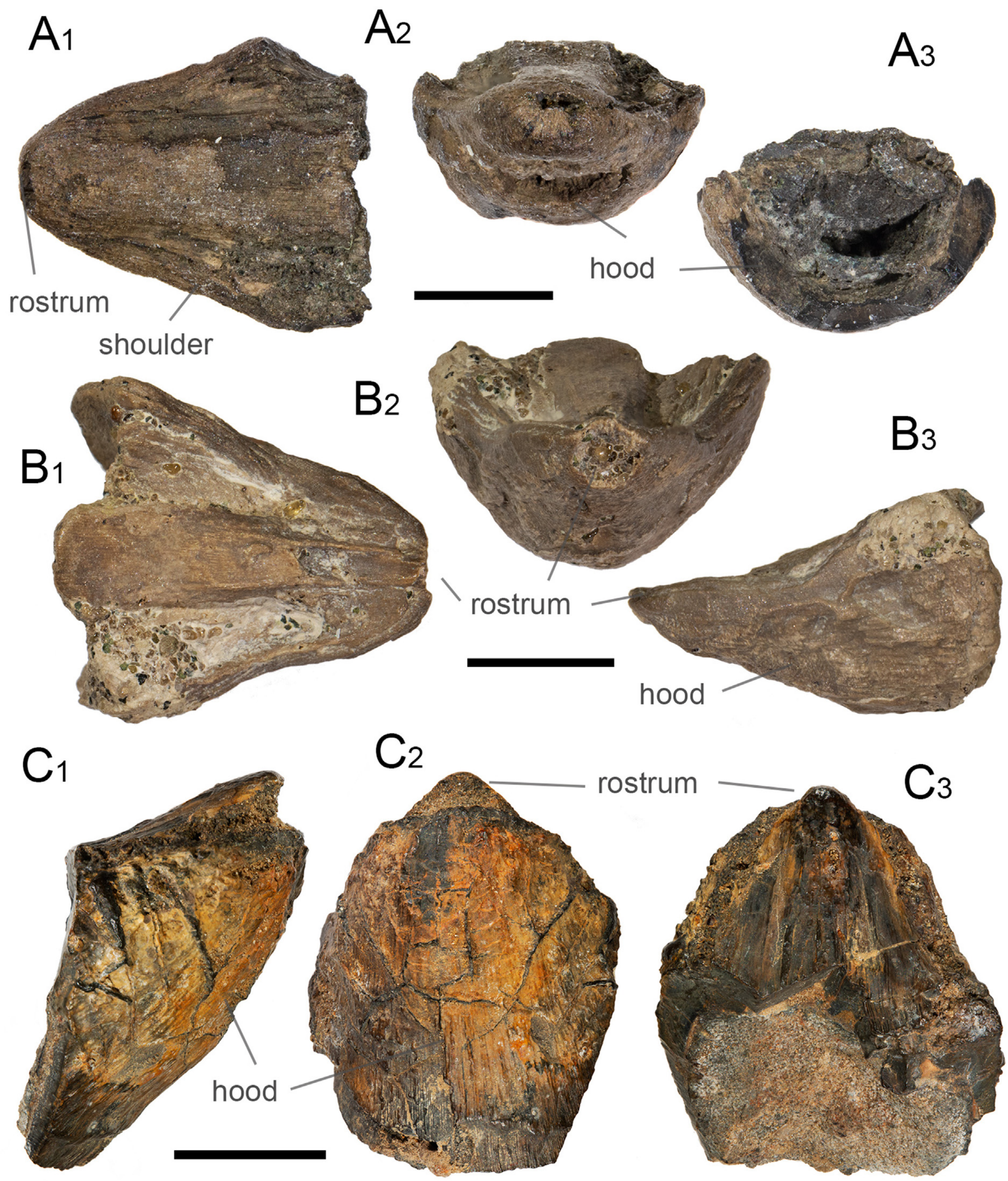

Fig. 8. Presumable coleoid lower jaws from various localities. A — PIN 5877/17 from Kapotnya locality (Upper Jurassic, Volgian), A1 — dorsal view; A2 — anterior view, A3 — posterior view; B — PIN 5877/15 from Beloe ozero locality (Campanian), B1 — dorsal view, B2 — anterior view, B3 — lateral view; C — PIN 5877/16 from Yangoda river (Turonian), C1 — lateral view, C2 — ventral view, C3 — dorsal view. Scale bars 5 mm for A and B and 1 cm for C.

easily distinguished from those of Decabrachia by having a widely open and larger outer lamella (see Clarke 1986: fig. 126; Tanabe 2012: fig. 3.9a,b).

Among fossil decabrachian coleoids, Belemnitida has the most abundant fossil record. The abundance of belemnites in the Jurassic and Cretaceous strata is caused by the presence of a solid structure - a rostrum in their body. The rostrum is mostly composed of low-magnesium calcite and can be well preserved under a wide variety of conditions. Sometimes belemnite rostra form massive accumulations called “belemnite battlefields” (Doyle and Macdonald, 1993). However, paradoxically, the jaws of belemnites are among the rarest and poorly known cephalopod jaws. Reitner and Urlichs (1983) described a belemnite *Acrocoelites (Toarcibelus) raui* from the lower Toarcian (Posidonienschiefer) of Germany with jaws *in situ*, but its poor preservation does not allow any recognition of morphological details. Klug et al. (2010a) described a belemnite arm crown with both well-preserved upper and lower jaws. The authors assigned this specimen to *Hibolithes semisulcatus*, however, due to the absence of a rostrum in this specimen, this definition remains speculative. Upper and lower jaws of coleoids, probably belemnites, have also been described from the upper Callovian of Poland by Dzik (1986), and the lower Callovian of Russia by Keupp and Mitta (2013). Two large jaws, upper and lower, were recently described from the Aalenian of Switzerland (Klug et al., 2020b) and assigned to megateuthidid belemnite *Acrocoelites conoideus*. However, both these Aalenian and Callovian specimens were found separately from the rostra or body imprints of mollusks and their relation with belemnites is determined only tentatively. Another isolated upper jaw with a pointed and slightly curved rostrum, most likely belonged to belemnites, has recently been described from the upper Bajocian (Middle Jurassic) of the Northern Caucasus (Mironenko and Mitta, 2020).

Findings of the jaws of another decabrachian group, teuthids, are also very rare. Whereas the oldest imprint of an unambiguous squid body known to date is described from the lower Oligocene of Russia (Mironenko et al., 2021), the upper jaws of possible teuthid affinity are known from the Campanian of Hokkaido, Japan. They are assigned to the species *Yezoteuthis giganteus* (Tanabe et al., 2006). As is clear from the species name, the jaw has a large size (the length of the holotype is 97 mm). The lower jaws with possible teuthid affinity, from the upper Santonian of Hokkaido, assigned to the species *Haboroteuthis poseidon*, are somewhat smaller (67 mm long), but this is also a very large size for teuthid jaws. The detailed stratigraphic distribution of these Pacific coleoid jaws is described in Tanabe et al. (2017). All decabrachian jaws, both lower and especially upper, are distinguished by pointed tips (rostra).

The jaws of “fossil teuthids”, gladius-bearing Mesozoic coleoids, which are currently considered by most researchers as octobrachians, are more common in fossil state. Numerous findings of such jaws, including specimens preserved *in situ*, are known from the upper Kimmeridgian Lithographic Limestone of Nusplingen, Germany. The jaw elements of following taxa are described from these famous deposits: *Trachyteuthis hastiformis*, *Plesioteuthis prisca*, and *Leptotheuthis gigas* (Klug et al., 2005, 2010b). From the Toarcian Posidonienschiefer of Holzmaden, Germany two coleoids *Parabelopeltis fexuosa* and *Jeletzkyteuthis coriacea*, have recently been described as dying together, with a preserved jaw apparatus, however, the shape and structure of their jaws are difficult to recognize (Klug et al., 2021b). The possible jaws of Vampyromorpha and Cirroctopoda were also described from the lower Callovian of Russia (Keupp and Mitta, 2013). However, this assumption is most likely erroneous since these specimens are almost identical to the outer lamellae of the upper jaw of aptychophoran ammonites (see Mitta and Mironenko 2021: fig. 7 and Mironenko and Mitta 2023: fig. 5A-C) and most likely belonged to the kosmoceratid and cardioceratid ammonites, the inner lamellae of the upper jaw of which are found in the same concretions (Keupp and Mitta, 2013: fig. 17). Moreover, these jaws were originally described as ammonite upper beaks (Mitta and Keupp, 2007). It is also likely that some of the coleoid jaws described by Dzik (1986) also actually belong to ammonites (upper jaws of coleoid type A, Dzik 1986: fig. 2B,C,D).

Findings of the jaws of octobrachians are especially numerous in the Upper Cretaceous strata. Some of them are preserved *in situ*, such as in the specimens, which were identified as *Glyphiteuthis libanotica* from the Cenomanian and the Santonian of Lebanon (Fuchs and Larson, 2011). Others are found as isolated specimens, which makes it somewhat difficult to determine their hosts, such as individual lower jaws from the upper Maastrichtian of Greece, which may belong to Vampyromorpha, but also resemble the ammonoid anaptychi (Klug et al., 2020a). The most interesting findings of octobrachian jaws come from the Turonian, Santonian, and Campanian of the Pacific regions, from several localities of Hokkaido, Japan and Vancouver Island, Canada. The lower jaws of Vampyromorpha are described from there, assigned to the genus *Nanaimoteuthis* in Tanabe et al., 2008 (the species *Nanaimoteuthis jeletzkyi*, *Nanaimoteuthis hikidai*, *Nanaimoteuthis yokotai*) and to the Cirroctopoda: *Paleocirroteuthis* in Tanabe et al., 2008 (the species *Paleocirroteuthis pacifca*, *Paleocirroteuthis haggarti*) (Tanabe et al., 2008, 2015b, 2017; Tanabe and Hikida, 2010; Tanabe 2012). It is worth noting that all these jaws are very large, for example, the holotype of *N. jeletzkyi* is 54.0 mm in maximum length (Tanabe et al., 2008), *N. hikidai* is even 90.4 mm in length and 87 mm in width (Tanabe et al., 2015b), and *P. haggarti* - 78.2 mm in maximum width of outer lamella (Tanabe et al., 2008), etc. Such big jaws indicate very large sizes of their hosts, much larger than the size of modern Vampyromorpha and Cirroctopoda. Although the upper and lower jaws of the various modern and fossil octobracians differ from one another, they can generally be distinguished from the jaws of the decabrachian jaws by their more rounded anterior tips.

4.3. Comparison of the studied specimens with previously described coleoid jaws

Therefore, fossil coleoid jaws show some important differences. The jaws of “fossil teuthids”, currently considered as jaws of octobrachians, such as *Trachyteuthis hastiformis*, *Plesioteuthis prisca* and *Leptotheuthis gigas* have a distinctly rounded anterior margin (Klug et al., 2005). Exactly the same rounded rostral tips are visible in the jaws from the Upper Cretaceous of Hokkaido, and Vancouver Island (Tanabe et al., 2008, 2015b, 2017; Tanabe and Hikida, 2010; Tanabe 2012). All lower jaw specimens from the sandy deposits studied here also have broad anterior rostra that are more rounded than pointed, suggesting that most likely they belong to octobrachian coleoids.

The upper jaws of decabrachians also differ from those of octobrachians in having a more pointed and often hooked rostrum (Tanabe et al., 2006: fig. 1; Klug et al., 2020b: fig. 2d). There is no such downwardly curved tip on the upper jaws described herein, which also confirms the hypothesis that their hosts belonged to octobrachians.

It is difficult to precisely determine which taxa among octobrachian coleoids were the hosts of these jaws. Although lower jaws of both Vampyromorpha and Cirroctopoda are known from the Upper Cretaceous strata of the Pacific region (*Nanaimoteuthis* and *Paleocirroteuthis* respectively), they were found not *in situ* and the taxonomic affiliation of their hosts was determined by indirect evidence. Moreover, they were found in concretions and, in general, are better preserved than findings from sandy deposits. Therefore, comparison of our specimens with them will not lead to reliable conclusions. Given the limitations in the degree of preservation of specimens and of our knowledge of the Late Cretaceous coleoid fauna, a more detailed definition of the taxonomic affiliation of their hosts would be too speculative.

It is also worth considering that, as a recent study showed (Roscian et al. 2022), the shape of the jaws of modern coleoid cephalopods is related with their feeding strategies and habitats. In the Mesozoic seas, representatives of the octobrachians and decabrachians could have occupied ecological niches that differed from those of their modern descendants. Therefore, the close resemblance of their jaws with the jaws of modern coleoids in some cases can be associated not only with a close genetic relationship, but also with a convergence due to a similar mode of life, and this fact may limit our interpretations.

4.4. Giant coleoids from the Boreal and epeiric seas

It is interesting to note that although the aforementioned jaws from the Pacific region (Tanabe et al., 2008, 2015b, 2017; Tanabe and Hikida, 2010; Tanabe 2012; Tanabe and Misaki, 2023) are the largest fossil coleoid mouth parts known so far, some of the findings described herein are also very large. The largest among these specimens are the central part of the lower jaw from Yangoda river (Fig. 8C), in which the thickness of the outer lamella exceeds 5 mm, and the anterior part of the upper jaw from Inokovka-2 locality (Fig. 7A), whose original size could exceed 6–7 cm. Albian lower jaws from Malogolubinsky locality are also large: their size exceed 2.5 cm and their anterior parts are not fully preserved. All these specimens are quite comparable in terms of their size with the findings from Hokkaido and Vancouver Island (Tanabe et al., 2008, 2015b, 2017; Tanabe and Hikida, 2010; Tanabe 2012; Tanabe and Misaki, n 2023). Therefore, very large coleoids inhabited not only in the North Pacific Ocean., but also the Boreal seas and even the epeiric seas of Central Russia during the Late Cretaceous Period. Nevertheless, of course, the sizes of most jaw specimens from coastal deposits of shallow epeiric seas are much smaller.

5. Conclusions

Phosphatized jaws of cephalopods have been found for the first time not only in concretions or layered clays and shales, but in sandy facies, formed in a shallow-water coastal environment. Most of the cephalopod jaws from the Mesozoic (mostly Upper Cretaceous) sandy deposits, judging by their shape and proportions, belong to octobrachian coleoids. A more precise identification is not possible to date due to the imperfect preservation of the specimens and general lack of knowledge about octobrachian coleoid fauna of the Cretaceous of the studied region. However, it can be assumed that most of the jaw specimens belonged to the Vampyromorpha, the most widespread group of Mesozoic octobrachians. Only one of the lower jaws, judging by its shape, likely belonged not to coleoids, but to a representative of Nautilida. Some of the studied coleoid jaws are quite large, indicating a large body size of their hosts.

The dynamic environment of the coastal waters and the abrasive properties of sand prevented the preservation of soft tissues of cephalopods and even (in most cases) their shells. However, under these conditions, as it turned out, the jaws of cephalopod mollusks were preserved due to phosphatization process. And now these jaws provide a “window” into the past, which allows researchers to assess the diversity and abundance of cephalopods that lived in shallow-water coastal environments. This is especially important for the study of non-belemnoid coleoids, the findings of which are extremely rare in a fossil state outside of Konservat-Lagerstätten localities.

Although the vast majority of specimens were found in Upper Cretaceous deposits, the discovery of one of the jaws in the Upper Jurassic sands shows that the conditions for the preservation of coleoid jaws were not unique to the Cretaceous Sea. Therefore, such findings are possible not only in the Cretaceous beds, but most likely in all coastal sandy localities of the Mesozoic and Cenozoic. Cephalopod researchers should pay attention to sections, characterized by a large number of vertebrate findings (such as shark teeth, bones and teeth of marine reptiles and cartilaginous fish), because among these specimens the phosphatized cephalopod jaws can still be hidden and unidentified.

Author statement

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Uncited reference Q2

Mironenko, 2014.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

I am very grateful to Irina Shahurina (Ryazan), Dmitry Kucher (“Moscow children and youth center of ecology, local history and tourism”, Moscow), Maxim Arkhangelsky and A. Shchetinkin (Saratov State Technical University and Saratov State University, Saratov), Nikolay Zverkov and Mikhail Rogov (Geological Institute of Russian Academy of Sciences, Moscow), Sergei Lavrov (Moscow) for donation the findings of cephalopod jaws for this study and to Alexander Lebedev (Moscow) for providing photos from the Malyy Prolom quarry. The study of Cretaceous deposits of Yangoda river is supported by RFBR grant no. 20-55-26006. The excavations on the Q1 locality of Beloe Ozero were carried out by M.S. Arkhangelsky in 2017–2022 under the license from Saratov State Technical University, SRT 01881 PD. I am also very grateful to reviewers Kazushige Tanabe (University of Tokyo, Japan) and Martin Košťák (Charles University of Prague, Czech Republic)and the editor Eduardo Koutsoukos for their very useful comments, advice and criticism, which helped to greatly improve the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105687.