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Ventral Bite Marks (Ichnospecies *Bicrescomanducator rolli*): Lethal Injuries on the Shells of Jurassic Ammonites

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Abstract—Ichnofossils are fossilized traces of the biological activity of ancient organisms, which often shed light on the paleoecological interactions of extinct animals. Mesozoic ammonites are no exception: holes in the walls of their body chambers, attributed to the ichnospecies *Bicrescomanducator rolli* Donovan et al., indicate predator attacks that were lethal for the ammonites. In this paper we describe numerous findings of *B. rolli* (also known as ventral bite marks) on ammonite shells from the Middle and Upper Jurassic of European part of Russia. These findings demonstrate that the pressure of predators, which left ventral bite marks on the ammonite shells, gradually increased and reached a maximum at the end of the Jurassic. These predators were most likely various coleoids, including the ancestors of modern squids and octopuses. Not only *B. rolli* but other rare ichnofossils were found on the Jurassic ammonites: *Oichnus ovalis* Bromley and *Podichnus centrifugalis* Bromley et Surlyk.

Keywords: ventral bite marks, paleoecology, ammonites, Jurassic, ichnofossils, *Bicrescomanducator*, *Bicrescomanducator rolli*

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INTRODUCTION

In the Jurassic, ammonites were a significant component of marine ecosystems, being numerous and diverse. They were hunted by a wide variety of predators: marine reptiles, fish, crustaceans, and cephalopods (nautilids, coleoids, and other ammonites). To better understand which predators preyed on ammonites in each particular case, and how strong the pressure of these predators was in different ecosystems, paleontologists study injuries of ammonite shells (Hölder, 1956; Keupp, 2012; Mironenko, 2017a).

Typically, these are healed injuries, which are relatively easy to recognize on fossil shells, and, in the case of healed injury, it must have been inflicted during the life of the ammonite. However, in order to obtain a complete picture of the interactions between ammonites and their predators, it is necessary to also study the injuries that led to the death of the mollusks. This poses a problem, because they must be clearly distinguished from postmortem injuries that occurred on shells due to the action of scavengers, bottom-boring organisms, compaction of the sediment in which the shell was buried, or other taphonomic factors.

Except for rare cases when the shell bears direct imprints of the shape of the jaws and teeth of the predator that attacked it (Kauffman and Kesling, 1960; Tsujita and Westermann, 2001; Martill, 1990; Richter, 2009), there are two ways to distinguish fatal injuries from postmortem damage to shells. First, an analogy can be drawn between damage to shells that do not bear signs of healing, with similar healed damage. Thus, deep cuts on the ventral side of the shells of the Upper Volgian ammonites *Kachpurites* Spath and *Craspedites* Pavlow are found both healed and without signs of healing, their comparison leaves no doubt that both are traces of predator attacks, which ended differently for the ammonites (Mironenko, 2020). Secondly, injuries located in a strictly defined place on the shell and having a similar morphology can be confidently attributed to traces of predator attacks. These, about twenty years ago, served as the basis for the first identification of such injuries as ventral bite marks.

Larson (2003) was the first to draw attention to these injuries. He provided images of four scaphitid shells from the Upper Cretaceous of the USA, belonging to the genera *Discoscaphites* Meek and *Hoploscaphites* Nowak with holes in the base of the body chambers and noted that such uniform damage was present on 17 of the 57 specimens he studied. Six years later, in 2009, a fundamental study was published describing ammonites with uniform holes in the base of the body chamber, slightly anterior to the last septum of the phragmocone. The authors of this study examined several dozen large collections of the Triassic, Jurassic and Cretaceous ammonites (Klompmaker et al., 2009). The geography of the studied collections covered almost all of Western Europe; ammonites from Indonesia, Africa and Australia were also studied. This study showed that between 5% and 50% of ammonites from Mesozoic deposits have characteristic holes at the base of the body chamber. The authors coined a new term to describe these holes: ventral bite marks.

Later, ventral bite marks were described from the Lower Jurassic of Great Britain (Andrew et al., 2010, 2015; Maddra, 2015) and Japan (Takeda and Tanabe, 2015), the Upper Jurassic of Great Britain (Wright et al., 2014), and the Upper Cretaceous of Mexico (Ifrim, 2013) and the USA (Landman et al., 2012; Takeda et al., 2016; Tajika et al., 2025). In 2010, new ichnotaxa were established for such injuries: the ichnogenus *Bicrescomanducator* Donovan et al. with the ichnospecies *Bicrescomanducator rolli* Donovan et al. (Andrew et al., 2010).

Ventral bite marks (=*Bicrescomanducator rolli*) are holes, usually located at the base of the body chamber at a short distance from the last septum (Andrew et al., 2010, text-figs. 4–6) (Fig. 1). However, in some cases, this ichnotaxon includes holes located quite far from the phragmocone, in the middle of the body chamber or even closer to the aperture (Klompmaker et al., 2009, text-fig. 6D; Andrew et al., 2010, text-fig. 8). In rare cases, the injury may also affect the last 1–3 septa of the phragmocone. The holes are usually asymmetrical and on one side of the shell can be one and a half times to twice as deep as on the other, although specimens with relatively symmetrical holes are also known. The edges are often uneven, but on one of the lateral sides a semicircular hole with a relatively smooth edge may be observed (Mironenko, 2012, pl. I, fig. b). In some cases, a section of the shell may be broken off together with the umbilical wall. The apertural margin of the shell usually remains intact. The hypothesis that such damage appeared while the animal was alive is also supported by the absence of broken fragments in the immediate vicinity of the damaged shell, while such fragments are preserved nearby when a shell is damaged by taphonomic processes (Klompmaker et al., 2009; Andrew et al., 2010). As noted by many researchers (Klompmaker et al., 2009; Andrew et al., 2010; Tajika et al., 2025), the holes located in the posterior part of the body chamber often correspond to the so-called ventro-lateral muscle scars—the areas of attachment to the shell of the largest ammonite retractor muscles (Doguzhaeva and Mutvei, 1991; Mironenko, 2015a; Mironenko, 2017b). Due to the additional layers of aragonite in the area of muscle attachment, this part of the body chamber has the thickest walls, which eliminates the possibility of accidental destruction of these areas during taphonomic processes. However, a bite in this area was guaranteed to destroy the two largest muscle attachment sites and could damage the three remaining retractor muscles, the attachment sites of which were located behind, directly at the last septum of the phragmocone (see Mironenko, 2017b)

Ventral bite marks from Russian localities have been described and illustrated three times (Mironenko, 2012, 2017a; Sherstyukov and Shekhanov, 2017). Occurrences from the upper Volgian, middle Callovian, and upper Bajocian were described. However, the distribution of the ichnotaxon *Bicrescomanducator rolli* from the Jurassic of Russia has not been studied in detail. In this paper, we describe occurrences of *Bicrescomanducator rolli* from 19 Jurassic localities in Central Russia, the Volga region, and the Northern Caucasus. They were found on ammonite shells from the upper Bajocian to the upper Volgian inclusive.

MATERIAL AND METHODS

We studied extensive material on ammonites collected by the staff of the Geological Institute of the Russian Academy of Sciences and amateur paleontologists from 25 Jurassic localities in European Russia during 2010–2024. Traces of ventral bites (ichnospecies *B. rolli*) were found on ammonites from 19 localities in 10 regions, including 18 localities on the Russian platform (Fig. 2). These ammonites belong to the following genera: *Rarecostites* Beznosov et Kutuzova, *Gulielmiceras* Buckman, *Kepplerites* Neumayr et Uhlig, *Kosmoceras* Waagen, *Indosphinctes* Spath, *Anaplanulites* Buckman, *Binatisphinctes* Buckman, *Sublunuloceras* Spath, *Brightia* Rollier, *Perisphinctes* Waagen, *Dichotomosphinctes* Buckman, *Cardioceras* Neumayr et Uhlig, *Amoeboceras* Hyatt, *Paramoeboceras* Gerassimov, *Plasmatites* Buckman, *Prionodoceras* Buckman, *Glochiceras* Hyatt, *Aulacostephanus* Tornquist, *Zaraiskites* Semenov, *Pavlovia* Ilovaisky, *Craspedites* Pavlow, *Kachpurites* Spath, and *Garniericeras* Spath. The stratigraphic reference of the finds is as follows: Middle Jurassic–Upper Bajocian, Lower and Middle Callovian (Fig. 3), Upper Jurassic–Lower Oxfordian (Fig. 4), Upper Oxfordian (Fig. 5), Lower and Upper Kimmeridgian (Fig. 6), Middle Volgian (Fig. 7) and Upper Volgian (Fig. 8). For more details, see Table 1.

Ammonites with *B. rolli* were found in lithologically different beds: in black bituminous clays, black shales, spongolite and marl nodules, nodules of phosphatized sand and even in sandy strata (Table 1). All these deposits were formed in the epicontinental Central Russian Sea, but at different depths and distances from the coastline. Thus, thin-layered black clays and shales were formed in relatively deep-sea environments below the storm wave base, and nodules of oolitic marl and sand strata with phosphatized nodules arose in much shallower waters closer to the coast.

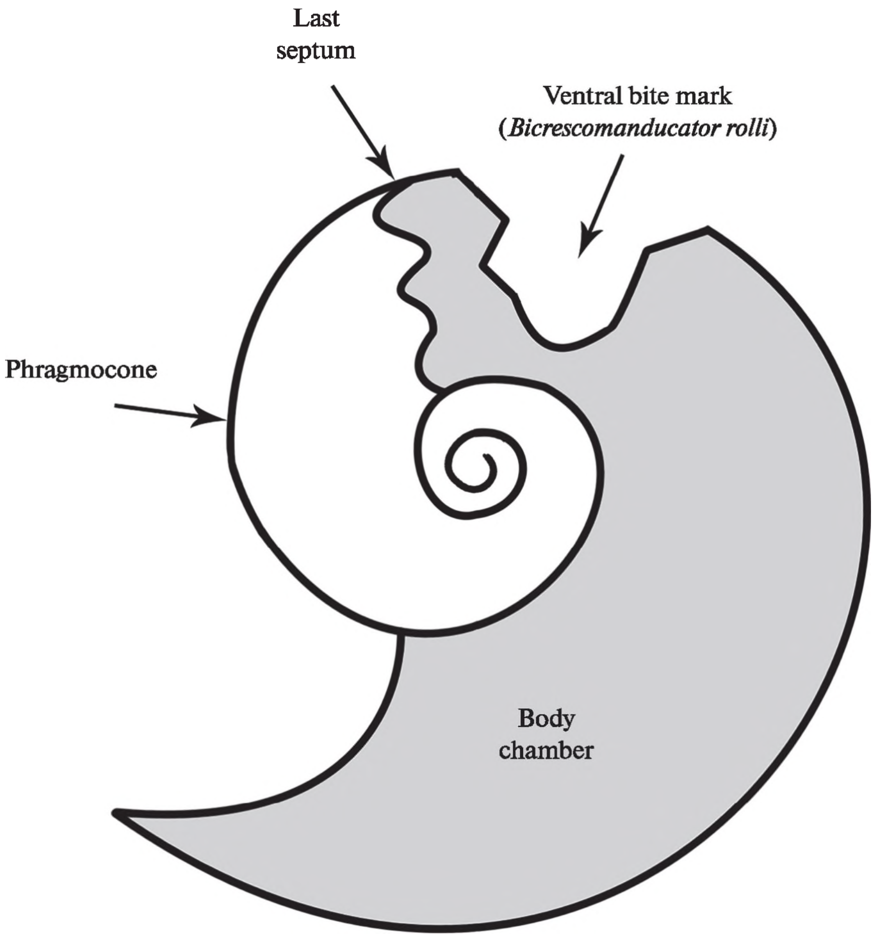

Fig. 1. Schematic drawing of a ventral bite mark (*Bicrescomanducator rolli*) on a Jurassic ammonite shell.

The main condition for searching for traces of ventral bites is the good preservation of the body chambers of ammonites. Firstly, they should be preserved (which is not observed everywhere), and secondly, they should not have been subjected to significant postmortem damage, which could lead to the appearance of holes which may be confused with bite marks. For these reasons, for example, the Upper Volgian zones *Catenulatum* in Eganovo and *Catenulatum–Nodiger* in Kashpir (see Rogov, 2017, 2021) were excluded from the study, where the body chambers of ammonites were subjected to very strong postmortem destruction. At the same time, those localities are quite suitable for searching for ventral bites in which only body chambers filled with lithified sediment from the aperture to the last septum have been preserved, and the remaining empty phragmocones were completely or partially destroyed.

In some localities (Mikhailovcement, Markovo, Rybaki—see Table 1), pyritized ammonite phragmocones with an original aragonite shell layer are well preserved (see Mironenko, 2015b), but the body chambers in most cases were flattened and fragmented during compaction of the clay sediment. Very careful collection of ammonites with a section of the host rock in these localities makes it possible to detect and preserve traces of ventral bites on the crushed body chambers. However, it is impossible to establish the percentage of shells with ventral bites to the total number of ammonite occurrences in such beds, since most specimens in private and scientific collections are phragmocones without body chambers.

The ammonites were studied using light binocular microscopes. Most of the studied specimens are housed in the Geological Institute of the Russian Academy of Sciences (Moscow), collection No. GIN MPC 11. Specimens from the Kyafar River are housed in the collection of M.P. Sherstyukov (Stavropol). We also give a brief overview of other ichnofossils found on ammonite shells; they are stored in the collection of the Geological Institute No. GIN MPC 10.

RESULTS

The Jurassic ammonite shells that we found with *B. rolli* on the body chambers belong to 23 genera of

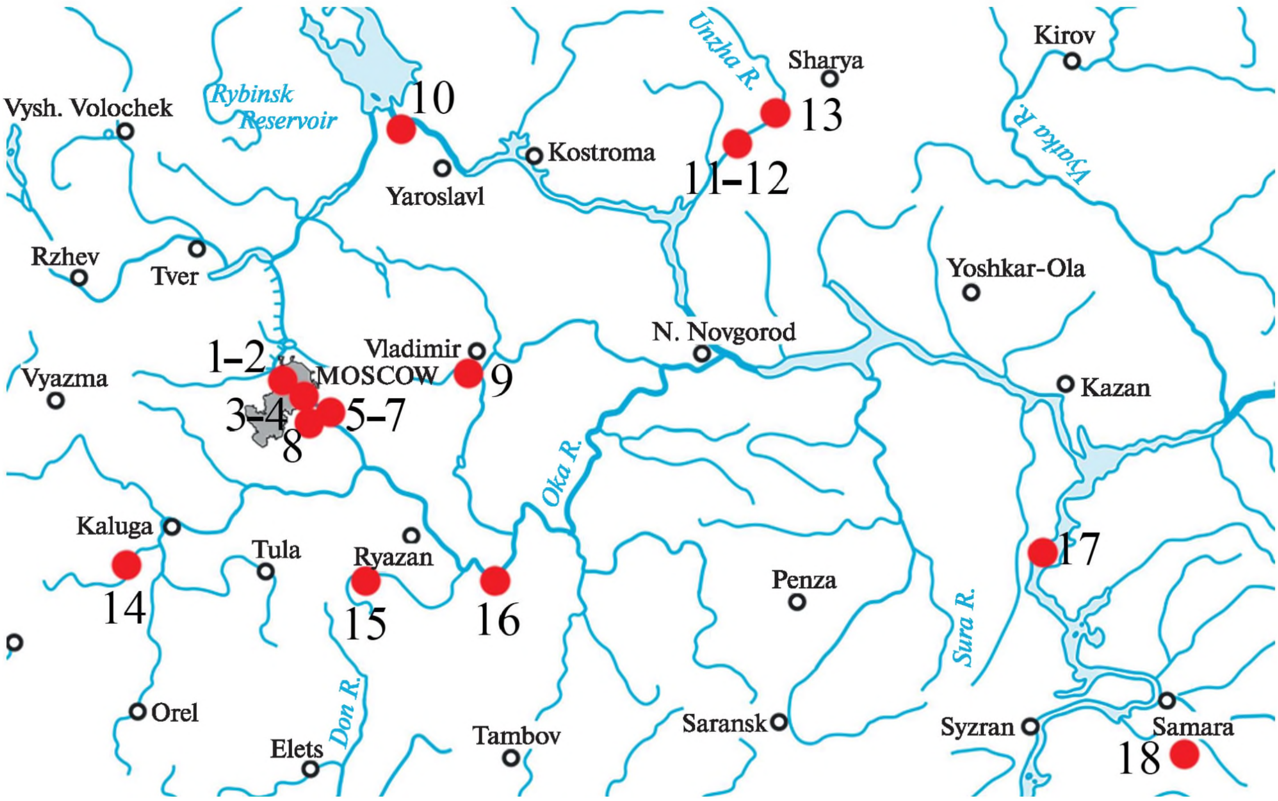

Fig. 2. Map of locations where Jurassic ammonites with ventral bite marks have been found. (1) Mnevniki (55°46′03.7″ N 37°28′26.4″ E), (2) Kuntsevo (55°44′30.8″ N 37°26′24.0″ E), (3) Moskvorechye (55°38′28.6″ N 37°42′00.1″ E), (4) Milkovo (55°36′34.9″ N 37°48′03.6″ E), (5) Rybaki (55°28′29.3″ N 38°13′28.6″ E), (6) Markovo (55°26′36.7″ N 38°15′06.9″ E), (7) Borsheva (55°23′49.4″ N 38°19′27.2″ E), (8) Eganova (55°32′15.7″ N 38°03′46.8″ E), (9) Bolgary (56°00′32.4″ N 40°06′31.3″ E), (10) Cheremukha River (57°58′08.4″ N 38°52′42.2″ E), (11) Mikhalenino (57°58′41.8″ N 43°59′38.8″ E), (12) Znamenka (58°23′23.1″ N 44°51′33.3″ E), (13) Ivkino (58°14′35.9″ N 44°39′28.8″ E), (14) Lipitsy (54°18′31.4″ N 35°33′04.6″ E), (15) Mikhailovcement (54°12′35.2″ N 38°56′10.8″ E), (16) Nikitino (54°21′13.5″ N 40°24′25.5″ E), (17) Gorodishchi (54°34′27.2″ N 48°25′02.1″ E), (18) Yablonovyy ovrag (52°50′38.9″ N 50°24′35.9″ E).

ammonites of eight families of the suborder Ammonitina. These are the families Parkinsoniidae, Perisphinctidae, Kosmoceratidae, Cardioceratidae, Hecticoceratidae, Dorsoplanitidae, Virgatitidae, Craspeditidae. The greatest number of ventral bite marks were found on the shells of cardioceratids, craspeditids and virgatitids, the least—on kosmoceratids. The frequency of *B. rolli* occurrence varies from single finds (a fraction of a percent) to 40% of the total number of ammonite shells in a particular horizon.

Ventral bite marks are clearly visible both on flat crushed body chambers and on three-dimensionally preserved specimens. However, *B. rolli* occurrences on 3-D-preserved shells (primarily Volgian Craspeditidae) provide more information: they allow the asymmetry of ventral bite marks to be evaluated. On almost all such shells, the bite depth on one side is twice as deep as on the other (Fig. 8).

The ventral bite marks in the ammonites studied here are mostly located in the posterior part of the body chamber at some distance from the last septum of the phragmocone, like in the previously described specimens. In the Callovian, Oxfordian and Kimmeridgian finds, the *B. rolli* holes are located approximately half a whorl away from the aperture, i.e., 160–180 degrees of circumference. This distance is almost independent of the length of the ammonite's body chamber (see Table 2). In the Volgian ammonites, primarily in the Virgatitidae and Craspeditidae, the distance from the aperture to the *B. rolli* hole is greater, ca. 250 degrees. This corresponds to the long body chamber of most representatives of these families. Only in the Upper Volgian craspeditids of the genus *Garniericeras* do ventral bite marks again appear half a turn from the aperture, since the body chamber of these ammonites was short.

In the vast majority of cases, traces of ventral bites were found on shells of relatively small size: 3–5 cm in diameter. The largest shells bearing such damage are the Middle Volgian *Zaraiskites* with a diameter of about 10–12 cm and the Upper Oxfordian *Dichotomosphinctes* with a diameter of 12–13 cm. This is consistent with the data from previous studies: the size of shells with *B. rolli* varies in the range of 1–4 cm and

Table 1. Finds of ventral bite marks (ichnospecies *B. rolli*) in the Jurassic deposits of Central Russia, the Volga region and the Northern Caucasus

Region, locality	Age	Taxon	Preservation type	Host rocks	Frequency of finds
Moscow Region, Milkovo (Rogov, 2017, 2021)	Upper Vogian, *Craspedites nodiger* Zone	*Craspedites*	Phosphatized three-dimensional body chambers	Sands with interbeds of phosphatized concretions	25%
Moscow, Mnevniki (Rogov, 2017)	Upper Volgian, *Kachpurites fulgens* Zone	*Kachpurites* *Craspedites*	Phosphatized three-dimensional shells, but often with poorly preserved phragmocones	Sands with admixture of clays and glauconite grains	5.5%
Moscow, Kuntsevo (Rogov, 2017)	Upper Volgian, *Kachpurites fulgens, Garniericeras catenulatum* Zones	*Kachpurites* *Craspedites* *Garniericeras*	Phosphatized three-dimensional shells, but often with poorly preserved phragmocones	Sands with admixture of clays and glauconite grains	5.8%
Yaroslavl Region, Cheryomukha River (Kiselev et al., 2018)	Upper Volgian, *Kachpurites fulgens, Garniericeras catenulatum* Zones	*Kachpurites* *Craspedites* *Garniericeras*	Clusters of phosphatized three-dimensional shells in concretions	Phosphatized sandstone concretion in sands	6%
Moscow Region, Eganovo (Rogov, 2017, 2021)	Upper Volgian, *Kachpurites fulgens* Zone	*Kachpurites* *Craspedites*	Phosphatized three-dimensional shells, often with poorly preserved phragmocones	Sands with admixture of clay and glauconite	5.5%
Kostroma Region, Ivkino (Gavrilov et al. 2008)	Middle Volgian, *Dorsoplanites panderi* Zone	*Pavlovia*	Flat impressions of whole shells in shale	Dark colored shale	16%
Samara Region, Yablonovy Ravine (Bukhman and Baranova, 2016)	Middle Volgian, *Dorsoplanites panderi* Zone	*Zaraiskites*	Flat impressions of whole shells in shale	Dark colored shales exposed to high temperatures	40%
Ulyanovsk Region, Gorodishchi (Rogov, 2021)	Middle Volgian, *Dorsoplanites panderi* Zone	*Zaraiskites*	Flat impressions of whole shells in shale	Dark colored shale	40%
Moscow, Brateevo-Moskvorechye	Middle Volgian, Dorsoplanites panderi Zone	*Zaraiskites*	Three-dimensional phosphatized molds	Phosphorite interbeds in clay	5%
Kaluga Region, Lipitsy (Rogov, 2021)	Upper Kimmeridgian, *Aulacostephanus eudoxus* Zone	*Aulacostephanus* *Glochiceras*	Three-dimensional molds with shell remains replaced by spongolite	Interbeds of spongolite concretions in clay	Very low
Vladimir Region, Bolgary (Rogov, 2017)	Lower Kimmeridgian, Plasmatites bauhinia Zone	*Plasmatites*	Flat impressions of whole shells in clay	Black clay	20%*
Moscow Region, Borsheva (Rogov, 2017)	Lower Kimmeridgian, Plasmatites bauhinia Zone	*Plasmatites*	Flat impressions of whole shells in clay	Black clay	14%*
Moscow Region, Rybaki (Rogov, 2017)	Upper Oxfordian, Zone Prionodoceras serratum	*Prionodoceras*	Phosphatized living chambers with pyritized phragmocones and flat impressions	Black clay	3.5%

Table 1. (Contd.)

Region, locality	Age	Taxon	Preservation type	Host rocks	Frequency of finds
Moscow Region, Markovo	Upper Oxfordian, *Amoeboceras alternoides* Zone	*Amoeboceras (Paramoeboceras)*	Three-dimensional pyritized shells and imprints	Black clay	1%**
Kostroma Region, Mikhalenino (Głowniak et al., 2010)	Upper Oxfordian, *Amoeboceras* alternoides Zone	*Amoeboceras Dichotomosphinctes*	Flat impressions of whole shells in clay	Black clay and shale	15%
Ryazan Region, Mikhailovcement (Kiselev and Rogov, 2018)	Lower Oxfordian, *Cardioceras cordatum* Zone	*Cardioceras Perisphinctes*	Three-dimensional pyritized shells	Dark colored clay	1%**
Ryazan Region, Mikhailovcement (Kiselev and Rogov, 2018)	Middle Callovian, *Erymnoceras coronatum* Zone	*Sublunuloceras Brightia Binatisphinctes Kosmoceras*	Pyritized phragmocones with flat impressions of body chambers and flat impressions of whole shells	Dark colored clay	1%**
Kostroma Region, Znamenka (Keupp and Mitta, 2013)	Lower Callovian, *Sigaloceras calloviense* Zone	*Rondiceras* juv. *Kepplerites* juv.	Phosphatized shells in concretions	Phosphated concretions in sands	Very low
Ryazan Region, Nikitino (Gulyaev, 2001)	Lower Callovian Zone *Sigaloceras calloviense*	*Anaplanulites Indosphinctes Gulielmiceras*	Three-dimensional shells with marl-filled body chambers	Oolitic marl concretions	Very low
Krasnodar Region, Kyafar (Mitta, 2017)	Upper Bajocian, *Parkinsonia parkinsoni* Zone	*Rarecostites*	Three-dimensional shells with marl-filled body chambers	Concretions in dark grey mudstones	3%

* Small sample of ammonites, ** small number of ammonites preserved with body chambers.

only two samples have a diameter of 5 and 10 cm, respectively (Andrew et al., 2010).

We also, for the first time, found two examples of healed ventral bites on Oxfordian perisphinctid ammonites of the genera *Perisphinctes* and *Dichotomosphinctes* (Figs. 4b, 9a).

DISCUSSION

First of all, it is noteworthy that not all damage to the ventral part of the shell can be attributed to the ichnotaxon *B. rolli*. Firstly, according to the definition of the taxon by the authors, *B. rolli* is located on the body chamber of the ammonite (Andrew et al., 2010). In some cases, one or more septa of the phragmocone are affected, but only on the marginal part of the opening. Of course, it is possible that a predator could have mistakenly bitten the phragmocone. This was the assumption made by the authors of a recent study, who described the first find of *B. rolli* on the phragmocone of the Jurassic nautilid *Cenoceras* Hyatt from Great Britain (Davis et al., 2023). However, in our opinion, this interpretation is erroneous: the edge of the opening has several rounded bends, while *B. rolli* is characterized by a maximum of one such bend. Most likely, in this case, the hole in the phragmocone appeared as a result of a fish attack on the head section of the nautilid, similar to the holes in the phragmocone of the modern *Nautilus macromphalus* Sowerby (Mapes and Chaffin, 2003, text-fig. 3) or the upper Callovian *Quenstedtoceras lamberti* Sowerby (Mironenko and Parkhomenko, 2023). Therefore, this damage to the phragmocone cannot be considered as *B. rolli* or a ventral bite mark in its original sense. In our study, no damage to the phragmocone morphologically similar to *B. rolli* was found on Jurassic ammonites.

It should also be taken into account that the width of *B. rolli* on the body chambers of ammonites cannot be very large. Apparently, it corresponds to a single bite of a predator. However, it cannot be ruled out that for some reason the predator could have inflicted two bites in a row: because of this, the width of the hole may be larger than usual. Nevertheless, if the specimen is missing half of the body chamber, then even if this is due to predator attack, it must be a different predator than that responsible for the ventral bites, i.e.

Table 2. The most abundant Jurassic ammonite taxa with ventral bite marks: body chamber length and position of *B. rolli* (in degrees of circumference)

Age	Taxon	Body chamber length	Average distance to the center of *B. rolli* from the last septum	Average distance to the center of *B. rolli* from the aperture
Volgian	*Garniericeras*	190°–200°	20°–30°	160°–180°
	Craspedites	320°–340°	60°–70°	250°–270°
	Kachpurites	270°–320°*	40°–60°	220°–250°
	Zaraiskites	320°–340°	70°–80°	250°–260°
Kimmeridgian	*Plasmatites*	190°–200°	10°–30°	160°–180°
Oxfordian	*Amoeboceras, Prionodoceras*	190°–200°	10°–30°	160°–180°
	Perisphinctes, Dichotomosphinctes	340°–360°	170°–180°	170°–180°

* The length of the body chamber of Kachpurites gradually shortened over the course of its evolution; in the more ancient species of this genus from the lower parts of the Fulgens Zone it is longer, in the younger species from the upper parts of the same zone it is shorter. In addition, in all taxa the length of the terminal body chamber may differ slightly from the length of the juvenile body chamber.

one capable of destroying a significantly larger part of the shell at once. In addition, long holes in the ventral part of the shell could have occurred as a result of the damaging effect of sediment in high energy settings, as was shown in experiments with modern nautiluses (Wani, 2004). Therefore, specimens with too much damage to the body chamber were also not taken into account in our study.

Geographical and Stratigraphic Distribution of B. rolli in Jurassic Deposits in Russia

Isolated single finds of ventral bite marks on ammonite shells are known from Paleozoic and Triassic deposits (Klompmaker et. al. 2009), but they become widespread starting from the Lower Jurassic. Thus, in the Sinemurian and Toarcian deposits of Great Britain and Germany, the number of specimens with such damage ranges from 6–25% (Andrew et. al., 2010, 2015) to 50% of the total number of shells studied (Klompmaker et. al. 2009).

In Russia, the oldest traces of ventral bites to date were found in the Bajocian of the Northern Caucasus on the ammonites *Rarecostites* from the Krasnodar Region (Sherstyukov and Shekhanov, 2017; Fig. 3a here). There are no reliable finds from the Aalenian, although concretions containing hundreds of perfectly preserved *Leioceras* Hyatt ammonite specimens with intact body chambers are known from localities on the Kyafar River in Karachay-Cherkessia (Mitta et al., 2018; Mitta and Sherstyukov, 2018), but not a single trace of a ventral bite has been found on them yet. A gradual increase in the number of ventral bites is observed in Callovian deposits. On Lower Callovian ammonites from such localities as Nikitino in the Ryazan region, as well as Znamenka in the Kostroma Region (see Keupp and Mitta, 2013), such damage is extremely rare (single finds are encountered), despite the very good preservation of the body chambers (Figs. 3b, 3c). However, in the middle Callovian deposits in the Mikhailovcement section in the Ryazan Region (Kiselev and Rogov, 2018), they are already more numerous (Mironenko, 2017a), despite the poor preservation of the body chambers in these beds (Fig. 3d).

Ventral bite marks become more numerous in the Upper Jurassic deposits of Central Russia. They are found on the shells of cardioceratids of the genera *Cardioceras* in the Lower Oxfordian of the Ryazan Region (Mikhailovcement, Fig. 4a) and *Amoeboceras* (*Prionodoceras, Paramoeboceras*) in the Upper Oxfordian of the Moscow (Markovo and Rybaki localities) and Kostroma (Mikhalenino) regions (Figs. 5a, 5c). From the Oxfordian deposits, there are also known finds of ventral bite marks, including healed ones (we will discuss them below), in ammonites of the genera *Perisphinctes* and *Dichotomosphinctes* (Figs. 4b, 9a).

Even more frequently, traces of ventral bites are found on the shells of *Amoeboceras* descendants—representatives of the genus *Plasmatites* in the lower Kimmeridgian of the Moscow (Borsheva) and Vladimir (Bolgary) regions (Fig. 6a). However, in the Late Kimmeridgian, the situation changed. Thus, in the deposits of the Kimmeridgian *Eudoxus* zone in the Lipitsa section in the Kaluga Region, traces of ventral bites become extremely rare: only 2 specimens were found among many hundreds of shells (Fig. 6b). In this section, the absence of *B. rolli* finds on the shells of ammonites of the genus *Sutneria* Zittel is also unusual—these aspidoceratid microconchs never reached a large size, and usually it is their size class (up to 5 cm) that accounts for the maximum number of finds with traces of ventral bite marks.

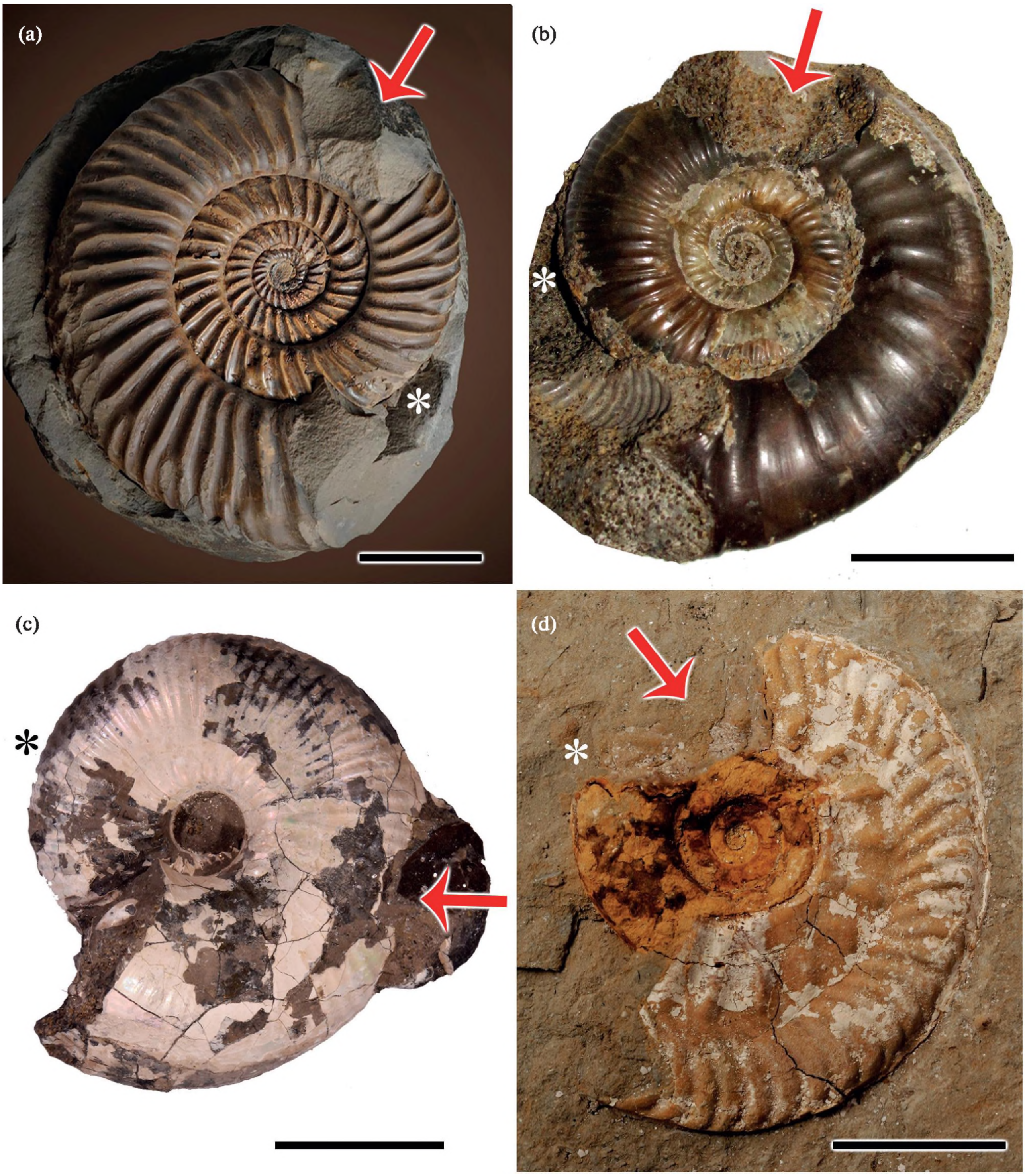

Fig. 3. Middle Jurassic ammonites with *B. rolli*. (a) *Rarecostites subarietis*, Upper Bajocian, Kyafar River, Karachay-Cherkessia (coll. and photo by M. Shersyukov); (b) *Anaplanulites nikitinoensis*, lower Callovian, Nikitino, Ryazan Region, sample GIN MPC no. 11/26; *Rondiceras* juv., lower Callovian. Znamenka, Kostroma Region, sample GIN MPC no. 11/27; *Sublunuloceras lonsdalii*, Middle Callovian, Mikhailovcement, Ryazan Region, sample GIN MPC no. 11/22; Symbol * denotes the boundary of the phragmocone and the body chamber, the arrow shows the hole of *B. rolli*. Scale bars: (a) 1 cm, (b) 2 cm, (c) 1.5 cm, (d) 2 cm.

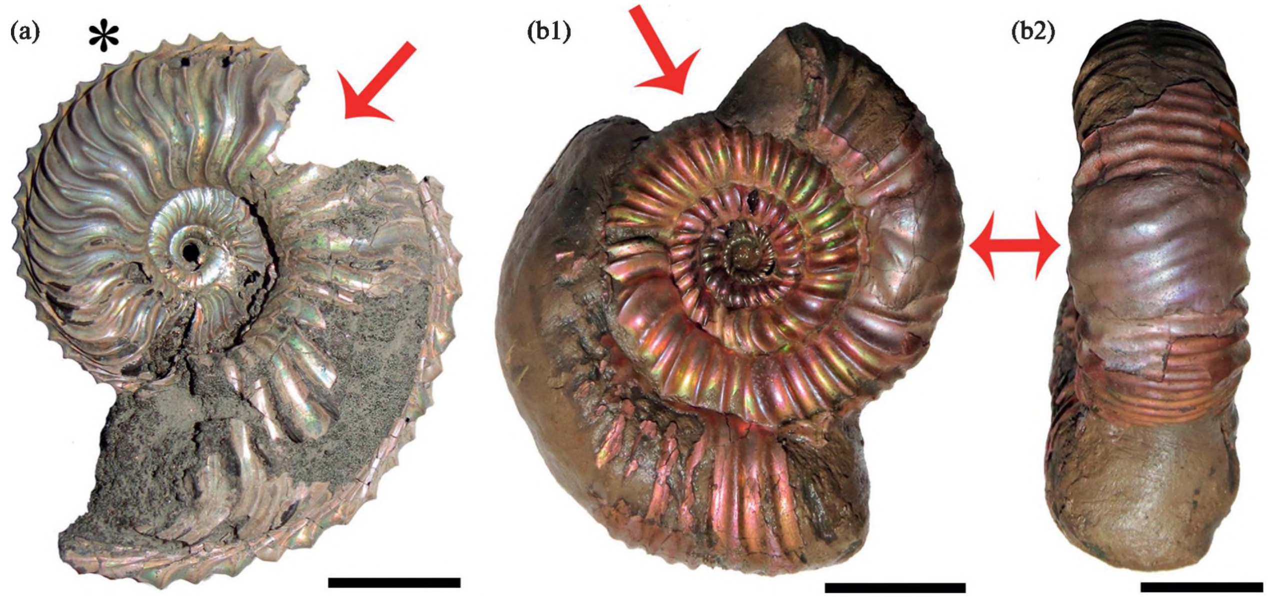

Fig. 4. Lower Oxfordian ammonites with *B. rolli* and a healed ventral bite mark: (a) *Cardioceras* sp., sample GIN MPC no. 11/32; (b) *Perisphinctes* sp. with a healed ventral bite mark (marked with a double arrow), lateral (b1) and ventral (b2) view, sample GIN MPC no. 11/35. Both samples are from the Lower Oxfordian of the Mikhailovcement section, Ryazan Region. The * symbol denotes the boundary of the phragmocone and the body chamber, the arrow shows the opening of *B. rolli*. Scale bars: (a) 1 cm, (b) 1.5 cm.

The most common traces of ventral bites are found in the Volgian deposits. Thus, from the Middle Volgian of the Volga Region—from the Samara and Ulyanovsk regions (Yablonovy Vrag and Gorodishchi, respectively) and from the territory of Moscow (Moskvorechye), many *Zaraiskites* ammonites with characteristic holes in the base of the body chamber are known, they make up about 40% of all finds (Figs. 7a–7b). However, it is worth noting that such numbers of *B. rolli* occurrences are recorded only in the *Zaraiskites kuteki* biohorizon, while in the next biohorizon—*Zaraiskites regularis* (see Rogov, 2021) in the mentioned sections they are almost absent, but they are found on dorsoplanitid shells in the Ivkino locality in the Kostroma Region (Fig. 7d).

Less numerous, but also widespread are traces of ventral bites on the shells of ammonites *Kachpurites, Garniericeras* and *Craspedites* from the Upper Volgian deposits of Moscow (Kuntsevo and Mnevniki), Moscow (Eganovo and Milkovo) and Yaroslavl (Cheryomukha) regions (Fig. 8). At the same time, in the overlying *Nodiger* ammonite Zone in Milkovo, damaged shells of *Craspedites* make up more than 25% of the finds of this genus, while in the more ancient deposits of the *Fulgens* and *Catenulatum* zones they are about 5–6%.

Thus, it can be concluded that the number of predators responsible for inflicting ventral bites gradually increased, albeit with numerous fluctuations, throughout the Middle and Late Jurassic. The first maximum of their numbers was reached at the end of the Oxfordian—beginning of the Kimmeridgian, followed by a slight decrease in the Late Kimmeridgian. The second and higher maximum was reached by the very end of the Jurassic, in the Middle and Late Volgian.

Habitats of Ammonites Bearing B. rolli on Their Shells

Most of the ammonite shell finds with ventral bite marks from the territory of the European part of Russia come from dark-colored bituminous clays and shales formed in relatively deep-water conditions far from the coast (Figs. 5; 6a, 7, 9). These are Upper Oxfordian and Lower Kimmeridgian black clay and shales in the Moscow, Kostroma and Vladimir regions, dark-colored shales of the Middle Volgian in the Kostroma, Samara and Ulyanovsk regions. Since the benthic fauna in these deposits is usually either rather uniform of not very numerous, it can be concluded that the conditions in the bottom water layer were not the most favorable, probably due to oxygen deficiency. Most likely, most ammonites in such environments lived in the epipelagic zone.

However, *B. rolli* finds are also very numerous in the much shallower upper Volgian deposits of the Moscow and Yaroslavl regions, represented by sands with phosphatized nodules containing both isolated ammonite shells and large accumulations of them (Fig. 8). Nevertheless, the phosphatized nodules in the Kostroma Region (Znamenka) and oolitic marls of the Ryazan Region (Nikitino), which were formed

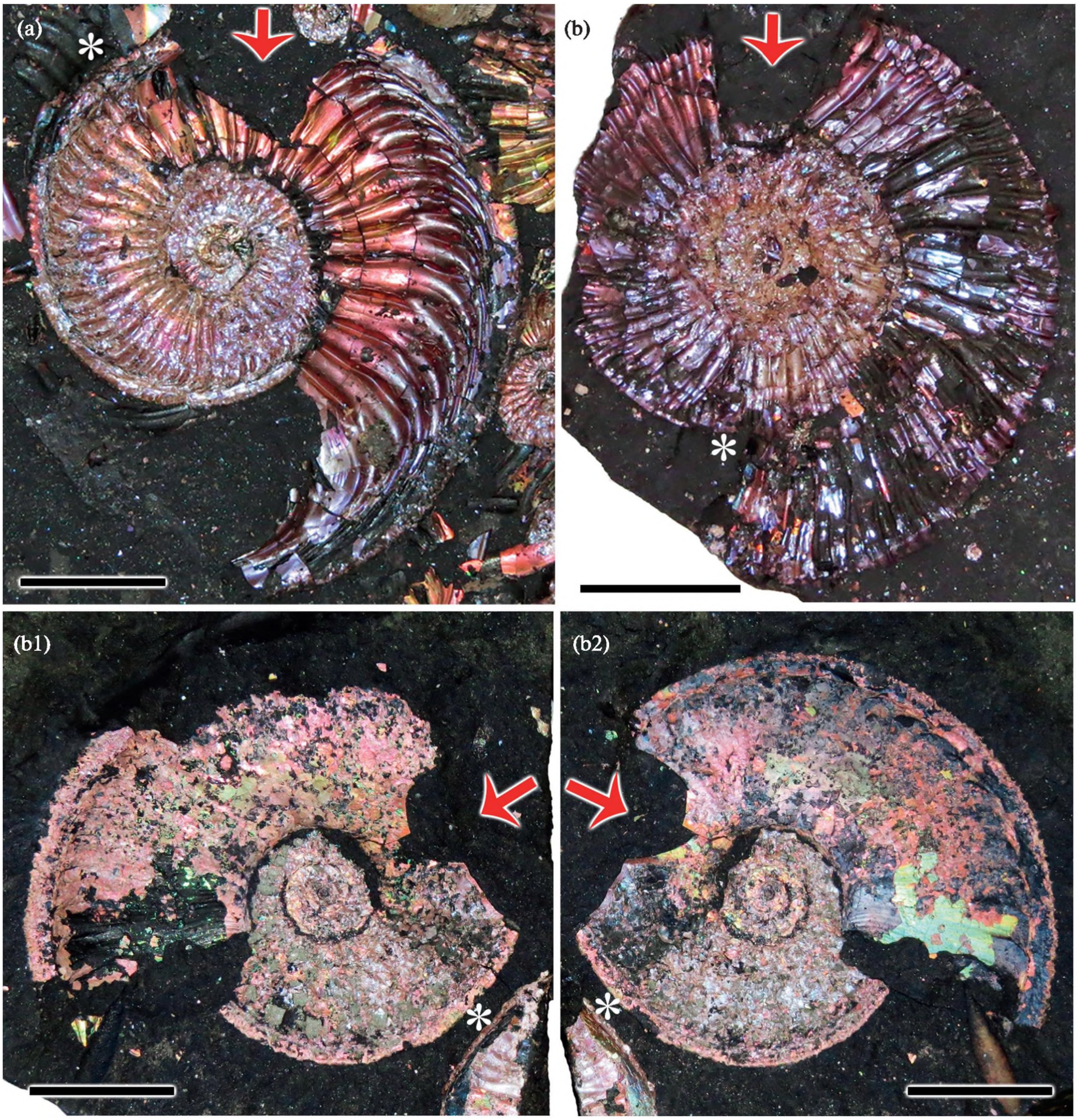

Fig. 5. Upper Oxfordian ammonites with *B. rolli*. (a) *Amoeboceras (Paramoeboceras) ilovaiskii,* sample GIN MPC no. 11/55; (b) *Dichotomosphinctes elisabethae*, sample GIN MPC no. 11/56; both from the Upper Oxfordian of Mikhalenino, Kostroma Region; (b) *Prionodoceras serratum*, imprint and counterpart imprint, Upper Oxfordian, Rybaki, Moscow Region, sample GIN MPC no. 11/47. The symbol * denotes the boundary of the phragmocone and the body chamber, the arrow shows the opening of *B. rolli*. Scale bars: (a) 1 cm, (b and c) 2 cm.

in similar shallow water conditions in the early Callovian, contain significantly fewer finds of ventral bite marks.

It should also be noted that the shells of the Upper Volgian ammonites of the genera *Craspedites* and *Kachpurites* bear approximately the same number of injuries caused by *B. rolli*. However, these ammonites vary greatly in the number of injuries caused by crustaceans: in *Craspedites*, they account for almost 10% of all finds and almost all of them are healed, while in *Kachpurites*, the picture is the opposite: only 1% of shells have damage, and there are almost no healed ones among them (Mironenko, 2020). This suggests that these two genera differed in their lifestyle: repre-

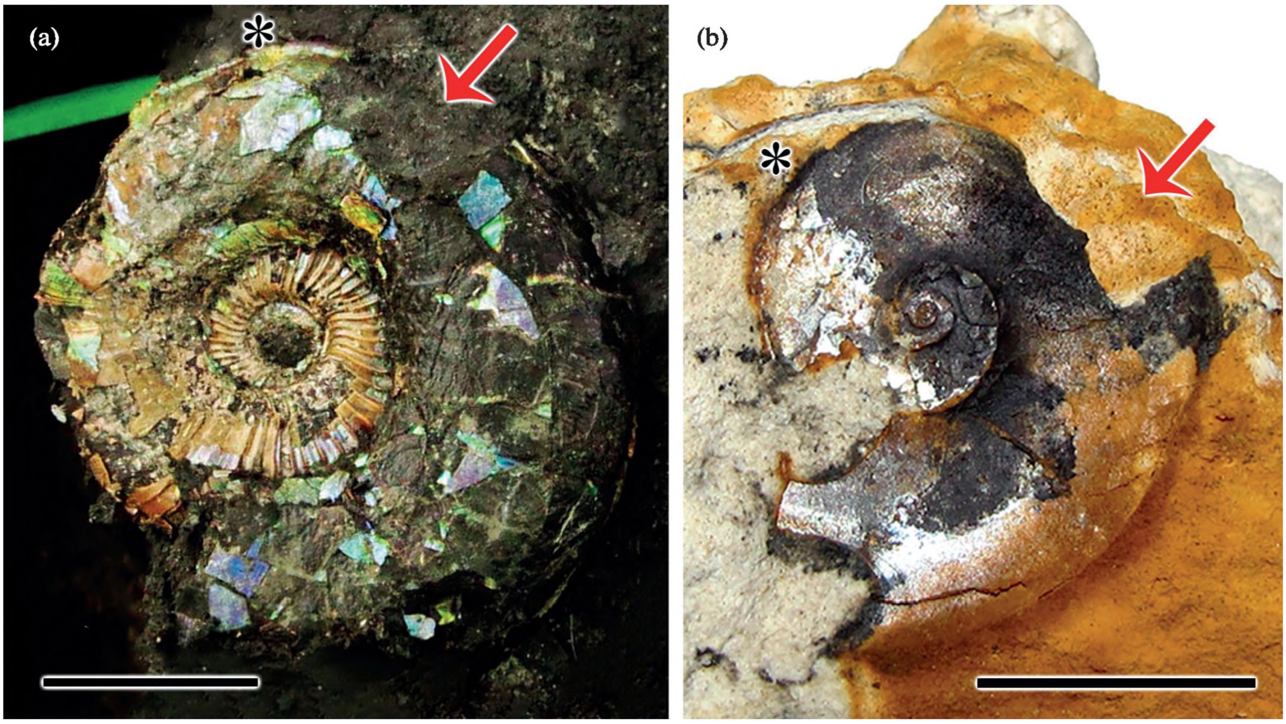

Fig. 6. Kimmeridgian ammonites with *B. rolli*. (a) *Plasmatites lineatum*, Lower Kimmeridgian, Bolgary, Vladimir Region, sample GIN MPC no. 11/41; (b) *Glochiceras nimbatum*, Upper Kimmeridgian, Lipitsy, Kaluga Region, sample GIN MPC no. 11/54; The symbol * denotes the boundary of the phragmocone and the body chamber, the arrow shows the hole of *B. rolli*. Scale bars for a and b 1 cm.

sentatives of *Craspedites* lived near the bottom, often encountered crayfish and were adapted to their attacks, while *Kachpurites* lived in the water column and rarely occurred near the bottom, possibly only when already weakened (Mironenko, 2020). The presence of approximately the same number of ventral bite marks on the shells of these taxa suggests that the predators responsible for inflicting them could have attacked ammonites throughout the entire water column, from the bottom to the surface layers.

Thus, apparently, the activity of predators hunting by ventral bites did not directly depend on the depth of the sea and the distance from the shore, and both bottom demersal and epipelagic species of ammonites were subjected to their attacks.

Distribution of B. rolli Occurrences among Taxa and Morphotypes of Jurassic Ammonites

A study of *B. rolli* finds shows that the ammonites most susceptible to bites were those with wheel-shaped shells with a moderately narrow venter: evolute and semi-evolute serpenticons, platycones and discocones (for a classification of morphotypes, see Westermann, 1996), lacking tubercles and spines. Ammonites of the superfamily Perisphinctoidea suffered most from ventral bites: Callovian *Anaplanulites*, Oxfordian *Perisphinctes* and *Dichotomosphinctes*, Volgian *Zaraiskites*, *Kachpurites* and *Craspedites*. The presence of ribs on the shell apparently did not affect the frequency of damage (for example, it is approximately the same for smooth *Kachpurites* and ribbed *Zaraiskites*—see Figs. 7 and 8). Similar data were previously reported for the ribbed *Dactylioceras* Hyatt and the smooth keeled *Hildoceras* Hyatt and *Harpoceras* Waagen (Klompmaker et al., 2009).

Also, very susceptible to ventral bites were the narrow discocones of the Cardioceratidae family (*Cardioceras, Amoeboceras, Plasmatites, Prionodoceras*), which had a predominantly ribbed ornamentation and a pronounced ventral keel (Figs. 4a, 5a, 5c). Although the keel can be considered as a ventral stiffening rib of the shell, it clearly did not protect against ventral bite attacks. Wright et al. (2014) also noted a high frequency of ventral bite marks in the cardioceratids *Cardioceras* and *Goliathiceras* Buckman from the Oxfordian of Great Britain.

Other preferred victims of predators that typically attacked the venter were ammonites with oxyconic shells—Callovian *Sublunuloceras* and *Brightia* (Fig. 3g), Kimmeridgian *Glochiceras* (Fig. 6b), and Upper Volgian *Garniericeras* (Fig. 8d). Traces of ventral bites are unknown for the Aalenian oxycones *Leioceras*, but in this case the issue may be the absence or rarity of appropriate predators in the habitat of these ammonites during the formation of the bottom sediments that contain their shells, and not their abil-

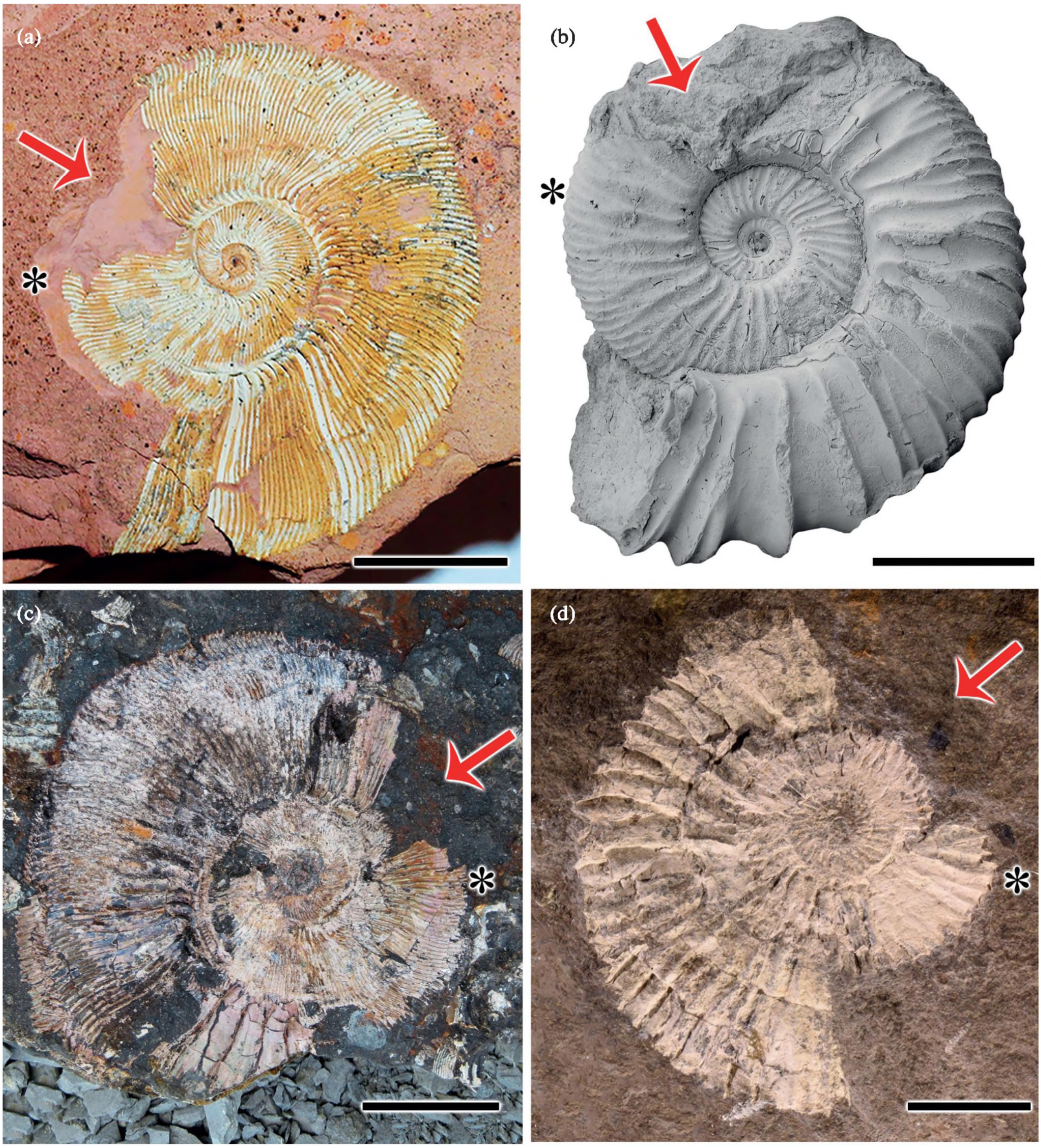

Fig. 7. Middle Volgian ammonites with *B. rolli*. (a) *Zaraiskites densecostatus*, Yablonovy Ovrag, Samara Region, sample GIN MPC no. 11/73; (b) *Zaraiskites mikhalskii*, Moskvorechye, Moscow (photo by M. Rogov), sample GIN MPC no. 11/81; (c) *Zaraiskites densecostatus*, Gorodishchi, Ulyanovsk Region, sample GIN MPC no. 11/79; (d) *Pavlovia pavlovi*, Ivkino, Kostroma Region, sample GIN MPC no. 11/80. The * symbol denotes the boundary of the phragmocone and the living chamber, the arrow shows the hole of *B. rolli*. Scale bars: (a–b) 2 cm, (d) 1 cm.

ity to avoid bites. Note that the oxyconic shells of *Harpoceras* in the lower Toarcian of Germany bear a great many traces of ventral bites (Klompmaker et al., 2009).

On shells with prominent protective ornamentation consisting of sharp spines, traces of ventral bites are almost never found. Thus, in representatives of the family Kosmoceratidae, they are very rare. They were

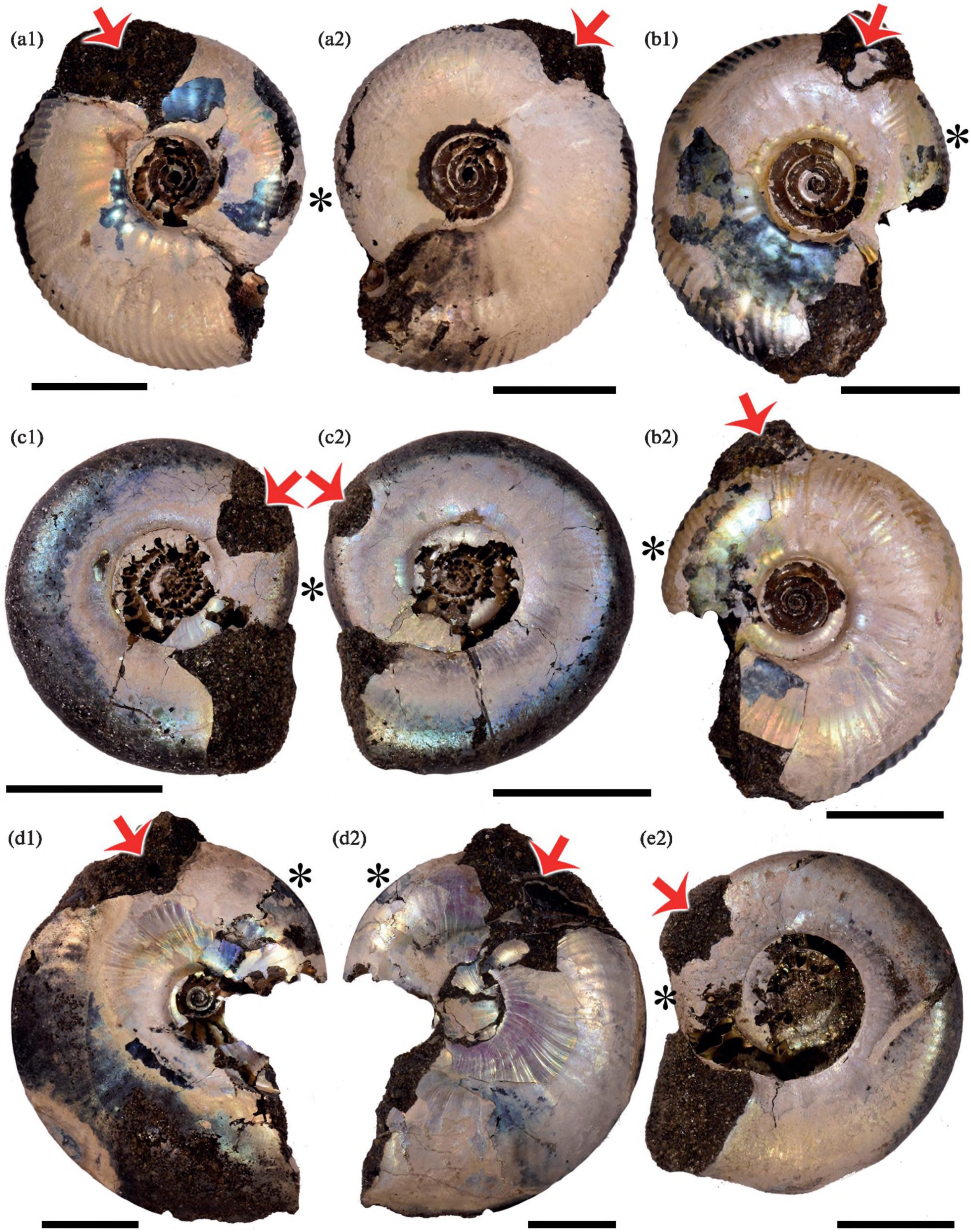

Fig. 8. Upper Volga ammonites with asymmetrical *B. rolli*. (a and b) *Craspedites nekrassovi*, view from both sides of the shell, Cheryomukha River, Yaroslavl Region, samples GIN MPC no. 11/7 and GIN MPC no. 11/8, respectively; (C AND D) *Kachpurites fulgens* (c1 and c2—view from both sides of the same shell), Eganovo, Moscow Region, samples GIN MPC no. 11/5 and GIN MPC no. 11/14, respectively; (d) *Garniericeras catenulatum*, view from both sides of the shell, Cheryomukha River, Yaroslavl Region, sample GIN MPC no. 11/16. The * symbol denotes the boundary of the phragmocone and the body chamber, the arrow shows the hole of *B. rolli*. All scale bars = 1 cm.

not found at all on the shells of the Lower Kimmeridgian macroconch *Aspidoceras* Zittel, but since they are also absent on the spineless shells of the microconch *Sutneria* from the same deposits, it is possible that this is not linked to the defensive function of the spines, but to the rarity of the predators that produced traces of ventral bites. In the literature, only one find of *B. rolli* on a shell with pronounced spines was mentioned—in the Upper Cretaceous (Turonian) *Pseudaspidoceras* Hyatt (Ifrim, 2013).

Not surprisingly, ventral bite marks are completely unknown on shells with wide venters, such as adult Callovian macroconchs of the subfamily Cadoceratinae (cadicones or sphaerocones) and juvenile shells of the genus *Erymnoceras* Hyatt of the family Pachyceratidae (extremely wide cadicones). This is unlikely to be due to the rarity of ventral bite marks themselves in the Callovian; more likely, the ventral regions of such shells may have been too wide to be effectively bitten. It can be assumed that the unusually rapid increase in whorl width early in *Erymnoceras* served precisely as protection against ventral bites, which were common on ammonite shells with narrower venters (especially oxycones), which lived in close proximity with *Erymnoceras*.

Unevenness of Temporal Distribution of B. rolli

Paleontologists are usually forced to study the past only on a very broad scale; changes that occurred over individual years and especially seasons remain out of sight. However, some features of phosphatized sand nodules related to the Upper Volgian *Fulgens* and *Catenulatum* ammonite zones in sections on the Cheremukha River indicate that they could have formed very quickly, but not simultaneously, over several years or even seasons (see Mironenko, 2017c). Although in ordinary sections of this age, ammonites *Craspedites* and *Kachpurites* (in the *Fulgens* Zone) and *Craspedites* and *Garniericeras* (in the *Catenulatum* Zone) are found mixed together, on Cheremukha, in some nodules, there are monospecific assemblages of these ammonites, of similar sizes. Examination of these ammonites for traces of ventral bites showed an interesting unevenness of their distribution. Of the four *Garniericeras* shells with *B. rolli*, three were found together in a same concretion (Mironenko, 2017c, text-fig. 2). One concretion contained three *Craspedites* shells of almost the same size with the same damage. Another concretion contained a mixed assemblage of *Kachpurites subfulgens* and various *Craspedites* species, and in it, ventral bite marks were found on several ammonites (Mironenko, 2017c, text-fig. 1). However, in at least seven of the studied concretions, no ventral bite marks were found.

If the assumption that these concretions were formed in different years or seasons is correct, then this implies that the predators responsible for inflicting ventral bites had uneven periods of activity. During some short periods of time, these predators actively hunted ammonites (sometimes larger, sometimes smaller), and during other periods, the ammonites were practically free from their pressure.

At present, this observation is unlikely to help reliably identify the predator responsible for the formation of *B. rolli*, since both fish and coleoids are subject to seasonal and annual fluctuations in abundance and can also change migration routes depending on various factors. However, it does show that the pressure of predators of ammonites was not constant and uniform, and that even in the Late Volgian, which was the time of high activity of ventral bite producers, there were intervals when ammonites rarely encountered them.

Cases of Survival after Ventral Bites

Until now, there have been no published examples of ammonites surviving ventral bites. However, the authors have two specimens of ammonites of the family Perisphinctidae (*Perisphinctes* and *Dichotomosphinctes*) from the Oxfordian of Central Russia with clear traces of healing of large ventro-lateral holes in the shell. One specimen, belonging to the genus *Perisphinctes*, comes from the lower Oxfordian of the Ryazan Region (Fig. 4b), the other, *Dichotomosphinctes*, from the upper Oxfordian of the Kostroma Region (Fig. 9a). In both specimens, peculiar "patches" are visible on the body chamber, clearly distinguished from the rest of the shell by larger and smoothed ribs, as well as a different direction of curvature of these ribs. According to the classification of paleopathologies by Hölder (1956), these healed lesions belong to *Forma aegra fenestra*, a formal type of paleopathology that unites all healed holes in ammonite shells, regardless of their origin.

The differences in the size of the ribs and the distance between them on the "patches" and the surrounding part of the shell are due to the fact that the ammonite, healing the holes with the edge of its mantle, formed ornamentation of the same size as in the aperture of the shell immediately before and after receiving the injury. This fact allows us to estimate where the aperture of the ammonite was at the time of the bite (since it is in this place that the parameters of ornamentation will be approximately the same as in the restored area). Comparison of the sizes of the ribs and the step between them shows that at the time of healing the injury, the aperture was located approximately half a whorl in front of the hole made by the predator.

It is important to note that different ammonite taxa vary greatly in the length of the body chamber. The cardioceratids *Cardioceras, Amoeboceras, Prionodoceras and Paramoeboceras* have a body chamber length of about 180–200 degrees of circumference. *Cardioceras* and *Amoeboceras* are the most abundant ammo-

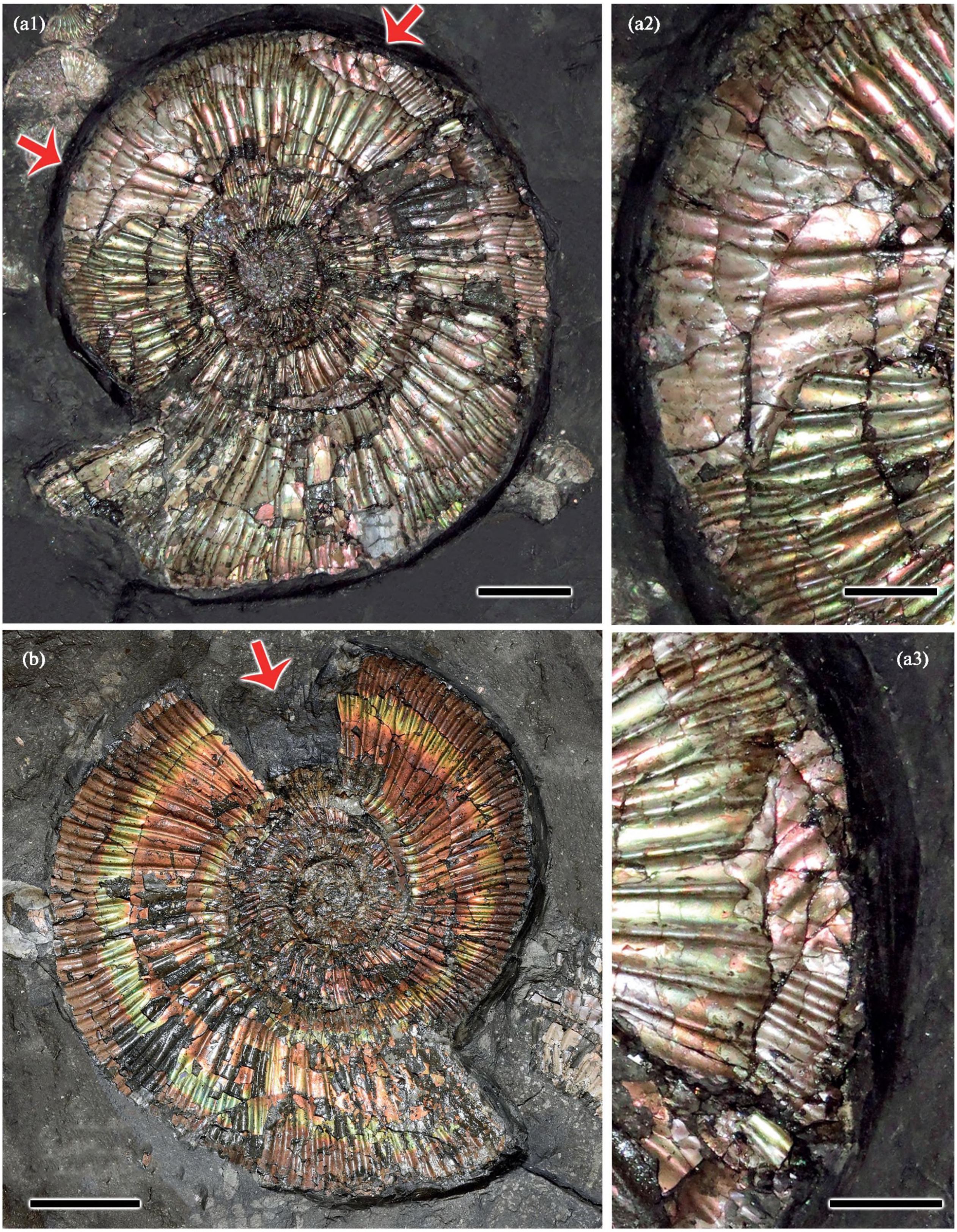

Fig. 9. An example of survival after a ventral bite. (a) *Dichotomosphinctes elisabethae* shell with two healed ventral bite marks ("patches"—marked with arrows and shown separately in a2 and a3). Specimen GIN MPC no. 11/57. The healed areas differ in size and rib angle. (b) ammonite *Dichotomosphinctes elisabethae* of similar size that died after a predator attack and carried *B. rolli* (marked with an arrow), specimen GIN MPC no. 11/58. Upper Oxfordian, Mikhalenino, Kostroma Region. Scale bars: for (a1 and b) 2 cm, (a2 and a3) 1 cm.

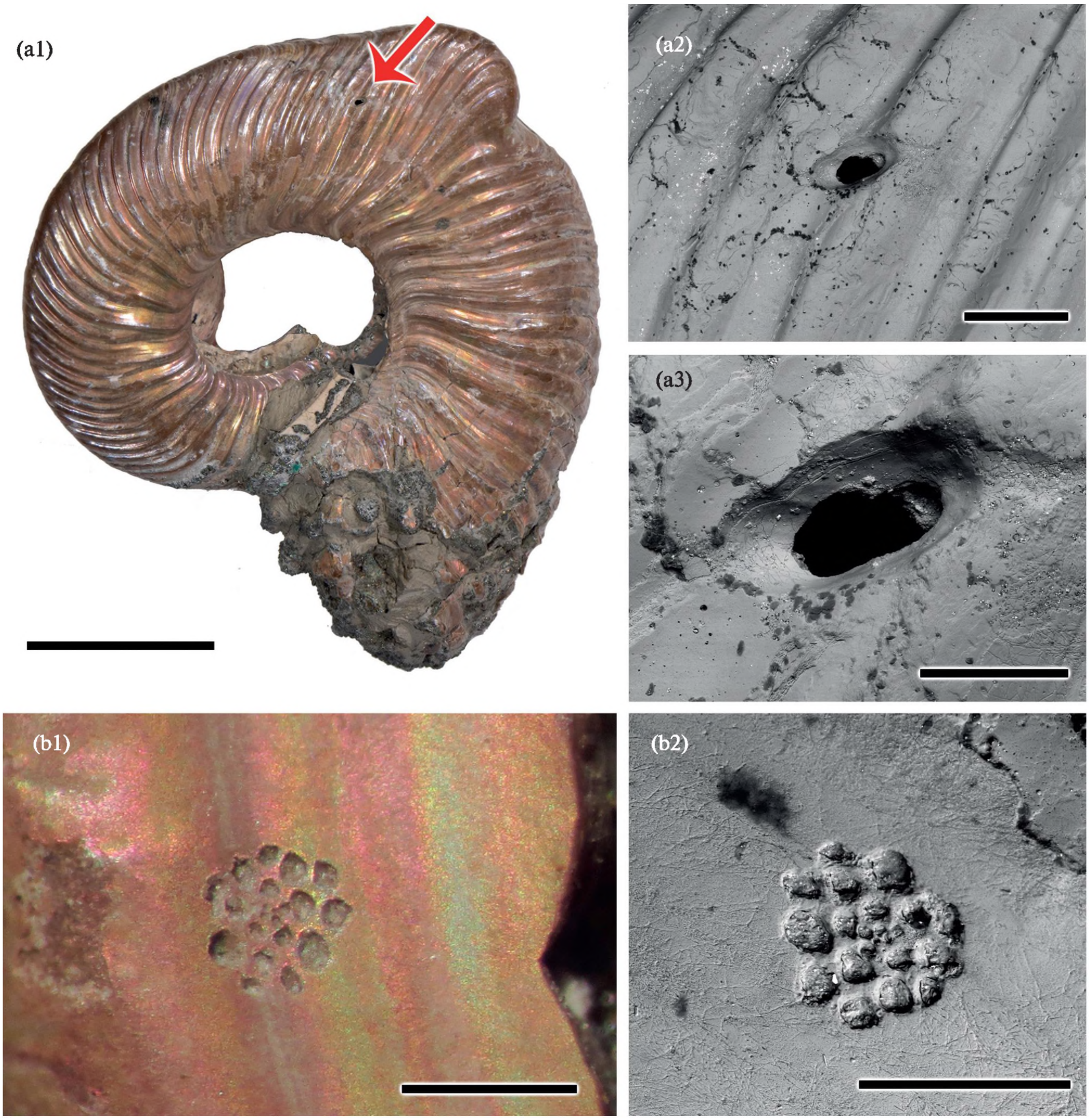

Fig. 10. Ichnofossils *Oichnus ovalis* and *Podichnus centrifugalis* on ammonite shells from the upper Callovian of the Saratov Region. (a) drilling of *Oichnus ovalis* on the shell of *Quenstedtoceras lamberti* (marked with an arrow). Specimen GIN MPC 10/20. (a1) general view, (a2 and a3) SEM images of *Oichnus ovalis*. Scale bars: (a1) 1 cm, (a2) 1 mm, (a3) 0.5 mm. Modified after Mironenko and Klompmaker, 2025.

nites in the Lower Oxfordian in Mikhailov and Upper Oxfordian in Mikhalenino, respectively. In both localities, they significantly outnumber perisphinctids. In the perisphinctid genera *Perisphinctes* and *Dichotomosphinctes*, to which the surviving ammonites belong, the length of the body chamber is significantly greater: 340°–360°. Consequently, a bite inflicted on the shell half a whorl behind the aperture in cardioceratids fell precisely on the area of attachment of the muscles in the rear part of the body chamber, and in perisphinctids—on the central part of the body chamber. It cannot be said that damage in the middle of the body chamber was safe for ammonites: many perisphinctids died from such bites (Figs. 5b, 9b), although some managed to survive. Among cardioceratids with their relatively short body chambers and bites that fell on the places of muscle attachment, no shells are yet known with traces of healing of these injuries.

Hunting Tactics of Predators That Used the Ventral Bite Method

The case of the surviving Oxfordian ammonites, which had a longer body chamber than their more numerous ecosystem neighbors, helps to explain how the predators chose their bite sites. Apparently, in most cases in the Oxfordian, they simply bit the shell about half a whorl from the aperture, regardless of the species of the prey. However, some of the predators were apparently able to learn from previous attacks.

In the Toarcian Sea of Germany, ammonites of the genera *Hildoceras* and *Harpoceras* with relatively short body chambers (around 240°) coexisted with *Dactylioceras*, which had body chambers 310° long (Klompmaker et al., 2009). Both often had the ventral bite in the same place, around 180° from the aperture (Klompmaker et al. 2009, text-figs. 2C, 2D). Although survivors of ventral bites have not yet been described among *Dactylioceras*, it is logical to assume that they will be found in the future. However, the damage pattern diagrams shown in Fig. 3 (Klompmaker et al., 2009: text-fig. 3, C—*Dactylioceras*, D—*Harpoceras*, E—*Hildoceras*) show that *Dactylioceras* exhibit the greatest variation in the location of the ventral bite, with a significant portion of the damage still located closer to the phragmocone. It can be assumed that predators could, through the accumulation of individual experience, gradually learn to distinguish ammonites by the shape of their shells and change their hunting behavior accordingly over time.

Almost all authors of previous works on ventral bite marks noted that predators attacked ammonites from a "blind spot": it is possible that the surprise of the attack for the ammonite was of great importance in the success of the hunt. After all, if the ammonite had no time to retract into the shell, then after its retractor muscles were broken, it could no longer hide, and the predator could easily kill its prey. If the ammonite managed to retract into the body chamber, the predator had to shake it out, and it could resist for some time, holding on inside with the help of its tentacles or the aptychi valves spread apart. One of the reconstructions of a coleoid hunting ammonites using the ventral bite method (Klug et al., 2021, text-fig. 7) shows the belemnoid *Acanthoteuthis* Wagner pulling the ammonite's body directly through the ventral bite hole. In reality, this could not have happened: the ammonite's aptychi (the lower jaw, which served to protect the aperture opening in times of danger) were almost as large as the shell's aperture, and they would have certainly become stuck somewhere in the middle of the body chamber, or, at worst, in the ventral bite opening itself. Thus, the predator had to pull the ammonite out from the apertural side, and of course it was more advantageous for the attacking predator to paralyze the ammonite's muscles before it had time to escape.

Significantly, in the Oxfordian, most *B. rolli* are located at a distance of about 180 degrees from the aperture, while on the Volgian ammonites, which had longer body chambers, the holes are mainly located at 250 degrees. Consequently, in the Volgian, predators adapted to feed on ammonites with a longer body chamber. Here, predators had to attack the ammonite if not "head-on", then in the area of the shell located above the head of the mollusk. It is difficult to say whether the effect of surprise was preserved in this case, perhaps the ammonite did not see this part of the space, or perhaps the accuracy of hitting the area of muscle attachment was still more important than surprise during the attack. At the same time, ammonites of the genus *Garniericeras*, which appeared at the end of the Volgian and had short body chambers, were attacked by predators again at a distance of 180 degrees from the aperture, which was apparently optimal for this taxon.

In summary, it can be concluded that in the Callovian, Oxfordian, and Kimmeridgian, most predators that made ventral bites attacked ammonites with a rapid lunge from the "blind spot," aiming at the shell area opposite the aperture, regardless of the prey species. In the Volgian, the situation changed: predators adapted to ammonites with long body chambers. This did not prevent them from adapting to the appearance of a new taxon with short body chambers (*Garniericeras*) in the late Volgian, which may indicate the evolution of the cognitive abilities of the attackers. After the attack, the predator either killed the prey, which could no longer be pulled into the body chamber, or shook the prey out through the aperture.

Potential Predators Responsible for Ventral Bite Marks

Previous studies on ventral bite marks have compiled an extensive list of potential predators that could have been responsible for this damage to ammonite shells. Among them were vertebrates—fish and marine reptiles (Larson, 2003; Klompmaker et al., 2009; Takeda and Tanabe, 2015; Takeda et al., 2015; Tajika et al., 2025), as well as cephalopods: nautilids (Takeda et al., 2015; Takeda and Tanabe, 2015; Takeda et al., 2015), various ammonoids (Andrew et al., 2010; Takeda and Tanabe, 2015; Takeda et al., 2015), and most often—coleoids (Larson, 2003; Klompmaker et al., 2009; Andrew et al., 2010, 2015; Wright et al., 2014; Maddra, 2015; Takeda and Tanabe, 2015; Takeda et al., 2015; Klug et al., 2021; Tajika et al., 2025).

The discovery of numerous ventral bite marks on ammonite shells from Central Russia and the Volga Region and the characteristics of these injuries help to significantly reduce the list of "suspects" in causing such injuries. It becomes possible to exclude ammonoids with a rhynchaptychus type of jaw apparatus, which was characterized by calcified tips of both jaws (Tanabe et al., 2015; Mironenko and Gulyaev, 2018; Mironenko and Rogov, 2018). The rhynchaptychus type of jaw apparatus, which appeared in the Early or Early Middle Jurassic, was characteristic only of representatives of the suborders Lytoceratina and Phylloceratina (Tanabe et al., 2015; Mironenko and Gulyaev, 2018; Mitta and Mironenko, 2024). Ammonites with such jaws were probably durophagous predators capable of penetrating the tough covers of their prey, and at first glance they seem to be good candidates for ventral-biting predators (Andrew et al., 2010; Takeda and Tanabe, 2015). However, they never lived in the epicontinental Central Russian Sea. Therefore, they should be excluded from the list of potential predators that may have inflicted the ventral bites, at least on the territory of the Russian Platform.

For similar reasons, nautilids (order Nautilida) should also be excluded from the list of potential predators. Beginning in the middle Triassic, they had calcite beak tips and were quite capable of piercing ammonite shells (Klug, 2001). Unlike Lytoceratina and Phylloceratina, they lived in the Central Russian Sea, but their peak in numbers and diversity occurred in the Callovian, an epoch when ventral bites were relatively few. In the Late Jurassic, nautilids became extremely rare in the Russian Platform, although it was precisely at this time that the number of ventral bites increased sharply.

Vertebrate predators such as marine reptiles and fish can be mostly ruled out based on the size of the ventral bite marks. Most often, these injuries are found on small shells (up to 5 cm in diameter), and the width of the injury rarely exceeds 1 cm. This is too small for marine reptiles and many fish. However, in some cases, injuries are found on fairly large shells, over 10 cm in diameter, for example, in the Upper Oxfordian *Dichotomosphinctes* and the Middle Volgian *Zaraiskites*. However, undoubted fish bites, both on modern nautiluses (Saunders et al., 2010) and on ammonites (Martill, 1990), have a characteristic shape with two or more rounded dents—tooth marks. Ventral bites of this shape have never been observed on ammonite shells, which casts doubt on the involvement of fish in their formation even when damaged shells are of suitable sizes.

Thus, the most likely predators that could have attacked ammonites using the ventral bite method remain coleoids and larger ammonites. Although such ammonites, namely representatives of the genus *Placenticeras* Meek, have only once been mentioned in the literature as potential predators (Takeda et al., 2015), the morphology of their jaws makes this assumption quite likely. The lower jaw, consisting of a pair of aptychi, was not well adapted to holding prey or destroying its covers. However, Lehmann and Kulicki (1990) suggested that the aptychi could have been a kind of passive "anvil" on which the prey was held (possibly with the help of arms), and the upper jaw served as a movable "hammer", piercing the protective covers of the victim ("The lower jaw was probably rather immobile in the biting cycle, most or all of the biting movement being achieved by the upper jaw"). Considering that there was a channel inside the upper jaw through which poison could be immediately injected into the punched hole (Mironenko, 2021), this method of hunting could be very effective. The noticeable asymmetry of most ventral bites indirectly confirms this assumption (although it could also occur with bites of coleoids, whose upper and lower jaws are also not identical). However, judging by the finds from Western Europe, ventral bites on ammonites became widespread back in the Sinemurian, before the emergence of the aptychi type of jaw apparatus (see Tanabe et al., 2015). Sinemurian ammonites had a more ancient anaptychus type of jaws, in principle very similar to the jaw apparatus of coleoids, therefore they could also pierce the shells of their relatives. On the other hand, the theory that ammonites were the main predators responsible for the ventral bite marks is refuted by the rarity of these injuries in many beds of the lower and middle Callovian, as well as the upper Kimmeridgian in Russian Platform, rich in ammonites, the size of which was well suited to both being hunters and prey. This version is also contradicted by the above-mentioned situation with the Upper Volgian concretions, which could have formed in different seasons: it is unlikely that the same ammonites began to hunt other ammonites at a specific time of the year, and suddenly stopped such hunting with the change of the season.

Belemnites and non-belemnoid coleoids (the Mesozoic ancestors of modern squids and octopuses) have been considered the most likely predators since the beginning of ventral bite research for two reasons: first, they are sufficiently intelligent to attack the ammonite not just anywhere, but in the most vulnerable place, which is undoubtedly the area of muscle attachment; second, they have developed arms and tentacles that allow them to manipulate objects and rotate the ammonite shell into a position convenient for biting (Klompmaker et al., 2009). However, the second argument seems unconvincing, since in a three-dimensional water column, a predator does not necessarily need to rotate the ammonite shell, as it is enough to swim up to it at the right angle. In addition, manipulation of prey is incompatible with the effect of a surprise attack, which many authors suggested.

Regarding intelligence, the situation is not as simple as it seems: modern predatory marine gastropods can also drill into the shells of their prey, but not everything remaining inside the body chamber was always available for the predator, or it had to spend energy and bite the rapidly sinking shell again. Thus, a forward miss, closer to the middle of the body chamber, was still better than a backward miss—on the phragmocone. The fact that the predators hunting *Dactylioceras* at least in some cases bit them at a significantly greater distance from the aperture than when hunting the sympatric *Harpoceras* and *Hildoceras*, suggests that predators were able (or gradually learned from experience) to distinguish the shells of these ammonites by appearance, and understood what taxon needed to be bitten in what position. This testifies to the analytical abilities of predators and is an argument in favor of coleoids – "primates of the sea" in the words of Akimushkin (1963). The swiftness of the attack from the "blind zone", which was mentioned above, is also an indirect argument in favor of coleoids, since they are characterized by rapid assaults on prey.

Thus, coleoids, both belemnoids and their relatives with no rostrum (having a gladius) (primarily Vampyromorpha), could have hunted ammonites using ventral bites, and they are the most likely predators that used this method. In the Central Russian Sea, they were numerous and diverse (Hecker and Hecker, 1955; Rogov and Bizikov, 2006). The size of these predators allowed them to hunt small and medium-sized ammonites and judging by the finds of coleoid statoliths (aragonite structures from their equilibrium organs), this diversity may be even greater than previously thought (Mironenko et al., 2025).

Other Rare Ichnofossils on Jurassic Ammonite Shells

B. rolli is not the only ichnotaxon found by the authors on the shells of Jurassic ammonites from European Russia. Thus, a boring trace belonging to the ichnospecies *Oichnus ovalis* Bromley, 1993 (Mironenko and Klompmaker, 2025) was recently found on the shell of the ammonite *Quenstedtoceras lamberti* from the Upper Callovian of the Dubki Quarry in the Saratov Region. This type of boring is often found on the hard covers of modern marine animals: crustaceans, bivalves and nautiluses. In modern seas, such borings are produced only by octopuses of the superfamily Octopodoidea (Saunders et al., 1991). Until recently, fossil ichnofossils of *O. ovalis* were known only from the Cenozoic (Bromley, 1993; Klompmaker et al., 2014) and Upper Cretaceous, where they were found on bivalves (Klompmaker and Landman, 2021). The first find of *O. ovalis* in the Jurassic, discovered on an ammonite shell, indicates that either the earliest octopuses or their ancestors from the order Vampyromorpha hunted ammonites by drilling into their shells in the same way as modern octopuses do with nautilus shells (Mironenko and Klompmaker, 2025). It is interesting that the drilling of *O. ovalis* on the ammonite shell is located in the same place as most of the *B. rolli* occurrences: in the rear part of the body chamber, slightly in front of the last septum, in the area of attachment of the lateral retractor muscles. That is, regardless of the hunting method (bite or drilling), predators preferred to attack this area of the ammonite's body chamber. It can even be assumed that it was the ancestors of these drilling octopods that inflicted ventral bites and adaptation to attacking the vulnerable spot in ammonites developed during their long evolution. On the other hand, the habit of drilling this area of the shell could well have arisen independently.

In the case of drilling, there could, of course, be no element of surprising the ammonite, but modern octopuses inject poison into the hole, dissolving the muscle attachment sites, and then shake the prey out of the shell—their Callovian ancestors could have done the same.

Another example of ichnofossils, no longer associated with predation, was also found on a fragment of the ammonite *Q. lamberti* shell from the same locality in the Saratov Region (Mironenko, 2018). This is the ichnospecies *Podichnus centrifugalis* Bromley et Surlyk 1973—an etching trace of the brachiopod pedicle to a hard substrate. It is difficult to say whether this pedicle was attached during the life of the ammonite, or the brachiopod settled on an empty shell lying on the seabed. Both versions can be true, since in conditions of a muddy bottom and oxygen deficiency, the shells of ammonites, both living in the water column and already dead and at least slightly rising above the bottom, were the most common and convenient option for a hard substrate. Nevertheless, as far as we know, except for this find, *Podichnus* have never been recorded on ammonites from the territory of Russia.

Both ichnospecies are known from single ammonite specimens, but their rarity is most likely due to their very small size (slightly more than 1 mm in the case of *O. ovalis* and 0.5 mm in the case of *P. centrifugalis*)—they are simply very difficult to notice. Targeted searches on well-preserved shells will certainly lead to new finds.

CONCLUSIONS

In European Russia, the ichnospecies *B. rolli* is found in Jurassic deposits from the Upper Bajocian to the Upper Volgian. The frequency of occurrence of this ichnospecies in the Middle Jurassic (especially in the Lower Callovian) is not high but increases significantly in the Upper Jurassic. The peaks of the number of finds occur in the Upper Oxfordian–Lower Kimmeridgian, as well as in the Middle and Upper Volgian. In terms of proportions, ventral bite marks are most commonly found in the *Panderi* Zone in the Volga region, where they are present on almost 40% of ammonites of the genus *Zaraiskites*. Ventral bite marks were found in 21 ammonite genera with different shell shapes. Ribs and keels could not have served as protection against ventral bites, but the particularly wide venter apparently protected against them. *B. rolli* are mainly found on shells up to 5 cm in diameter, the maximum size of shells with such damage that we found was 12–13 cm. Therefore, the victims of ventral bite attacks were mainly small-sized ammonites. The activity of predators hunting by ventral bites in the Central Russian Sea did not directly depend on the depth and proximity of the coast. Both bottom demersal and epipelagic ammonite species were equally subject to their attacks. However, there is reason to believe that the numbers of these predators were subject to seasonal or long-term fluctuations.

Since ammonites with a rhynchaptichous jaw apparatus (Lytoceratina and Phylloceratina) did not inhabit the Central Russian Sea, and the peak of nautilid abundance occurred in the Callovian (the time of minimal prevalence of ventral bites), these cephalopods should be excluded from the list of "suspects" in the formation of *B. rolli*. Vertebrate predators seem unlikely due to the small size and shape of *B. rolli*. The assumption that ammonites with an aptychus jaw apparatus themselves could bite their smaller relatives is contradicted by the absence of finds of traces of ventral bites in many beds rich in ammonites. Therefore, it is most likely that the predators that inflicted ventral bites were coleoids—both belemnites and gladius-bearing ancestors of octopuses and squids.

In general, the pressure from predators producing ventral bite marks increased during the Middle and Late Jurassic. It was aggravated by the more flexible behavior of attackers in the Volgian: in the Callovian, Oxfordian, and Kimmeridgian they attacked all ammonites at a distance of about 180–200 degrees of circumference from the aperture, which allowed some of them to survive the attack, while at the end of the Volgian they confidently distinguished *Craspedites* with a long body chamber (which were attacked in the area of 250 degrees from the aperture) and *Garniericeras* with a short body chamber (they were attacked in the area of 180 degrees).

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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