Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

First record of the ichnospecies *Oichnus ovalis* in a Jurassic ammonite

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LETHAIA

Among various drill holes located in ancient shells, the ichnospecies *Oichnus ovalis* is particularly important for understanding the presence and behaviour of cephalopods. In modern seas, incirrate octopuses of the superfamily Octopodoidea produce small, oval drill holes ascribed to *O. ovalis* in the shells of various molluscs and crustaceans. Until now, fossil *O. ovalis* has been primarily known mostly from the Pliocene and Pleistocene, whereas the oldest examples have been reported from the Late Cretaceous (Campanian). Here, we describe the first Jurassic record of *O. ovalis*, found in the ammonite *Quenstedtoceras lamberti* from the Middle Jurassic (latest Callovian) of Russia. The oval drill hole measuring 1.0 to 0.5 mm is located on the ammonite body chamber in the area of attachment of retractor muscles, which suggests this hole most likely was made by a predator that attacked a living ammonite in the water column. If this drill hole had been found in the Late Cretaceous or Cenozoic, it would have been attributed to an octopodoid predator. However, body fossils of octopodoids are still unknown from the Jurassic. Nevertheless, judging by some molecular clock data, incirrate octopuses might have already existed in the Late Jurassic and probably even earlier. Therefore, the Jurassic *O. ovalis* may have been drilled by one of the oldest octopodoids, their ancestors, or an unknown predator. Regardless of the identity of the predator, this finding expands our knowledge on the Middle Jurassic predators of ammonoids and suggests drilling on active pelagic prey arose during the Jurassic phase of the Mesozoic Marine Revolution.
Oichnus, Oichnus ovalis, □ *Jurassic, Callovian, ammonites, ichnotaxa*

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Trace fossils, also known as ichnofossils, represent a fossil record of biological activity of ancient animals. They provide a window into the past that sheds light on the behaviour of extinct creatures. They can preserve without the fossilized remains of their producers. On the one hand, this makes it difficult to identify the producers of trace fossils, but on the other hand, if these producers are already known from today's environments, ichnofossils can significantly expand our knowledge on the stratigraphical and palaeogeographical distribution of the animals that produced them.

Among the ichnofossils, there are traces of movement, crawling, burrowing, as well as traces of predation, including drilling into the hard skeletons of marine organisms (e.g. Seilacher 2007; Knaust 2017; Klompmaker *et al.* 2019). The last category includes the ichnogenus *Oichnus* Bromley, 1981, which represents drill holes of various shapes and sizes in the hard shells of animals. According to Bromley (1981), these drill holes may penetrate the shell wall, or end within it as a shallow to deep depression or short, subcylindrical pit. Several ichnospecies of *Oichnus* have been established to date (Wisshak *et al.* 2015). They differ in the shape of the external and internal holes, the ratio of their sizes and the angle of inclination of the walls.

For researchers of the evolution of cephalopod molluscs, the ichnospecies *Oichnus ovalis* Bromley, 1993, is of particular interest. These trace fossils are elongated oval holes, in which the diameter of the internal hole is smaller than the diameter of the external one. It was repeatedly shown that in modern seas such holes are drilled by octopuses of the superfamily Octopodoidea (Pilson & Taylor 1961; Arnold & Arnold 1969; Nixon 1979; Nixon & Maconnachie 1988; Saunders *et al.* 1991; Runham *et al.* 1997; Blustein & Anderson 2016; Pech-Puch et *al.* 2016), although octopodoids can also produce more circular, irregular holes (e.g. Arnold & Arnold 1969). For drilling, the octopuses use the radula, traces of which can be found on the walls of the holes, and the hard tip of the salivary gland (Nixon & Maconnachie 1988; Saunders *et al.* 1991). In modern seas, octopodoid holes are found on the shells of various molluscs, including representatives of cephalopods: the genera *Nautilus* and *Allonautilus* from the order Nautilida (Saunders *et al.* 1991), and crustaceans.

Most fossil evidence of *O. ovalis* is known from Cenozoic deposits. They were mainly described from the Pliocene and Pleistocene and found on the shells of bivalves, gastropods, and crustaceans (Bromley 1993; Harper 2002, 2005; Pasini & Garassino 2012; Klompmaker *et al.* 2013, 2014, 2015; Klompmaker & Kittle 2021). The only known Mesozoic example of *O. ovalis* are drill holes in Late Cretaceous (Campanian) lucinid bivalves from South Dakota, USA (Klompmaker & Landman 2021). The fact that octopuses were producers of these drillings has not been challenged to date.

However, octopuses, including those belonging to the superfamily Octopodoidea, have been known from body fossils starting from the beginning of the Late Cretaceous (Cenomanian). Judging by the presence of two separate families of octopodoids in the Cenomanian, they likely evolved much earlier (Fuchs *et al.* 2009; Fuchs 2020). According to current thinking, the order Octopoda existed at least from the Middle Jurassic (Fuchs 2020), thoughuntil now *O. ovalis* has not been reported from pre-Campanian sediments. Here, we describe the first record of *O. ovalis* from the Middle Jurassic (late Callovian) from the Saratov region of Russia in a body chamber of the ammonite *Quenstedtoceras lamberti* Sowerby, 1821 (Fig. 1).

Material and methods

The material studied herein comes from the uppermost part of the Callovian dark clay beds (*Quenstedtoceras lamberti* ammonite Zone) of the well-known Dubki locality (51°40´19.35″ N; 46°1´15.91″ E) in the Saratov region of Russia (Seltzer 1999; Larson 2007; Kiselev *et al.* 2013; Mironenko 2015a).

The drill hole in the shell of the ammonite *Quenstedtoceras lamberti* was discovered by chance during a study of an ammonite shell anomaly known as forma *aegra augata* (Kröger 2000; Keupp 2012). In search of the reasons of its presence, one of us (A.M.) studied the microsculpture of ammonite shells with this anomaly using an optical microscope and found an opening located not far from the anomalous

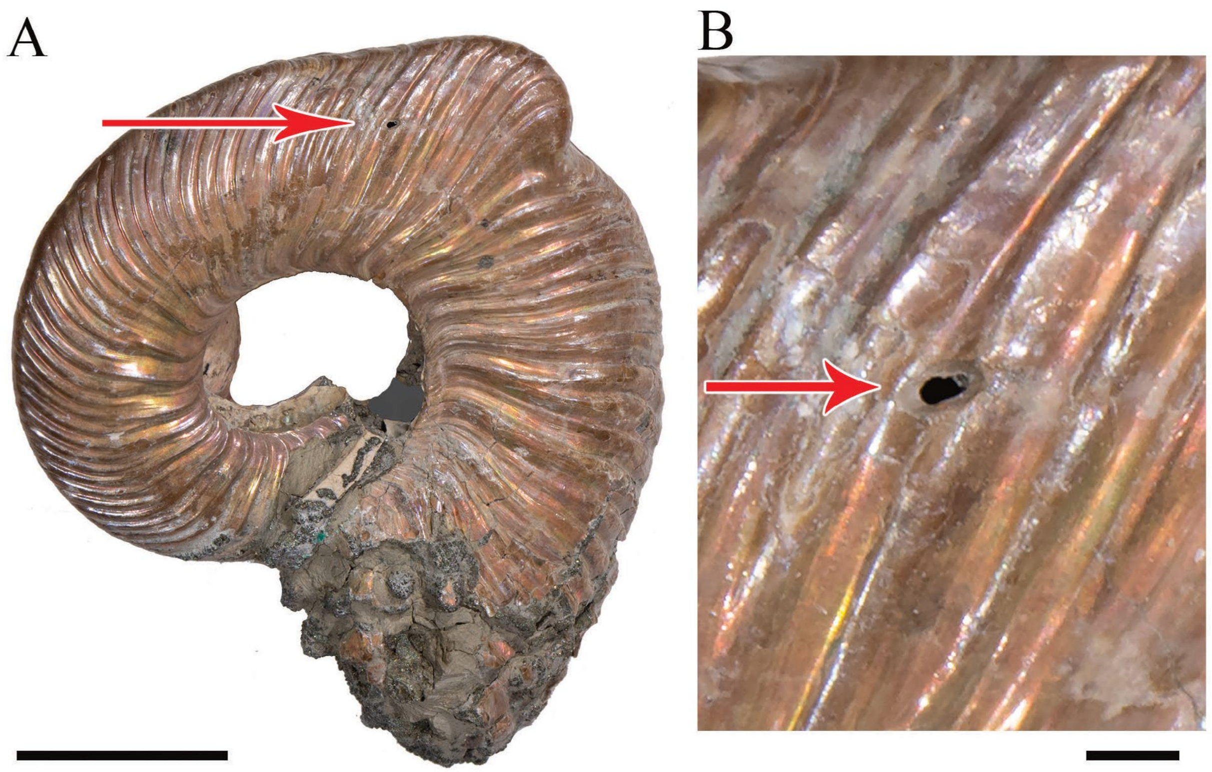

Fig. 1. Upper Callovian ammonite *Quenstedtoceras lamberti* (specimen GIN MPC 10/20) with a palaeopathology, forma *aegra augata* Kröger, 2000, and a drill hole attributed to *Oichnus ovalis* Bromley, 1993 (marked by an arrow). Scale bars are 1.0 cm for A and 1.0 mm for B.

protuberance in one specimen. Subsequently, the authors studied a collection of ammonites from the Dubki quarry, consisting of almost 200 specimens, which are housed in the collection of the Geological Institute of the Russian Academy of Sciences (number GIN MPC 10). It includes mainly the ammonites *Quenstedtoceras* Hyatt, 1877, as well as *Kosmoceras* Waagen, 1869, and *Peltoceras* Waagen, 1871. Twenty-eight bivalves of the genus *Nucula* Lamarck, 1799 from the same layers of Dubki section were also examined.

The specimen of *Quenstedtoceras lamberti* with the drill hole was studied with a Neoscan X-ray microtomograph with an X-ray source voltage 110 Kv and a 1-mm-thick copper filter, and scanning electron microscope (SEM) TESCAN VEGA II with secondary electron (SE) mode at the Paleontological Institute of the Russian Academy of Sciences (PIN RAS) in Moscow. A small part of the specimen which includes the hole was coated with gold and inspected in high-vacuum conditions at 20 kV. The specimen is housed in the collection of the Geological Institute of the Russian Academy of Sciences (GIN RAS) in Moscow under the number GIN MPC 10/20.

Results

On a single specimen of *Quenstedtoceras lamberti* (GIN MPC 10/11), a 1.0 mm long and 0.5 mm wide drill hole is located on the left side of the shell (Fig. 1). The general shape of the opening is oval to somewhat rhomboidal with slightly wavy edges. A short groove leads into the main penetration (Fig. 3 A-C, oriented to the right). The X-ray micro-CT scan made it possible to establish that the hole is located in the body chamber at a distance of 5 mm from the last septum (Fig. 2). In this ammonite, the body chamber was preserved due to the infilling of this cavity with pyrite. Pyritization is typical for hollow phragmocone chambers at this locality, but is rare for ammonite body chambers. A SEM examination showed that the internal diameter of the hole is smaller than the external one (0.45mm to 1mm), the walls are flat and bear traces of drilling (Fig. 3). It is also worth noting that although the body chamber and phragmocone of ammonite shells are filled with pyrite, the shell wall itself retains its original aragonitic structure in which the drill hole is located.

Study of an extensive collection of additional ammonites from the same locality (nearly 200 specimens, both normal and bearing various pathologies) did not yield additional specimens containing similar drill holes. The probable reason for this is that most of the studied ammonites were represented by phragmocones because their body chambers were not replaced with pyrite and, thus, were not preserved. Traces of drilling were also not found on the benthic bivalves *Nucula* (nearly 30 specimens), but the studied specimens of this genus were not numerous.

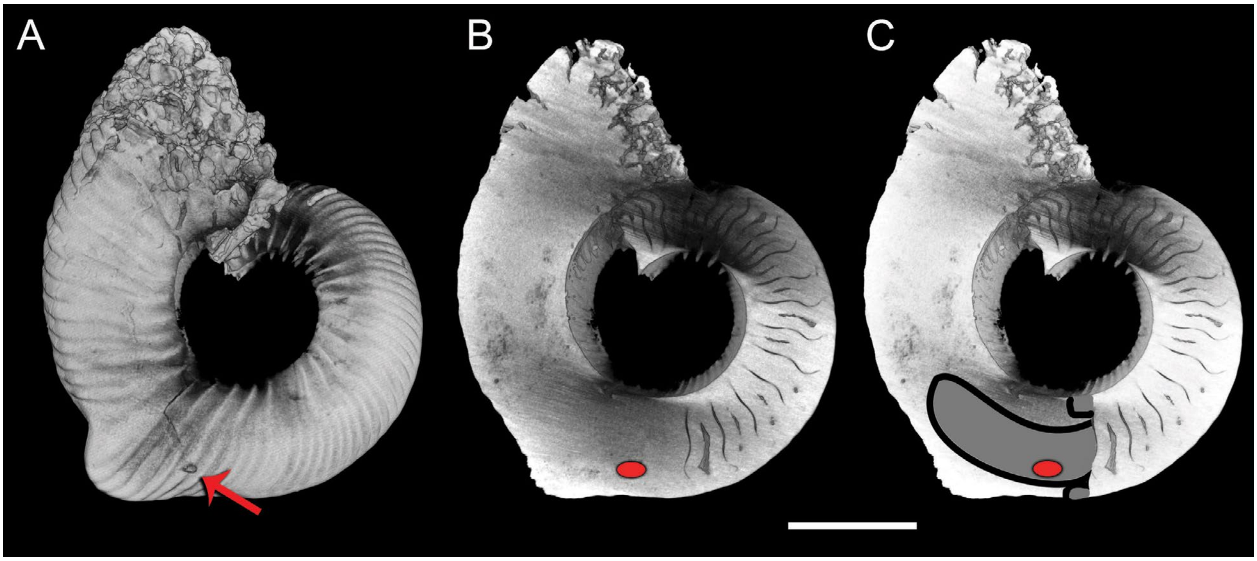

Fig. 2. X-ray micro-CT images of specimen GIN MPC 10/20. A – external view, B – longitudinal section of the shell, C – longitudinal section of the shell with a reconstruction of the position of muscle scars (based on Doguzhaeva & Mutvei 1991, pl. 7 figs 1–2). The position of *O. ovalis* is marked by an arrow for A and indicated by an oval on B and C. Scale bar – 1.0 cm.

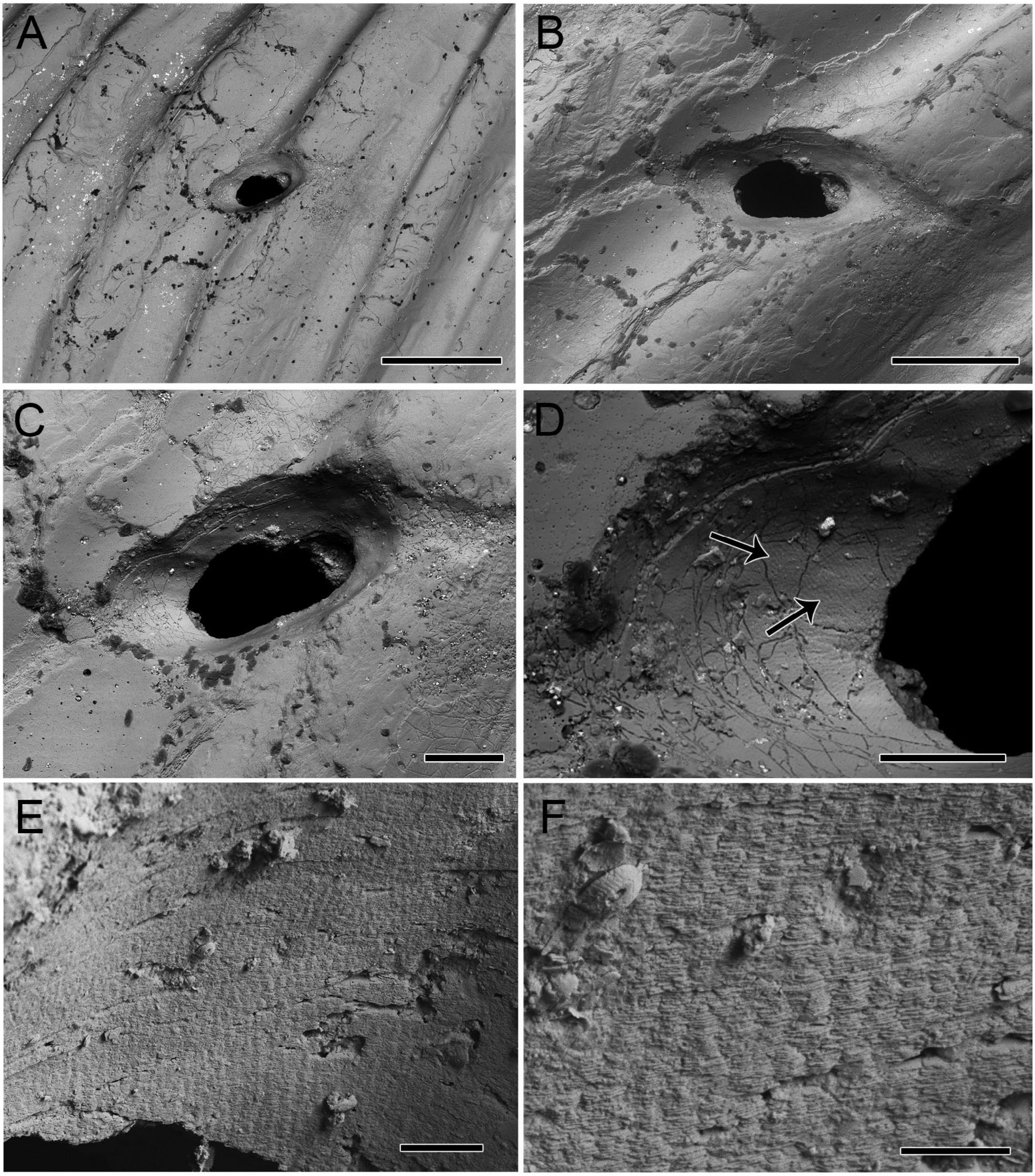

Fig. 3. SEM images of *O. ovalis* on the *Q. lamberti* shell. Scale bars for A – 1.0 mm, B – 500 μm, C – 200 μm, D – 100 μm, E – 25 μm. F – 10 μm. A-C – general view of the drill hole, D – erosion of the wall of the hole (marked by arrows). Note that long worm-shaped borings and pinholes are likely traces of post-mortem microbioerosion and are not related to the creation of *O. ovalis*. Similar traces are seen in the lower rightmost part of C. E, F – details of the structure of erosion of the aragonitic structure of the shell wall is visible. The platy horizontal structure represents aragonite crystals.

Discussion

In today's oceans, oval drill holes of similar size that can be ascribed to *Oichnus ovalis* are produced only by incirrate octopuses of the superfamily Octopodoidea (Pilson & Taylor 1961; Arnold & Arnold 1969; Nixon 1979; Nixon & Maconnachie 1988; Saunders *et al.* 1991; Hiemstra 2015; Blustein & Anderson 2016; Klompmaker & Landman 2021; Markaida 2023). For drilling, these octopuses use not only the radula (e.g. Pech-Puch *et al.* 2016), but also the hard tip of the salivary gland (Nixon & Maconnachie 1988; Saunders *et al.* 1991). They also use saliva for dissolution of the calcium carbonate shell at the place of drilling (Runham *et al.* 1997).

Until now, trace fossils of the ichnospecies *O. ovalis* have not been described from Jurassic and Lower Cretaceous deposits. The vast majority of finds of *O. ovalis* in the fossil record were described from the Pliocene and Pleistocene (Bromley 1993; Harper 2002, 2005; Pasini & Garassino 2012; Klompmaker *et al.* 2013, 2014, 2015; Klompmaker & Kittle 2021). All examples were attributed to octopodoid predation. Villegas-Martín *et al.* (2019) reported two examples of *O. ovalis* in Paleocene ostracods, but did not attribute them to a specific predator. Unequivocal Mesozoic examples of *O. ovalis* attributed to octopodoids were described only once from the shells of Late Cretaceous (Campanian) lucinid bivalves (Klompmaker & Landman 2021). Fatka *et al.* (2022) described two openings on the pygidium of a trilobite from the Middle Ordovician and assigned them to *O. ovalis*. However, these holes are symmetrically located, which is highly unlikely if they represent two separate drillings. Moreover, each hole is surrounded by a shallow depression (Fatka *et al.* 2022: fig. 3D), which may not have been created by drilling but could have resulted from a bite or puncture. The morphological dissimilarity of these holes to *O. ovalis* renders assignment to this ichnotaxon unlikely.

In contrast, the oval opening located on the shell of the upper Callovian *Quenstedtoceras* described herein corresponds to the characteristics of *O. ovalis*: it has an oval shape with a somewhat wavy outer edge, shallow walls and a diameter of the external opening which is larger than the internal one (Fig. 3). The short groove or gutter which leads into the main hole (Fig. 3A-C, to the right) is frequently observed for octopodoid predation traces (Arnold & Arnold 1969, fig. 2D; Guerra & Nixon 1987, pl. 3; Nixon & Maconnachie 1988, pl. 7B; Bromley 1993, fig. 4; Harper 2002, fig. 1; Klompmaker *et al.* 2014, fig. 1) but is not characteristic of muricid borings (e.g. Bromley 1993). According to the definition of Bromley (1993, p. 171), *O. ovalis* 'is normally elongatedly oval in shape but commonly has a somewhat rhomboid form', matching the drill hole herein (see Fig. 3B).

On the walls of some *O. ovalis* drill holes, a wavy relief is visible (Arnold & Arnold 1969, fig. 3; Nixon & Maconnachie 1988, pl.1f- h; Fig. 3D, E, F herein). This morphology could be considered either as traces of a radula (Arnold & Arnold 1969) or erosion of the internal structure of the shell (Nixon *et al.* 1980; Nixon & Maconnachie 1988). The SEM images show the structure of aragonite on the walls of the hole and support the latter hypothesis (Fig. 3 E, F). The size of the opening of 0.5 to 1.0 also falls within the size range of modern and fossil *O. ovalis* – from 0.5 to 4.0 mm in length (Saunders *et al.* 1991; Klompmaker & Landman 2021). Moreover, a typical modern octopodid drill hole is ~0.8 mm long and ~0.6 mm wide (Pilson & Taylor 1961; Hiemstra 2015), which is nearly equal to the size of the Callovian drill hole.

In the absence of signs of healing of the hole in the *Quenstedtoceras* shell, this damage was either caused during a predatory attack that turned out to be fatal for the ammonite, or it was an empty shell lying on the sea floor which was drilled. The second hypothesis seems unlikely for several reasons. First, the absence of epibionts and substantial other traces suggests that the shell was not exposed for long time at the bottom and was quickly buried. Secondly, this ammonite lacks signs of final septal crowding. Septal crowding is a phenomenon in which the distance between the last two or three septa is less than the previous ones. It is characteristic of adult individuals of both ammonoids and nautiloids (Klug *et al.* 2015). The absence of crowding of the last septa in the studied specimen indicates the premature death of this individual before the end of puberty. The drill hole in its shell is likely the result of a predatory attack that led to its death. Moreover, the location of the drill hole in the area of attachment of the retractor muscles (Doguzhaeva & Mutvei 1991; Mironenko 2015b) also suggests a predatory attack. Jurassic ammonites had five main areas of retractor muscles attachment (or 'muscle scars'): one mid-ventral, two dorso-lateral and two large ventro-lateral areas. All of them were located in the rear part of the body chamber (Doguzhaeva & Mutvei 1991; Mironenko 2015b).

Although the muscle scars are not preserved on this specimen, their size and shape can be established by analogy with other *Quenstedtoceras* ammonites in which muscle scars were previously described (Doguzhaeva & Mutvei 1991, pl. 7, figs 1, 2). This comparison shows that the drill hole occurs precisely in the area of the attachment of the large ventro-lateral muscle scar (see Fig. 2C). For cephalopod prey, modern octopuses predominantly drill into *Nautilus* Linnaeus, 1758 and *Allonautilus* Ward & Saunders, 1997 shells in the rear part of the body chamber, where the large lateral retractor muscles are attached, and inject a venom that paralyzes and relaxes the prey's muscles (Pilson & Taylor 1961; Saunders *et al.* 1991; Pech-Puch *et al.* 2016). About 98% of drill holes on the body chambers of nautiluses occur in this part (Saunders *et al.* 1991, fig. 4). Durophagous predators that hunted ammonites in Mesozoic seas also often attacked the same area on the shell, at a small distance from the last septum, leaving characteristic holes – ventral bite marks (Klompmaker *et al.* 2009; Andrew *et al.* 2015; Klug *et al.* 2021). Therefore, it seems unlikely that the drill hole could have accidentally occurred precisely in the area of attachment of the largest ventro-lateral retractor muscle of the ammonite. The absence of drill holes on ammonite phragmocones from the same locality also supports our hypothesis that a predator that could have hunted in the water column and selected a place on the ammonite shell convenient for drilling.

Had the drill hole described herein been found in Upper Cretaceous or Cenozoic deposits, its producer would be considered an octopodoid. No other predators are known to drill similar holes in the shells (Klompmaker & Landman 2021). Rare oval/elliptical holes attributed to drilling gastropods in annelid tubes that are considered a geometric artefact (Klompmaker 2012; Martinell *et al.* 2012) are more regularly shaped. We cannot conclude unequivocally that, in the case of the Callovian specimen, *O. ovalis* was drilled by an octopodoid because there is no evidence of the existence of incirrate octopuses in the Jurassic. In the mid-Cretaceous (Cenomanian), octopuses were already diverse: there were at least two genera in two families – Octopodidae and Palaeoctopodidae, which suggests that these molluscs may have been present in pre-Cenomanian times (Woodward 1896; Fuchs *et al.* 2009; Fuchs 2020). However, it is still unclear when exactly octopuses of suborders Cirrata and Incirrata arose. Molecular clock data suggest that two modern genera of octopodoids, *Octopus* and *Enteroctopus*, likely diverged about 150 million years ago during the Late Jurassic (Kröger *et al.* 2011, suppl. fig. 2). If correct, then Octopodoidea already existed in the Late Jurassic.

Soft body imprints of octopuses are rarely preserved in the fossil record. For example, until very recently there were no reports of fossil octopuses from the Cenozoic, even though they existed throughout this era. Only recently, three specimens of incirrate octopuses were described from the Eocene of Italy (Mironenko *et al.* 2024). The putative ancestors of octopuses belonging to the suborder Teudopseina of the order Octopoda have been known starting from the Toarcian stage of the Early Jurassic (Fuchs 2020). In the Callovian, the genus *Pearceiteuthis* Hewitt & Jagt 1999 from the family Patelloctopodidae already existed, and is considered as the possible ancestor of octopuses of both Cirrata and Incirrata suborders (Fuchs *et al.* 2020, Fuchs, 2020). It cannot be ruled out that these octopus ancestors could have begun to use the drilling method for hunting prey.

On the other hand, miniature trace fossils very similar in shape to octopod drill holes and confidently assigned to *O. ovalis* were discovered on the shells of ostracods (Villegas-Martín *et al.* 2019) and foraminiferans (Blissett & Pickerill 2007). However, they are much smaller (max. 0.09 mm for ostracods and 0.12 for foraminiferans) and could hardly have been drilled by octopuses; therefore, there were probably some other animals capable of producing similar drill holes. It cannot be ruled out that other drilling predators existed in the Jurassic. They could have been larger in size and have drilled large holes similar in size to modern *O. ovalis*.

This first record of Jurassic *O. ovalis* is found on an anomalous ammonite shell. The protuberance on the ventral side of the shell (forma *aegra augata sensu* Kröger 2000) must have decreased the hydrodynamic characteristics of the *Quenstedtoceras* shell and could have attracted the attention of predators. The predator could have selected this ammonite as prey because of the anomalous shape of its shell or its resulting decreased swimming abilities. On the other hand, it could have been coincidental. Many more specimens with preserved body chambers are needed to distinguish between these hypotheses, but ammonite body chambers at the Dubki section are rarely preserved. Unlike pyritized phragmocones, the body chambers are in rare cases filled with pyrite and are often crushed by the pressure of the overlying clay layers.

The drill hole discovered in the Callovian ammonite *Quenstedtoceras* is not the first known drilling on fossil cephalopod shells. Large round holes located on the body chambers not far from the aperture, are known from Silurian nautiloids of the genera *Octameroceras* Hyatt, 1900 and *Pentameroceras* Hyatt, 1884 from the order Oncocerida (Stridsberg 1985, fig. 23). The producer of these holes is unknown. Silurian oncocerids and their close relatives discosorids most likely were benthic cephalopods living near the sea floor, and it cannot be ruled out that they could have been attacked by crawling bottom predators, such as gastropods (for example, while resting).

Many ammonites, including *Quenstedtoceras*, were pelagic marine animals (Westermann & Tsujita 1999; Naglik *et al.* 2015, 2016). The discovery of *O. ovalis* on a Jurassic ammonite is the oldest likely trace of a drilling predator attack on a pelagic cephalopod in the water column. Therefore, it seems likely that drilling on active pelagic prey arose during the Jurassic phase of the Mesozoic Marine Revolution (see Vermeij 1977).

Conclusions

The drill hole found on the shell of the Upper Callovian ammonite *Quenstedtoceras lamberti* belongs to the ichnospecies *O. ovalis*. To date, this is the oldest known specimen of *O. ovalis* and the only one found in Jurassic deposits. The drill hole is located on the body chamber in the area of attachment of the largest retractor muscle and most likely was made by a predator in the water column. All modern drill holes of *O. ovalis* are made by octopuses of the superfamily Octopodoidea. They are found not only on benthic fauna, but also on the shells of modern nautilids, which octopuses hunt in the water column. Although neither soft-body imprints nor octopodid statoliths are known from the Jurassic, some molecular clock data suggest that these incirrate octopuses could have already existed in the Late Jurassic, and probably even earlier. One of them, one of their ancestors, or an unknown predator could have been the producer of this drill hole. One way or another, at the very end of the Middle Jurassic, ammonites were hunted not only by durophagous predators capable of breaking shells, but also by predators that employed drilling as a method of hunting.

Acknowledgments.– We are grateful to Roman Rakitov (PIN RAN, Moscow) for assisting with SEM and micro-CT scanning, to Sergei Kuznetsov and Vladimir Novikov (Saratov) for the donation of ammonite and bivalve specimens used in this study, and Ekaterina Parkhomenko (Samara Paleontological Society) for organizing the research of anomalous ammonites from Dubki quarry, during which the specimen with *O. ovalis* was found. We thank reviewers Max Wisshak (Senckenberg am Meer) and Christian Klug (University of Zurich) for useful comments that strengthened this paper.

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