Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Lower and upper jaws of the Early Permian goniatitid ammonoids

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LETHAIA

Ammonoids – cephalopod molluscs with external shells that existed from the Early Devonian up to the end of the Cretaceous – had well-developed jaws. During ammonoid evolution, several different types of their jaw apparatus arose, the study of which is of undoubted interest since it allows researchers to draw conclusions about the feeding strategies of ammonoids and their position in trophic chains. However, there is a lack of findings relating to the evolution of ammonoid jaws during the Permian. Here we describe a collection of almost thirty of cephalopod jaws from the Divjinskian Formation (Artinskian Stage, Cisuralian, Lower Permian), from the Sverdlovsk region of Russia. Most likely, these jaws belong to goniatitid ammonoid *Uraloceras*, the most abundant cephalopod mollusc in the Divjinskian (Divya) Formation. *Uraloceras* lower jaws are typical ammonoid anaptychi which have a rounded, wide and convex shape with smooth or slightly ribbed surface. They have a large inner lamella with a trapezoidal platform in the central part. One of the jaws bears a possible bite trace of a predator or scavenger. The upper jaws, described here for the first time, are slightly smaller than the lower jaws, their shape is narrow and pointed. Originally, both jaws were completely organic without calcareous elements. The absence of sculpture, consisting of frequent ribs and growth lines, characteristic of the more ancient Carboniferous goniatitid jaws, makes the jaws of the *Uraloceras* closer to the structure of the jaw apparatus of Triassic ammonoids. Judging by the pointed shape of the tips of both jaws, *Uraloceras* were active predators. □ *Permian, Cephalopoda, Ammonoidea, jaw apparatus, anaptychi, Artinskian*

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Ammonoids, like modern cephalopods, had a well-developed jaw apparatus that consisted of a pair of jaws – upper and lower, and a radula enclosed between them. Each jaw consisted of two lamellae – inner and outer. The size ratio of these lamellae varies cephalopods, but for ammonoids the outer lamella is always larger than the inner in the lower jaw, whereas in the upper jaw, on the contrary, the inner lamella is usually larger (see Tanabe *et al.* 2015). Finds of the elements of the ammonoid jaw apparatus are known from deposits of all periods when ammonoids existed: from the Devonian up to the end of the Cretaceous or even to the very beginning of the Palaeogene (Landman *et al.* 2012; Tanabe *et al.* 2015). Many publications are devoted to the study of the ammonoid jaw apparatus, however, the Palaeozoic stage of its evolution is still studied less than the Mesozoic one (see Tanabe *et al.* 2015 and Keupp *et al.* 2016 for review). Of the five types of ammonoid jaw apparatuses identified so far, four belong to the Mesozoic ammonoids and only one belongs to the Palaeozoic (Tanabe *et al.* 2015).

Ammonoids arose at the end of the Early Devonian, in the Emsian (Klug *et al.* 2015). For the Palaeozoic, findings of their jaws are known from the Devonian, Carboniferous and Permian deposits. However, the number of these findings in different periods and the state of their knowledge is very inconsistent. It is widely accepted that the oldest known ammonoid jaws to date come from the Late Devonian (Frasnian) deposits (Tanabe *et al.* 2015; Klug *et al.* 2016). Indeed, the largest number of Devonian ammonoid jaws comes from the Frasnian and belongs to Gephuroceratidae (Woodward 1885; Trauth 1927). A smaller number of ammonoid jaws is described from Famennian deposits (Fry & Feldmann 1991; Korn 2004; Klug *et al.* 2016). Initially, the lower jaws of the Devonian ammonoids were considered as crustacean phyllopods and were included in the suborder Discinocarina (e.g. Woodward 1882). One of the genera of discinocarins, *Lisgocaris*, was described by Clarke (1882) from the deposits, which, according to modern data, belong to the Givetian stage of the Middle Devonian (see Frye & Feldmann 1991; Jones & Olempska 2013). Therefore, it turns out that the oldest jaws of ammonoids are known from the Givetian. There is no doubt that the Emsian and

https://doi.org/10.18261/let.55.4.2

Eifelian ammonoid jaws must also have existed (Klug *et al.* 2016), and the absence of their findings is most likely due to taphonomic reasons (see Mironenko 2021).

Finds of ammonoid jaws are quite numerous in Carboniferous (both Mississippian and Pennsylvanian) deposits (Closs 1960, 1967; Mapes 1987; Bandel 1988; Tanabe & Mapes 1995; Doguzhaeva *et al.* 1997; Doguzhaeva 1999; Landman *et al.* 2010; Kruta *et al.* 2014). Findings of Triassic ammonoid jaws are also very numerous, which is reflected in a large number of publications that are devoted to these fossils (see Tanabe *et al.* 2015 for review). However, the knowledge about ammonoid jaws of the Permian is very scarce. The jaws of Permian ammonoids have been described to date only a few times. For the first time they were described at the end of the 19th century from the Artinskian stage of the Perm region of Russia (Krotov 1885). One ammonoid jaw, oddly identified as an aptychus, was described from the Artinskian deposits of the vicinity of the City of Krasnoufimsk by A.P. Karpinsky (1890, 1891). Frederiks (1915) also depicted a specimen from the Lower Permian of Krasnoufimsk and interpreted it as aptychus, but we re-examined this record and concluded that it is not related to cephalopod jaws. One ammonoid lower jaw (anaptychus) was described from the body chamber of the ammonoid *Paraceltites rectangularis* Miller from the Permian (Capitanian) deposits of Mexico in an unpublished Ph.D. dissertation by Spinosa (1968). Several small Permian lower jaws (anaptychi) were also described as a new formal species *Anaptychus ruzhencevi* by Ju.D. Zakharov (1979). However, these data are very limited, the number of specimens published so far is very insignificant, and in fact, we can only imagine how the ammonoid jaws changed throughout the Permian by comparing the older Carboniferous and younger Triassic specimens with each other. Permian ammonoid jaws themselves had still remained practically unexplored. The upper jaws of Permian ammonoids had never been described.

In this paper we describe a collection of Permian ammonoid jaws consisting of 28 specimens. All the jaws come from the Divjinskian Formation of the Artinskian Stage (Cisuralian, Lower Permian) outcropped in the vicinity of the City of Krasnoufimsk, the Sverdlovsk region, Russia (Fig. 1). All specimens

Fig. 1. Locality maps. A, Krasnoufimsk on the map of Russia. B, Krasnoufimsk surroundings. C, localities where ammonoid jaws have been found: 1, Krasnoufimskie Klyuchiki; 2, Za Selekciey; 3, Sobolya; 4, Cherkasovo.

studied are housed in the collection of the Vernadsky State Geological Museum (Moscow). The collection includes both well preserved lower and upper jaws. This is the largest set of Permian ammonoid jaws studied to date. Excellent preservation of many specimens allowed us to study the original shape of the jaws and make some assumptions about the ecology of their possible hosts — goniatitid ammonoids of the genus *Uraloceras* Ruzhencev, 1936.

Geological settings

Cephalopod jaws were collected by one of us (SVN) at four localities in the vicinity of the City of Krasnoufimsk, the Sverdlovsk region, Russia (Fig. 1). The localities are Krasnoufimskie Klyuchiki – from which the most of the specimens originated (22 jaws), Sobolya (3), Za Selekciey (2) and Cherkasovo (1) (see Naugolnykh 2018). All jaws were found in bluish-grey plate marls of the Divjinskian Formation, Sarginskian Horizon of the Artinskian Stage (Cisuralian, Permian). Besides cephalopod jaws, the Divjinskian Formation (Naugolnykh 2016, 2018; also known as Divya Formation, e.g. Lebedev 2009) in the area of the City of Krasnoufimsk contains carapaces of trilobites, numerous remains of fish (including tooth whorls of *Helicoprion bessonowi* Karpinsky), conulariids, and large shells of nautiloids and ammonoids. It should be noted that aragonitic layers of the shells of cephalopods of the Divjinskian Formation are completely dissolved, whereas their internal moulds are well-preserved. At the same time phosphatic fossils and carbonized organic matter of plant remains and cephalopod jaws are well-preserved in these beds. Due to findings of *Helicoprion* Karpinsky tooth whorls, the Divjinskian Formation is sometimes called '*Helicoprion* Marl Formation' (Naugolnykh 2016). However, the most common type of fossils in the Divjinskian Formation are trace fossils – winding tracks of crawling worm-like benthic animals, which lived in the bottom silt or on its surface (for example Naugolnykh 2016, fig. 2). These trace fossils can be attributed to the formal genus *Helminthoides* (Mikulash & Dronov 2006).

The Artinskian basin in the Krasnoufimsk area was a part of the Cisuralian Artinskian sea basin, which was connected to the Boreal Ocean in the north and the Tethys Sea in the south (Naugolnykh 2018). The rarity of findings of benthic animals with the dominance of ichnofossils and remains of pelagic organisms (cephalopods and fishes) indicates that these sediments were formed at a relatively considerable depth (Naugolnykh 2016, 2018). In addition, the presence of adverse factors, such as oxygen deficiency or increased salinity in the bottom water layer, cannot be excluded.

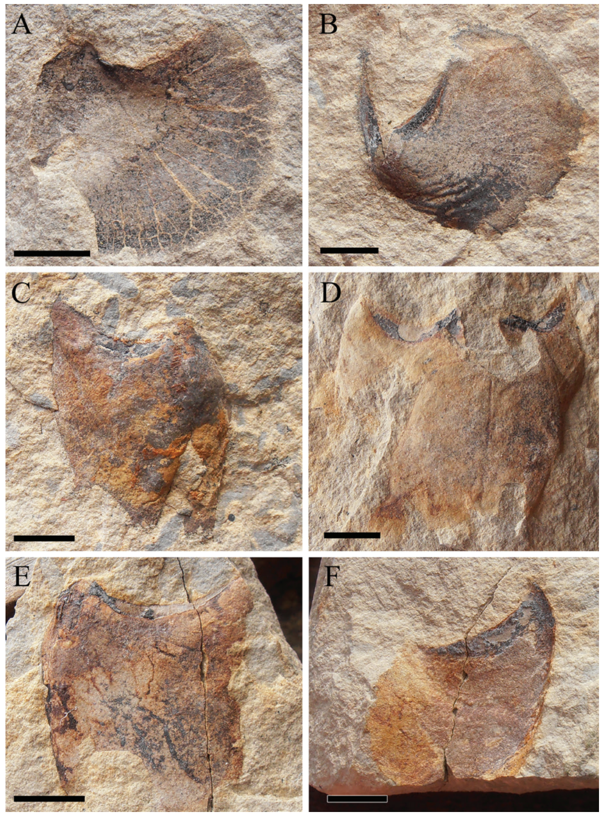

Fig. 2. Lower jaws in which only one outer lamella or its imprint is exposed. A, specimen K-R/9. B, K-R/8. C, K-R/5. D, K-R/11. E, K-R/21. F, K-R/12. Scale bars: 5 mm.

Methods and material

Specimens studied herein were examined both with an optical binocular microscope and under a scanning electronic microscope (SEM; TESCAN//VEGA with a retractable BSE detector) at the Palaeontological Institute of Russian Academy of Science (PIN RAS). However, the study on SEM did not bring significant results due to insufficient preservation of the organic layers of the jaws.

Among the 28 jaw specimens studied herein, 23 are identified as lower jaws (two of them – tentatively) and five are identified as upper jaws (one of them tentatively). Most of the findings are casts or imprints of one or two lamellae of the jaws, formed by fine-grained sediment. The organic layers of the jaws are usually absent. However, in some specimens of the lower jaws, the carbonized organic matter is preserved in the thickened parts along the anterior edge, at the sides of the tip, at the junction of the outer and inner lamellae, and in some cases even as a thin layer on the surface of the impressions of external lamellae. The lower jaws can be divided into three groups according to the degree of preservation.

The first and most numerous group comprises specimens in which only one outer lamella or its imprint is preserved or visible (Fig. 2). Such specimens allow us to understand the general shape of these lower jaws: they were wide, with a rounded posterior edge and a pointed anterior tip. The jaws were originally convex, some of them were flattened during the diagenetic compaction of the sediment and had cracked along the posterior edge with numerous cracks (for example, specimen K-R/9, see Fig. 2A). Such shape is typical of the Palaeozoic and Mesozoic ammonoid anaptychi (see Tanabe *et al.* 2015). In the vast majority of the jaws, the outer plate looks monolithic, but in the specimen K-R/11 (Fig. 2D) a thin groove runs along its central part. This groove is somewhat reminiscent of the symphysis of the aptychi of the Mesozoic ammonites. In some cases, the outer lamella of the lower jaws has slightly wavy shape with wide gently sloping ribs (Fig. 2B). Nevertheless, it is difficult to say whether this is its original shape or the result of post-mortem deformations. The anterior tips of the jaws are sharp.

The second group includes specimens in which an imprint of the inner lamella of the lower jaw is also visible together with the outer plate (Fig. 3). The inner lamella is wide and long, at least half the length of the outer lamella. In the central part of the inner lamella there is a flattened trapezoidal platform, which narrows towards the tip of the jaw and expands posteriorly (Fig. 3A,B,D).

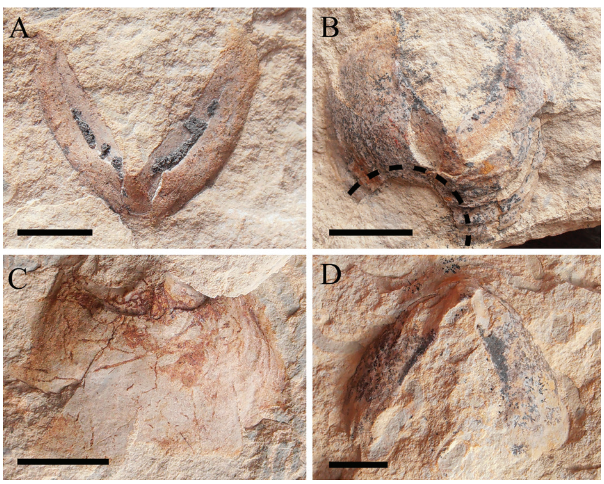

Fig. 3. Lower jaws in which an imprint of the inner lamella of the lower jaw is also exposed, together with the outer plate. A, specimen K-R/7. B, K-R/13. C, K-R/2. D, K-R/6. Scale bars: A, D, 5 mm; B, C. 1 cm.

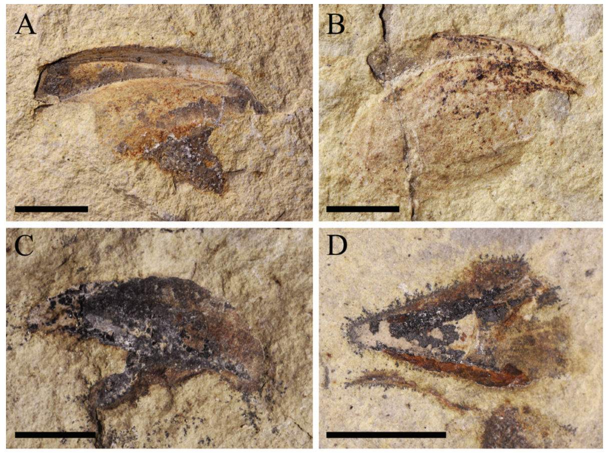

Fig. 4. Upper jaws. A, specimen K-R/22. B, K-R/26. C, K-R/19. D, K-R/27. Scale bars: 5 mm.

The third group of specimens studied includes fragmentary preserved jaws, the interpretation of which is often difficult due to incomplete preservation. We do not provide their images, since they are worth mentioning only in the sense of counting the number of findings, but are not of interest for the reconstruction of the structure of the jaws.

The upper jaws (Fig. 4) are much narrower and sharper than the lower ones. In most cases, only their outer lamella with an elongated anterior tip and lateral protrusions being visible (Fig. 4C,D). The size of the upper jaw specimens, on average, is smaller than the size of the lower ones, and although no pair of jaws was found (i.e. both the upper and lower jaws from the same animal), it can be assumed that the upper jaws were somewhat smaller in size than the lower ones. At the same time, the division of the inner lamellae into two elongated halves, typical for the upper jaws of the Mesozoic ammonites, was not detected in the specimens studied herein.

Both Permian upper and lower cephalopod jaws studied here contain no signs of calcareous elements. Whereas calcite and aragonite of mollusc shells are not preserved in the Divjinskian Formation, internal moulds and imprints of shells are preserved with excellent detail. Since the studied jaws did not contain any imprints of the calcareous rhyncholites or conchorhynchs, they most likely were completely organic.

Discussion

Affiliation of the hosts of the cephalopod jaws studied

In the marls of the Divjinskian Formation the internal moulds of nautiloid and ammonoid shells are present together with the cephalopod jaws. Nautiloids are represented by three orders: Oncocerida, Pseudorthocerida and Nautilida (Naugolnykh 2016, 2018) (Fig. 5). Oncocerids of the genus *Scyphoceras* Ruzhentsev and Shimanskiy from the family Scyphoceratidae (suborder Rutocerina) are the rarest cephalopods in these deposits (Fig. 5A). These unusual cyrtoconic nautiloids with a wide voluminous body chamber and a small phragmocone were previously considered as representatives of the order Nautilida (Ruzhentsev & Shimanskiy 1954). However, many researchers currently consider the Rutoceratina as a part of the Oncocerida (e.g. Manda & Turek 2011), therefore, *Scyphoceras* belongs to this order. Given the rarity of *Scyphoceras* in the Divjinskian Formation and the fact that the jaws have never been found in association with oncocerids (Mironenko 2021), it is unlikely that the jaws described herein belong to this genus.

Coiled nautilids (*Metacoceras artiense* Kruglov) are also rare in the Divjinskian Formation (Fig. 5B), and it is highly unlikely that the studied jaws belonged to them due to their rarity. Straight-shelled pseudorthocerids (*Dolorthoceras siphocentrale* (Krotov), *Dolorthoceras* sp.) are more common (Fig. 5C); however, there is a great deal that remains unclear about the jaws of this group of cephalopods. Very few findings of their jaws have been described to date. The Late Missisippian *Gordoniconus beargulchensis* Mapes, Weller & Doguzhaeva with a preserved jaw apparatus, which was originally described as orthoconic nautiloid (Landman & Davis, 1988) is currently considered a representative of Coleoidea (Mapes *et al.* 2010; Klug *et al.* 2019), so its jaws cannot be considered an example of nautiloid mandibles. The jaws of Carboniferous pseudorthocerid *Reticycloceras* Gordon have also been mentioned by Mapes (1987), nevertheless, the photos given in this publication are not enough to understand the shape and size of these jaws. Notwithstanding, Mapes (1987) cited an oral communication with R.S. Cox, relating to cephalopods collected in Mississippian (Carboniferous) beds of central Montana (USA), in which finds of the jaws of orthoconic nautiloids are much rarer than those of ammonoids from the same layers and localities.

Fig. 5. Cephalopods from the Divjinskian Formation. A, oncocerid *Scyphoceras*. B, nautilid *Metacoceras artiense*. C, pseudorthocerid *Dolorthoceras* sp. D, goniatitid ammonoid *Uraloceras* sp. with the lower jaw (specimen K-R/1). E, enlarged image of the lower jaw from D. Scale bars: 1 cm.

Therefore, it is most likely that Permian jaws from the Krasnoufimsk area belong to ammonoids, since the shells of these cephalopods are much more numerous in the layers of the Divjinskian Formation than the shells of nautiloids, and the size and shape of the jaws fully coincides with those of the previously described ammonoid lower jaws. Most likely, the jaws belong to the ammonoids of the genus *Uraloceras* Ruzhencev (Paragastrioceratidae, Goniatitida), the shells of which are most numerous in the Divjinskian Formation. This is also confirmed by the location of one of the jaws near the internal mould of the *Uraloceras* shell (specimen K-R/1, see Fig. 5D,E). Since fossils in these marls are rare and most of them are found at a great distance from each other, such a proximity is hardly accidental. The attribution of these jaws to goniatitid ammonoids is also confirmed by their similarity with the lower jaws of the Mississippian goniatitid *Cravenoceras* Bisat, which also have large inner lamellae (Kruta *et al.* 2014).

Some of the specimens (Fig. 3A,D) resemble Upper Cretaceous cephalopod jaws recently described as possible lower jaws of vampyropod coleoids (Klug *et al.* 2020). However, firstly, the findings of such coleoids have never been reported from the Artinskian deposits, and secondly, the trapezoidal shape of the central platform of the inner lamellae of these jaws is completely identical to that of the specimens K-R/2 and K-R/13 (Fig. 3C, 3B respectively) which are undoubtedly ammonoid anaptychi. Therefore, it is most likely that the shape of the specimens K-R/7 and K-R/6 is caused by their almost vertical arrangement in the sediment, whereas they are of the same type as the specimens K-R/2 and K-R/13. Therefore, we assume that all these lower jaws are ammonoid anaptychi.

Interpretation of the specimens of the upper jaws from the Divjinskian Formation is somewhat more complicated. They are similar to coleoid jaws, but in the absence of findings of coleoid guards or gladii mentioned above, we have no reason to consider the presence of these cephalopods in the Cisuralian Artinskian sea basin. The upper jaws of the Permian ammonoids, according to our knowledge, have not yet been described. In general, there is an interesting paradox which lies in the fact that the lower jaws of ammonoids in a fossil state, as a rule, greatly outnumber the upper jaws. Findings of the upper jaws are much rarer. According to Tanabe *et al.* (2015) *in situ* findings of jaw apparatuses are known from 109 ammonoid genera, whereas upper jaws are known only from 41 genera. This is well-reflected in the history of study of the ammonoid jaws. Whereas the aptychi and anaptychi (both are lower jaws) of ammonoids have been known since 1702 (see historical review in Trauth 1927), the first ammonoid upper jaw was only described a century and a half later, in 1864 (Meek & Hayden 1864). Following a long hundred-year break the second time that upper jaws were described was in 1967 (Closs 1967; Lehmann 1967). Fortunately, several specimens of Carboniferous (Closs 1967; Mapes 1987; Bandel 1988; Doguzhaeva *et al.* 1997) and one specimen of Upper Devonian (Klug *et al.* 2016) ammonoid upper jaws have been described to date. Our findings differ markedly from the Devonian upper jaw of the clymeniid ammonoid *Postclymenia* which, oddly enough, resembles the upper jaws of the Mesozoic ammonites. However, Permian specimens are very similar to the Carboniferous upper jaws of goniatitid ammonoids (Doguzhaeva *et al.* 1997). Therefore, we assume that the upper jaws described herein, as well as lower jaws belong to the goniatitid ammonoids of the genus *Uraloceras*.

Jaw apparatus of Uraloceras *and the question of the existence of Palaeozoic aptychi*

According to the ammonoid jaw type classification (see Tanabe *et al.* 2015), the jaws of Permian *Uraloceras* should be attributed to the normal type, as well as the jaws of Carboniferous ammonoids, due to the shape of the upper jaw. At the same time, the jaws of *Uraloceras* differ from the jaws of Late Carboniferous goniatitid ammonoids. Both the upper and lower jaws of these more ancient goniatitids usually bear a sculpture represented by fine ribs and growth lines (Doguzhaeva *et al.* 1997; Doguzhaeva 1999), whereas the Permian jaws are either smooth or covered with sparse undulating ribs. Therefore, the jaws of the Permian goniatitids from the Divjinskian Formation are more similar to later Triassic ammonoid jaws of the anaptychus type, than to the jaws of their Carboniferous ancestors.

Earlier, Karpinsky (1890, 1891) described an ammonoid lower jaw from the Artinskian deposits of the vicinity of Krasnoufimsk, interpreting it as an aptychus. Aptychi are paired symmetrical elements of the aptychus-type lower jaws, which, according to modern concepts, arose in the Toarcian (Early Jurassic). The lower jaws of the aptychus type are separated by a flexible ligament (symphysis) along the central line, which often disintegrated after the death of the mollusc, and the symmetrical halves of the jaw (the aptychi) were buried separately. Anaptychi, on the other hand, are monolithic lower jaws, which are not divided into easily separable halves. The only specimen depicted by Karpinsky does indeed resemble an aptychus. However, we assume, that the definition of the Artinskian specimen as an aptychus was erroneous. Judging by its schematic representation (Karpinsky 1890, fig. 56; Karpinsky 1891, fig. 15) this specimen is almost identical to the specimen K-R/12 described here (Fig. 2F), which is an imprint of the right half of the anaptychus. Judging by both this specimen and another similar specimen (Fig. 2E), the *Uraloceras* anaptychi were sometimes buried in a lateral position, folded along the middle line. It is possible that the median groove, which is visible in one specimen (Fig. 2D) could have facilitated such folding. Even though this groove may reflect the appearance of a more or less flexible symphysis between the two halves of the lower jaw, which subsequently facilitated appearance of the aptychi, the lower jaws of *Uraloceras* undoubtedly should be classified as anaptychi.

At the same time, it is premature to consider the discussion of the existence of the aptychi in the Palaeozoic as closed. Many reports of the Palaeozoic aptychi findings, as in the case of the Permian specimen mentioned above, are clearly erroneous (for example, specimens described by Kues (1983 are actually bivalves). However, in 1841 a pair of aptychi was described from the Eifel limestone (Eifelian/Givetian, Middle Devonian, d'Archiac & de Verneuil,1841: tabl. XXVI. fig. 9). Holzapfel (1899) questioned the age of this find, but confirmed that he had found similar specimens from the shales of Büdesheim (Frasnian, Upper Devonian). These aptychi surprisingly resemble the Frasnian anaptychi of the formal genus *Cardiocaris* which belonged to the goniatitid ammonoids (see Mironenko 2021). Another pair of aptychi has been described by Harper (1989) from the Carboniferous Ames Limestone of western Pennsylvania (see Harper 1989, fig. 2). Isolated findings always leave room for doubt, however among 'proto-jaws' of ammonoid ancestors – orthocerids (formal genera *Aptychopsis, Discinocaris* and *Peltocaris*) both the single- and double-valved forms had existed (Mironenko 2021). Therefore, it cannot be excluded that some evolutionary lineages with bivalved lower jaws could have existed among the early ammonoids, but this topic requires further research.

Ecological implications

Judging by the structure of the jaw apparatus (see Fig. 6), *Uraloceras* were either an active predator or a scavenger. This is evidenced by the lower jaws with a thick anterior margin, well preserved in the fossil state, and the pointed upper jaws. Although the Permian ammonoids did not have calcitic elements in their jaws (they appeared only in the Early Jurassic, see Mironenko & Gulyaev 2018), this could not have prevent them from being active predators, since modern squids and octopuses also have no such mineralized elements in their beaks, but able to hunt even such well-protected prey such as crabs and other crustaceans. It is difficult to say what kind of animals the *Uraloceras* hunted, however, based on the rarity of the benthic fauna in the Divjinskian Formation, it is most likely that they caught their prey in the water column. Most likely, fish were their prey, as well as small-sized cephalopods, such as other ammonoids and pseudorthocerids.

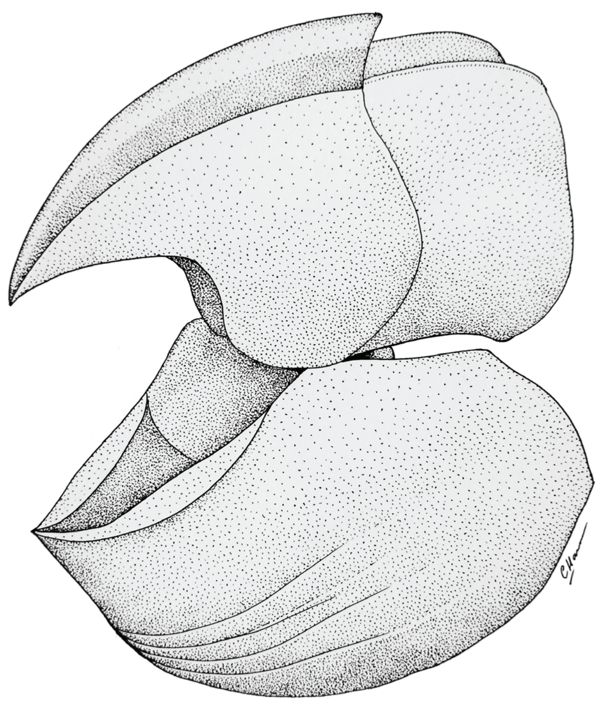

Fig. 6. General shape of the *Uraloceras* jaw apparatus. Both jaws are shown here of the same size, though the real ratio of their sizes could differ.

Many of the *Uraloceras* lower jaws studied herein show some damage (Fig. 2A,C,D), but almost all of them are most likely were caused by uneven compaction of the sediment and post-mortem deformations. However, in one case (specimen K-R/13 – Fig. 3B), in the posterior part of the jaw to the left of the centre, there is a wide semicircular opening whose formation cannot be explained by post-mortem deformations. Since the fragment of the jaw corresponding to this opening is missing, and the sediments in which the specimen was buried were formed under low-energy conditions without any strong currents, this opening is most likely the result of a predator attack or scavenger actions.

With the exception of two specimens (K-R/1, see Fig. 5A, and poorly preserved K-R/24), all the lower jaws studied herein were found separated from the shells of ammonoids and from the corresponding upper jaws. This suggests that the jaws were already separated from the shells while floating in the water column (see Klug *et al.* 2021), either as a result of decomposition of soft tissues or the activity of predators. The aforementioned damage on one of the lower jaws confirms that *Uraloceras* ammonoids could sometimes have fallen a prey to predators, including individuals of about more or less the same size as the ammonoids themselves.

Conclusions

Cephalopod jaws from the Divjinskian Formation of the Artinskian Stage (Cisuralian, Lower Permian) described herein most likely belonged to goniatitid ammonoids of the genus *Uraloceras*. The lower jaws are typical anaptychi, wide and convex, with a smooth or slightly ribbed outer lamella, and a relatively large inner lamella. A trapezoidal flat area is located in the central part of the inner lamella. The lamellae are fused together anteriorly, forming the pointed tip of the jaw and thickened 'shoulders' on its margins. A groove runs along the middle of the outer lamella of one of the specimens, somewhat reminiscent of the symphysis of the aptychi of the later Mesozoic ammonoids. The upper jaws of the *Uraloceras* are smaller than the corresponding lower jaws, they are narrow and have pointed tips. Both lower and upper jaws were completely organic, devoid of calcareous elements.

Due to the upper jaw having a large pointed hood, *Uraloceras* mandibles should be classified as a so-called normal type of ammonoid jaw (Tanabe *et al.* 2015). However, the absence of sculpture, consisting of the frequent fine ribs and growth lines, which are characteristic of the more ancient Carboniferous goniatitid jaws (Doguzhaeva *et al*. 1997, fig. 1; Doguzhaeva 1999: table 1, figs 1,3), makes the jaws of *Uraloceras* closer to the structure of the jaw apparatus of Triassic ammonoids. The presence of a central groove in one specimen and the fact that these lower jaws sometimes are folded along the central line, allow us to suggest that some sort of flexible symphysis could have appeared in the ammonoid jaws already in the Permian. Later in the Early Jurassic it led to the appearance of the aptychus-type of jaws.

Judging by the pointed shape of both jaws, the representatives of the genus *Uraloceras* most likely were active predators. Nevertheless, as they lacked reinforcing calcareous elements in their jaws, they hunted prey that had no strong outer shells. As evidenced by the finding of a damaged lower jaw, the *Uraloceras* themselves could also become victims of predators that were comparable to them in size.

Acknowledgements. – We are very grateful to the anonymous reviewers and the handling editor Peter Doyle, for their helpful and fruitful comments on the manuscript. We thank Mikhail Rogov (GIN RAN, Moscow, Russia) for the helpful and valuable comments on the draft version of the manuscript.

This work was fulfilled in a framework of the State Program of the Geological Institute of Russian Academy of Sciences, Moscow, Russia.

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