

New Ammonoids from the Devonian–Carboniferous Boundary Beds in Berchogur (Western Kazakhstan)

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Abstract—Old and new ammonoid collections from the Devonian–Carboniferous Boundary Section in Berchogur (Western Kazakhstan) are examined. The ammonoids come from the *Acutimitoceras* Genozone, from beds similar in age to the Stockum Fauna of Germany. The assemblage includes mostly species of the genera *Imitoceras* and *Acutimitoceras*, with diverse shapes of initial whorls. The new species *Acutimitoceras alabassense* sp. nov. and *A. dzhanganense* sp. nov. are described.

Keywords: ammonoids, Devonian–Carboniferous Boundary, Berchogur, Kazakhstan, *Acutimitoceras*

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INTRODUCTION

The Berchogur section in Western Kazakhstan is one of a few sections of the Devonian–Carboniferous boundary beds with ammonoids in the South Urals, including its southern termination, the Mugodzhary Mountains. Ammonoids from this locality were studied by Librovitch (1940), Balashova (1953), Kusina (in Barskov et al., 1984; Kusina, 1985 in Barskov et al., 1988) and Bogoslovsky (*Fauna i biostratigrafiya ...*, 1987). All researchers commented on the high significance of this section for solving the problem of the Devonian–Carboniferous boundary, because apart from ammonoids, the Berchogur section contains conodonts, foraminifers, spores and pollen, brachiopods, corals, conularians, gastropods, and trilobites (Simakov et al., 1985; *Fauna i biostratigrafiya ...*, 1987; Barskov et al., 1988). The study of assemblages of these organisms showed that ammonoids in this section come from the lowermost Carboniferous (*Fauna i biostratigrafiya ...*, 1987), because they belong to the *Acutimitoceras* Genozone. The Berchogur section was extensively studied in the 1980s, until the current D–C boundary level based on the FAD (First Appearance Datum) of the conodont *Siphonodella sulcata*, with a stratotype in La Serre (France), was ratified. From 2009, the Devonian–Carboniferous boundary is again under re-consideration because in the stratotype section, *S. sulcata* was discovered below the established boundary level immediately above the facies break (Kaiser et al., 2009). Because of this and because of the absence of conodonts immediately below the current boundary in La Serre, the new boundary level cannot be established there. Currently the Interna-

tional Working Group on the Devonian–Carboniferous boundary continue the search for a new boundary marker and new GSSP section, so the reference sections of all regions are being re-examined to provide the best correlation potential. In addition, it should be noted that changes in the biota and paleoenvironments in the boundary interval are best studied in the basins of Western Europe and Morocco (Walliser, 1984; Becker et al., 2016). There is also a great deal of information on sections in Kazakhstan and Central Asia (Simakov et al., 1985; Barskov et al., 1988) and China (Ruan, 1981; Sheng in Ji et al., 1989; Qie et al., 2015; Zhang et al., 2019).

Recently the examination of the Berchogur section in Western Kazakhstan was resumed aiming to precisely record the position of ammonoid occurrences relative to other fossils in the sections. Paleontology and sedimentology of all the localities are being studied. In two field seasons (2018 and 2019) a team from Moscow and Ufa (both Russia) and Almaty (Kazakhstan) re-sampled the sections and collected new ammonoid material alongside conodonts, foraminifers, corals, brachiopods, and crinoids. The first results of the re-examination of the ammonoids are presented in this paper.

MATERIAL

This paper is based on unpublished material of ammonoids from Western Kazakhstan collected in 1981–1983 by a team from the Paleontological Institute of the Academy of Sciences of the USSR under the leadership of B.I. Bogoslovsky, and a team from

the Geological Faculty of Moscow State University led by I.S. Barskov, and new material collected by the expeditions organized by the K.I. Satbayev University under the leadership of S.N. Mustapayeva in 2018–2019. All ammonoids come from several localities on the left bank of the upper reaches of the dry Burtybai (Dzhangansai) Creek (tributary of the Shyuldak River), in its meridional portion, 1 km north of the new Alabas Quarry in the Shalkar District of the Aktobe Region. The collecting sites are several closely situated localities in the Dzhangana Formation, which are traditionally named “Berchogur” after the nearby village of Berchogur (Birshogyr) and the railway station of the same name. Most ammonoids are from Member 3 of Section BK-3 on the left bank of Burtybai (Dzhangansai) Creek (coordinates 48°34′08″ N, 58°40′23″ E), which in the literature and various field labels of 1981–1983 is also referred to as “site 3”, “Trench BK-3, Sample 1”, “Trench BK-3, Sample 2”, “834 near BS-2”. The precise position of Sample 1, Sample 2 and 834 near BS-2 was not indicated on the original logs by previous authors. Additional material was collected from Locality 5, 10 m north of Section BK-3 (top surface of Member 3), Locality 6, 300 m north and upstream in the creek on the left bank (coordinates 48°34′15.77″ N, 58°40′26.01″ E), and Member 4 of Section BK-3 (loose, Locality 7) (coordinates 48°34′09.7″ N, 58°40′22.3″ E). The studied collections are housed in the Paleontological Institute of the Russian Academy of Sciences (PIN), Moscow, coll. nos. 1266, 4005, 5643.

ABBREVIATIONS

Dm—shell diameter, WH—whorl height, WW—whorl width, UW—umbilical width, W—whorl expansion rate; PIN—Paleontological Institute of the Russian Academy of Sciences (Moscow).

AMMONOIDS AT THE DEVONIAN–CARBONIFEROUS BOUNDARY

At the end of the Devonian, rich and diverse ammonoid faunas existed in the basins of the Urals, Tien-Shan, China, Western Europe, North Africa, and North America. They were represented by the orders Clymeniida, Agoniatitida, and Goniaticida. Clymeniids with their dorsal siphuncle and diverse shell morphology were particularly widespread and abundant. Agoniatitids were in decline, and goniaticids were mostly represented by one or two morphotypes with very involute whorls and a suture with undivided ventral lobe and simple lateral lobe. The umbilical lobe was located on the umbilical suture. At the very end of the Devonian all ammonoid orders were in a state of crisis, which resulted in the disappearance of clymeniids and agoniatitids and a profound decrease in the diversity and abundance of goniaticids. Ammonoids of the Devonian–Carboniferous bound-

ary beds are best studied in Germany, Austria, and France (Schindewolf, 1937; Vöhringer, 1960; Walliser, 1984; Korn, 1992; Becker, 1996; Bartsch and Weyer, 1996; Korn and Weyer, 2003; Korn and Feist, 2007, etc.), where they are found in cyclic series, including, among others, the Hangenberg Shales, Hangenberg Sandstone and Stockum and Hangenberg Limestones. The deposition occurred in a sequence of transgressive and regressive episodes that played a prominent role in the history of the Rhenish Massif and its adjacent areas (Price and House, 1984; Becker, 1993, 1996; House, 1993; Korn, 1993, 2000; Becker et al., 2016, etc.), and affected the diversity of its inhabitants. The extinction event at the end of the Devonian, the so-called “Hangenberg Event”, was associated with a brief flooding of the shelf and development of the dysoxic and anoxic environments and deposition of the Hangenberg Black Shale in the ammonoid phase UD-VI-E (within the Middle *praesulcata* conodont zone). The black shale contains goniaticids of the family Prionoceratidae and the last clymeniids. The presence of other ammonoid taxa is questionable. This event is also fixed in other regions of the world, e.g., in South China and North America (Becker et al., 2016). In general, the ammonoid assemblage from the Hangenberg Black Shale is strongly impoverished (genera *Mimimitoceras*, *?Sporadoceras*, *Postclymenia*, *Cymaclymenia*) (Zhang et al., 2019). This level can be considered as a completion of the Devonian history of the ammonoid evolution. The flooding was followed by a shallowing episode (Hangenberg Sandstone), and then by a new transgression (Stockum and Hangenberg Limestones), with a new ammonoid assemblage, containing none of the species that occur in the black shales (Walliser, 1984, 1996). The Hangenberg Sandstone (UD-VI-F) contains the earliest confirmed representatives of *Acutimitoceras*, and this is the level where the base of the ammonoid genozone is drawn (e.g., in the Rhenish Massif and adjacent regions). The appearance of abundant *Acutimitoceras* is fixed in the Stockum Limestone and its equivalents (=lowermost part of the Hangenberg Limestone) (upper part of UD VI-F to LC-I A₁) (Becker et al., 2016; Zhang et al., 2019). The assemblage of this genozone consisting exclusively of prionoceratids (genera *Imitoceras*, *Nicimitoceras*, and *Acutimitoceras*), differs in the presence of shells with evolute initial whorls, which apparently gave rise to the Tournaisian morphotypes (e.g., the genera *Gattendorfia*, *Zadelsdorfia*, *Voehringites* and the order Prolecanitida) (Korn and Weyer, 2003, etc.). The current Devonian–Carboniferous boundary drawn based on the first appearance datum of the conodont *S. sulcata* lies within the *Acutimitoceras* Genozone, above the level of the main extinction event (Becker et al., 2016) and possibly within the *A. prorsum* Zone (Korn and Weyer, 2003). A new boundary level, which is very likely to be chosen near the first appearance of the conodont *Protognathodus kockeli*, also lies within this zone, near the base of the Stockum Limestone.

AMMONOID ASSEMBLAGE
OF THE ACUTIMITOCERAS GENOZONE
FROM KAZAKHSTAN

In Kazakhstan, the earliest Carboniferous ammonoids are known from the Devonian–Carboniferous boundary beds in the Karaganda and Aktobe regions. The older, early Famennian ammonoid assemblages contain members of the three ammonoid orders (Clymeniida, Goniatiitida, Agoniatiitida). These assemblages were very diverse and were dominated by clymeniids. At the end of the Famennian (before the conodont *S. sulcata* phase) all these ammonoids became extinct, and the basins were inhabited by prionoceratid assemblages of the *Acutimitoceras* Genozone (genera *Acutimitoceras*, *?Nicimitoceras*, *Imitoceras*). In the Karaganda Region, Librovtich (1940) indicated localities with species presently assigned to the genus *Acutimitoceras*. These are (1) Aina-Su (left tributary of the Nura River), Outcrop 553 [*?Nicimitoceras* cf. *?carinatum* (Schmidt, 1924), *A. subbilobatum* (Münster, 1839) = possibly, *A. dzhanganense* sp. nov.], Outcrop 1375 [*A. subbilobatum* (Münster, 1839) = possibly, *A. dzhanganense* sp. nov.], (2) basin of the Sherubai-Nura River (Sulu Creek), Outcrop 2126 [*A. intermedium* (Schindewolf, 1923)], (3) vicinity of Tyugelbai Hill (Outcrop 1046) [*A. "rotiforme"* (Librovitch, 1940)], (4) Karamaysolgan, Outcrop 1349 [*A. intermedium* (Schindewolf, 1923)], (5) Maiuzek Hill, southern slope of Terekty Mountain (Outcrop 926) [*A. subbilobatum* (Münster, 1839) = possibly *A. dzhanganense* sp. nov.], Outcrop 103 [*A. intermedium* (Schindewolf, 1923)].

In the Shalkar District of the Aktobe Region, two areas with ammonoids of the Devonian–Carboniferous boundary beds—in the east and west of the Berchogur Depression (Syncline) are known. Balashova (1953) studied ammonoids from the western regions of the depression, and Kusina (1985), from the northeastern regions, in the upper reaches of Burtybai Creek (in its meridional portion, Section BK-3). Balashova (1953) indicated the following ammonoid occurrences in the Berchogur Depression: (1) Aktan and Kust-Kara dry rivers—*A. intermedium*, *A. cf. rotiforme*, *A. dzhanganense* sp. nov. (identified by Balashova as *I. subbilobatum*), (2) middle reaches of the Sarysai River—*A. cf. rotiforme*, *A. dzhanganense* sp. nov. (identified by Balashova as *I. subbilobatum*), (3) west of the Dzhan-Gana Range, Tungulyk-Bulak Gully—*A. alabasense* sp. nov. (identified by Balashova as *I. substriatum*), *I. bertchogurense*, *A. dzhanganense* sp. nov. (identified by Balashova as *I. subbilobatum*); (4) Kabaksai River—*A. dzhanganense* sp. nov. (identified by Balashova as *I. subbilobatum*). Most of these dry rivers and streams are shown in Fig. 1.

The studied “Berchogur” locality is in the eastern regions of the Berchogur Depression on the left bank of the Burtybai Creek (alternative name Dzhangansai Creek), east of the villages of Berchogur (Birshogyr)

and Alabas (Balashova, 1953; Barskov et al., 1984; Kusina, 1985; *Fauna i biostratigrafiya ...*, 1987; Barskov et al., 1988). The section is ca. 1 km north of the new “Alabas” Quarry, on the left slope of the dry creek, which is crossed by a road connecting the old and new quarries (Fig. 1). Ammonoids come from Members 3 and 4 of this section (see the description of the section in Barskov et al., 1988).

The assemblage from Member 3 in general corresponds to the fauna described by Kusina (1985) and contains *Imitoceras bertchogurense* (Balashova, 1953); *Acutimitoceras dzhanganense* sp. nov. [species identified by Kusina as “*I. (A.) subbilobatum*” (Münster, 1839)], *A. alabasense* sp. nov. [species identified by Kusina as “*I. (A.) substriatum*” (Münster, 1840)], *A. mugodzharense* Kusina, 1984, *?Nicimitoceras carinatum* (Schmidt, 1924), and *Sulcimitoceras yatskovi* Kusina, 1985. This assemblage belongs to the *Acutimitoceras* Genozone based on the occurrences of the index genus. A finer zonation is more problematic. The assemblage contains prionoceratids with involute initial whorls (*I. bertchogurense* and *?N. carinatum*). In addition, *A. dzhanganense* is similar to *A. subbilobatum*, which in its type region and in Morocco is found in the *prorsum* Zone (Becker et al., 2016). Therefore, the assemblage from Member 3 should probably be correlated with the *prorsum* Zone. The position of this fauna in relation to the conodont zonation is currently restudied. It is currently known that the level with the conodonts *S. praesulcata* in the Berchogur section is in Member 2b, approximately one meter below Member 3 with ammonoids, whereas the interval with ammonoids (Member 3) contains occurrences of *S. sulcata* (Barskov et al., 1984; *Fauna i biostratigrafiya ...*, 1987; Barskov et al., 1988). Thus, the current Devonian–Carboniferous boundary could be within or near the base of beds containing ammonoids (Member 3). If that is the case, Member 3 can be at least partly correlated with the upper part of the *prorsum* Zone, because in Western Europe, *S. sulcata* apparently appears within the *prorsum* Zone (Clausen and Korn, 2008). Limestones of Member 3 are overlain by shale interbedded with argillaceous limestone of Member 4 with *Acutimitoceras pulchrum* Kusina, 1985 [re-identified by Kusina from *A. aff. "rotiforme"* (Barskov et al., 1984)] and *A. alabasense* (see Kusina, 1985; Barskov et al., 1988). It is possible that beds of Member 4 can be correlated with the higher horizons of the Tournaisian Stage, but so far there is insufficient ammonoid-based data to make this correlation.

The ammonoid assemblage from Berchogur is similar to synchronous assemblages from other regions, in that it contains three main morphotypes of adult shells in relation to its width (wide, relatively narrow, and narrow, carinate). The first morphotype is represented by *A. alabasense*, second—by *I. bertchogurense* and *A. dzhanganense*, and the third—by *?N. carinatum*. Except for *I. bertchogurense* Balashova, 1953 and *A. pulchrum* Kusina, 1985, the shells have no constrict-

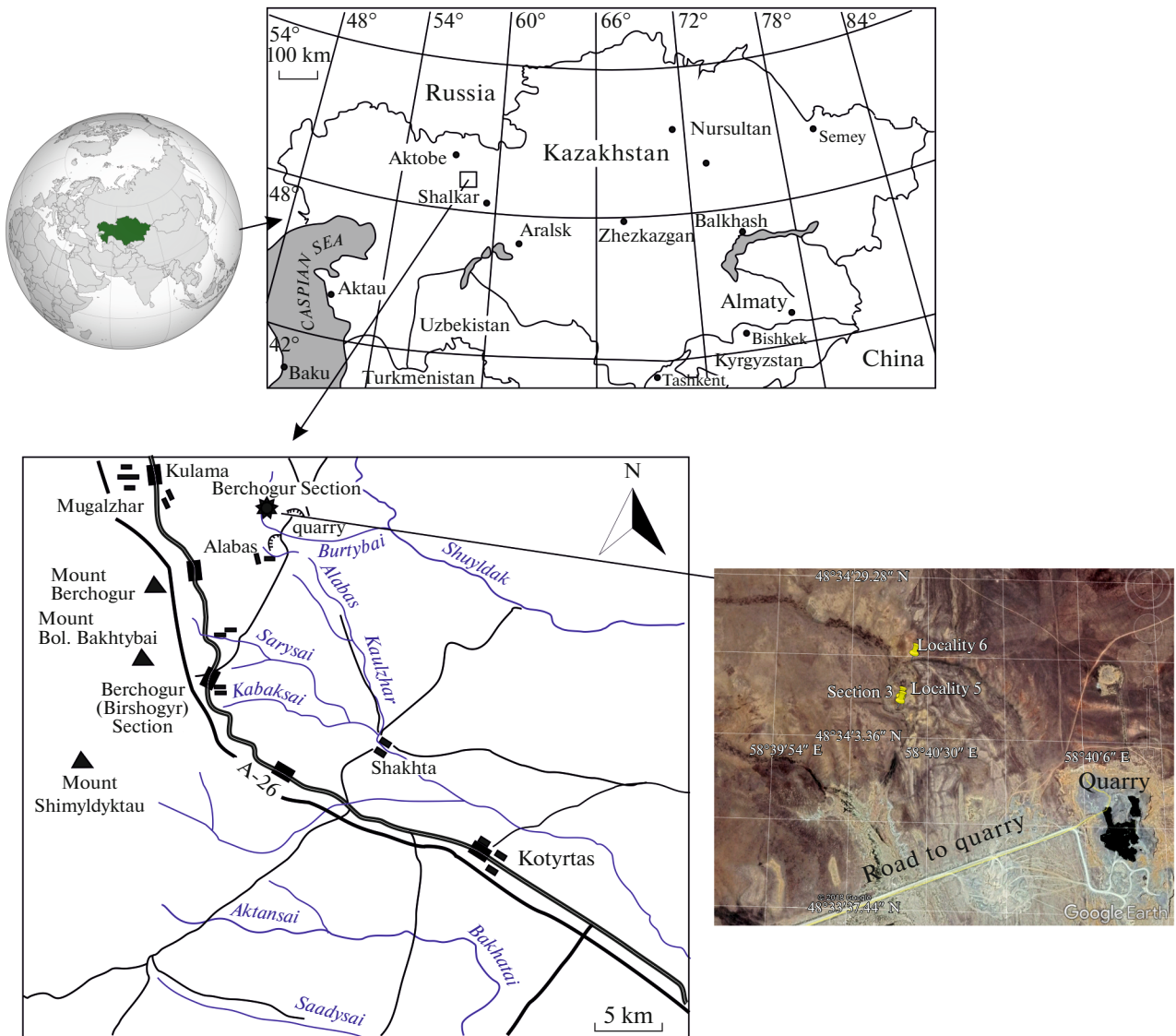


Fig. 1. Location of the Berchogur Section (Aktobe Region, Shalkar District) in Kazakhstan.

tions (in the latter species constrictions are only present on the mold). Juvenile shells are somewhat more variable in shape. Some are almost globular with a relatively wide umbilicus (*A. alabasense*), some are thickly discoidal with a wide and relatively wide umbilicus (*A. mugodzharensense*, *A. dzhanganense*, *S. yatskovi*), thickly discoidal with a narrow umbilicus (?*N. carinatum*), narrowly discoidal with a moderately wide umbilicus (*A. pulchrum*). These morphotypes break into smaller groups of juvenile morphotypes, e.g., shells with a ventral groove (*S. yatskovi*), with coarse ornamentation (*A. mugodzharensense*), etc. In addition, Kusina (1985) published an occurrence of an oxyconic shell 15 mm in diameter (this finding has not been repeated). House (1996, p. 182) interpreted the diversity of juvenile shells from the Stockum Limestone in Germany as a result of a considerable selection pres-

sure at the earliest stages of ammonoid ontogeny following large biotic crises, related to anoxic environments in the late Devonian basins. Interestingly, a similar high variety of early stages morphotypes in ammonoids of the *Acutimitoceras* Genozone is observed in such remote regions as Stockum (Rhenish Massif), Gröden (Carnian Alps, Austria) and Western Kazakhstan. For instance, similar juveniles include shells with a ventral groove (Kusina, 1985, pl. 3, fig. 10; House, 1996, text-fig. 23A), subspheroconic shells with an almost closed umbilicus (Kusina, 1985, text-fig. 1d; Schönlaub et al., 1988, pl. 2, fig. 4), subspheroconic and thickly discoidal shells with a partly evolute umbilicus (here, specimen 4005/115; Korn, 1984, pl. 2, figs. 9, 15). The diversity of early stages was likely to be connected with adaptation to variable feeding requirements and defense, rather than

locomotion, because ammonoid juveniles were probably planktonic. At that time paedomorphism was a dominant evolution strategy in ammonoids and was probably connected with the advantages of reaching maturity at earlier growth stages. Paedomorphism is observed in the evolution of prionoceratids and their descendants (gattendorfiids), in which both juvenile and adult whorls were evolute. It is likely that the survival of prionoceratids was related to the ability of species to adapt to various habitats, while a high diversity of juvenile morphotypes suggests adaptations in migrating to new biotopes.

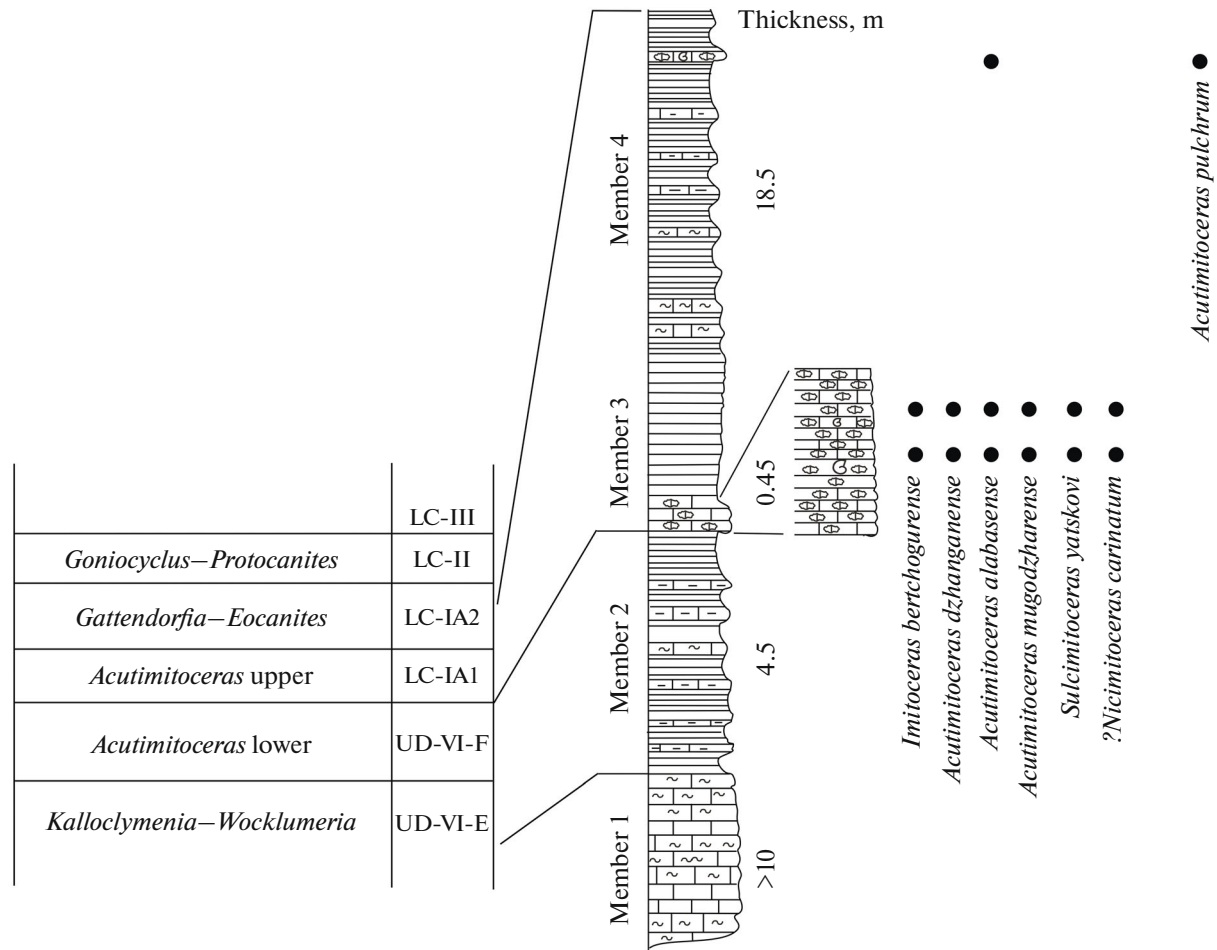
AMMONOID-BASED BIOSTRATIGRAPHY OF THE BOUNDARY INTERVAL AND SHELL MORPHOLOGY

The ammonoid genozone scale of the Devonian–Carboniferous boundary beds is undergoing continuous change. Some authors proposed the presence of two genozones in the boundary interval, *Acutimitoceras* (partly in the uppermost Famennian, partly in the Tournaisian) and *Gattendorfia* (Lower Tournaisian) (e.g., Becker, 1996); however, there are other opinions. Becker and Weyer (2004) showed three genozones: *Stockumites* (Famennian), *Acutimitoceras* and *Gattendorfia* (Tournaisian). In most scales the *Acutimitoceras* Genozone is subdivided into two zones, *Acutimitoceras prorsum* and *Acutimitoceras acutum* (Price and House, 1984; Shönlaub et al., 1988; Clausen et al., 1989; Becker, 1993; Korn and Weyer, 2003, etc.). However, in some scales the *Acutimitoceras acutum* Zone is not shown, and the *Acutimitoceras prorsum* Zone is followed by the *Gattendorfia subinvoluta* Zone (Korn and Klug, 2015, etc.). The Berchogur assemblage (genera *Imitoceras* and *Acutimitoceras*) is taxonomically similar to the assemblage of the Stockum Limestone, thereby suggesting the presence here of the *Acutimitoceras* Genozone (Kusina, 1985) (Fig. 2). A more detailed subdivision is based on the analysis of morphology of prionoceratids constituting this assemblage. It is established that most prionoceratids of this interval had evolute initial whorls, which is not characteristic of the Late Famennian prionoceratids. Considering that in the overlying *Gattendorfia–Eocanites* Genozone, most ammonoids have an evolute shell in the adult state, it is possible to suggest that evolution followed the paedomorphic pathway, when an evolute shell was retained into the adult stage. In addition, Becker (1996) proposed to take into account the size of shells with a carinate venter, suggesting that the appearance of the carinate venter is shifted to earlier stages in the phylogeny of the genus *Acutimitoceras*. For example, in *Acutimitoceras* sp., reported by Kusina from Berchogur (*Imitoceras* (*A.*) sp., see Kusina, 1985, pl. 3, fig. 6], the oxyconic shell appears at the diameter of 15 mm, whereas in *A. acutum* from the Tournaisian *acutum* Zone in the type region in Germany, it appears at the shell diameter of 10 mm. In *A. acutum*, the car-

inate venter appears in the four whorl, which is different from the somewhat earlier species *?N. carinatum* (Schmidt, 1924), in which the oxyconic shell is developed in the sixth whorl (Kusina, 1985, text-fig. 1i; Korn, 1994, text-fig. 37G). It is possible that the shift in the development of the oxyconic shell to earlier ontogenetic stages led to the appearance of *Voehringites* and some *Gattendorfia*, in which this shell shape is present in adults. Considering that the Berchogur section contains ammonoids, in which the oxyconic shell appears in the sixth whorl, and which were identified by Kusina (1985) as “*Imitoceras* (*Acutimitoceras*) *carinatum*”, her conclusion of the presence of equivalents of the *prorsum* Zone seems reasonable. In addition, Kusina (1985) noted that *I. bertchogurense* resembles *A. prorsum* and concluded that the Berchogur section most likely belongs to the *prorsum* Zone. It is noteworthy that in recent papers on the Devonian–Carboniferous boundary, “*A. carinatum*” is assigned to the genus *Nicimitoceras* Korn, 1993 (Korn and Klug, 2002), possibly because in the Rhenish representatives of this species the lateral lobe is considerably deeper than the ventral lobe, e.g., in *N. subacra* (Vöhringer, 1960), type species of the genus *Nicimitoceras*. In the Berchogur representatives of *?N. carinatum*, the lateral lobe illustrated by Kusina (1985, text-fig. 3b) is not deeper than the ventral lobe, but it should be said that the suture of the topotype of the species of *?N. carinatum* is drawn at the whorl height of 16.5 mm (Korn, 1994), and in Kusina’s specimen at the shell diameter of 7.6 mm, i.e., from a much smaller specimen. It is possible that the species described by Kusina as “*I. (A.) carinatum*”, represents a new species of *Nicimitoceras* or *Acutimitoceras*, but so far there is not sufficient material to resolve this problem. The ammonoid fauna of Berchogur can probably be correlated with that from the lower part of the Wangyou Formation in China, which is studied in the Muhua sections (Ruan, 1981; Qie et al., 2015), where thin-bedded limestones contain *A. wangyuense* Sun et Shen, 1965. The ammonoids *Acutimitoceras* sp. are found in this formation, in the *S. sulcata* conodont Zone or at the base of the *S. duplicata* Zone (Member C) in the Gedongguan Section, Youjiang Basin, Changshun County in the Guizhou, China (Qie et al., 2015, text-fig. 4). Ammonoids with a similar shell morphology are indicated from Faunule 1 (Bed RTB 10) of the Gara Bou Tlidat Section in the lower part of the Fez-zou Formation in Morocco (Becker et al., 2018).

TAXONOMY OF THE GENUS *ACUTIMITOCERAS* LIBROVITCH, 1957

Librovitch (1957) recognized the genus *Acutimitoceras* in a footnote on p. 263 and designated the type species *Acutimitoceras acutum* (Schindewolf, 1923), but with no description or revision of the species composition. He included this genus in the family Aganidae Smith, 1903, along with *Imitoceras* Schindewolf,



System	Stage	Genozones (Postanovleniya MSK, 2008)	This paper	Zonal index
Carboniferous	Tournaisian	<i>Protocanites–Gattendorfia</i> (including <i>Acutimitoceras prorsum</i>)	<i>Goniocyclus–Protocanites</i>	LC-II
			<i>Gattendorfia–Eocanites</i>	LC-IA2
			<i>Acutimitoceras</i> upper	LC-IA1
Devonian	Famennian	<i>Kalloclymenia–Wocklumeria</i>	<i>Acutimitoceras</i> lower	UD-VI-F
			<i>Kalloclymenia–Wocklumeria</i>	UD-VI-E

Fig. 2. A scheme of the Devonian–Carboniferous boundary beds and generalized section of the Dzhangana Formation in the Berchogur Section.

1923, *Gattendorfia* Schindewolf, 1920, *Kazakhstania* Librovitch, 1940, *Irinoceras* Ruzhencev, 1947, and *Neoganides* Plummer et Scott, 1937. Librovitch (1940) considered the genus *Imitoceras* in great detail

and assigned it to the family Cheiloceratidae Frech, 1923. Both points of view are currently considered outdated, and presently the genera *Imitoceras* and *Acutimitoceras* are assigned to the family Prionocerati-

dae (Kusina, 1985; Korn and Klug, 2002, etc.). Korn (1994) established the subfamily Acutimitoceratinae with the type species *Acutimitoceras* Librovitch, 1957, and included in it, apart from the type genus, *Costimitoceras* Vöhringer, 1960 (type species *C. ornatum* Vöhringer, 1960) and *Nicimitoceras* Korn, 1993. Kusina (1985, p. 37) noted that Librovitch considered the carinate venter to be the main character distinguishing *Acutimitoceras* from *Imitoceras*. She also noted that not everybody would consider this character to accurately distinguish the genera because the carinate venter appears in adults of many Carboniferous ammonoid taxa. In fairness it should be admitted that Librovitch (1957) did not write anything on the diagnosis of the new genus, but the mere fact that he chose *A. acutum*, in which the carinate venter appears very early in ontogeny, suggests that it is this feature that became the basis for the differentiation of this new genus. Vöhringer (1960) studied the shell morphogenesis of *A. acutum* and showed that the inner whorls in this species were evolute. Based on this, Korn (1984) assigned all prionoceratids with evolute early stages to the genus *Acutimitoceras*. Kusina (1985) questioned the correctness of this interpretation, because not all prionoceratids with evolute inner whorls develop a carinate venter in ontogeny and suggested that *Acutimitoceras* could be considered as a subgenus of *Imitoceras*. Becker (1996) accepted the genus *Acutimitoceras* but subdivided it into several subgenera. Apart from the nominotypical subgenus *Acutimitoceras* with the type species *A. acutum*, he recognized the subgenera *Stockumites* (type species *Imitoceras intermedium* Schindewolf (1923)) and *Streeliceras* (type species *Imitoceras heterolobatum* Vöhringer, 1960). Becker considered the genus *Sulcimitoceras* Kusina, 1985 as a subgenus of *Acutimitoceras* based on his opinion that the ventral groove (a distinguishing character of *Sulcimitoceras*) indicated by Kusina (1985) could not be considered as a generic character, because such a groove can be observed in many specimens of other, unrelated taxa. Besides, in Becker's opinion, ribs on the flanks (also a diagnostic character) are also present in other prionoceratids. These are justifiable considerations, but apart from those characters, *Sulcimitoceras* has a very unusual suture with a deep but rounded lateral lobe. Therefore, it is understandable that Kusina found it difficult to assign the Berchogur species to any other previously known prionoceratid genus. Korn

and Klug (2002) considered the subgenus *Stockumites* Becker as a junior synonym of *Acutimitoceras* Librovitch, and the genus *Streeliceras* Becker as a junior synonym of *Nicimitoceras* Korn, 1993, but retained the generic status of *Sulcimitoceras*. More studies of the type material from Germany are needed to resolve the problem with the subgenera. Here I accept the genus *Acutimitoceras* with an emended diagnosis (prionoceratids with evolute inner whorls) but note that the taxonomy of the genus *Acutimitoceras* and the family Prionoceratidae needs an extensive revision. Currently there is no available material for such a revision, as the morphology of the initial whorls is still unknown in some species, including those from Chinese sections.

SYSTEMATIC PALEONTOLOGY

Genus *Acutimitoceras* Librovitch, 1957

Acutimitoceras alabasense Nikolaeva, sp. nov.

Plate 3, figs. 1–6

Imitoceras substriatum (pars): Balashova, 1953, p. 196, pl. 12, figs. 1–9.

Imitoceras (Acutimitoceras) substriatum (pars): Kusina, 1985, p. 42, pl. 3, figs. 3, 4.

?*Acutimitoceras substriatum*: Ruan, 1981, p. 63, pl. 11, figs. 26–28. non *Goniatites striatus* Münster, 1839, p. 20.

non *Goniatites substriatus* Münster, 1840, p. 107.

E t y m o l o g y. After the village of Alabas near the Berchogur section.

H o l o t y p e. PIN, no. 4005/147; Kazakhstan, Aktobe Region, Shalkar District, northeast of the village of Berchogur (Birshogyr), left bank of the upper reaches of Burtybai dry creek, in its meridional portion, 1 km north of the new Alabas Quarry, Berchogur Section; Dzhangana Formation; Lower Carboniferous; *Acutimitoceras* Genozone.

D e s c r i p t i o n. Shell shape (Fig. 3c). Initial whorls are weakly evolute (Fig. 3c; Kusina, 1985, text-fig. 1z). In adults the shell is thickly discoidal, with a rounded venter, with wide, weakly convex flanks, gradually converging to the venter. The umbilicus in adults is closed.

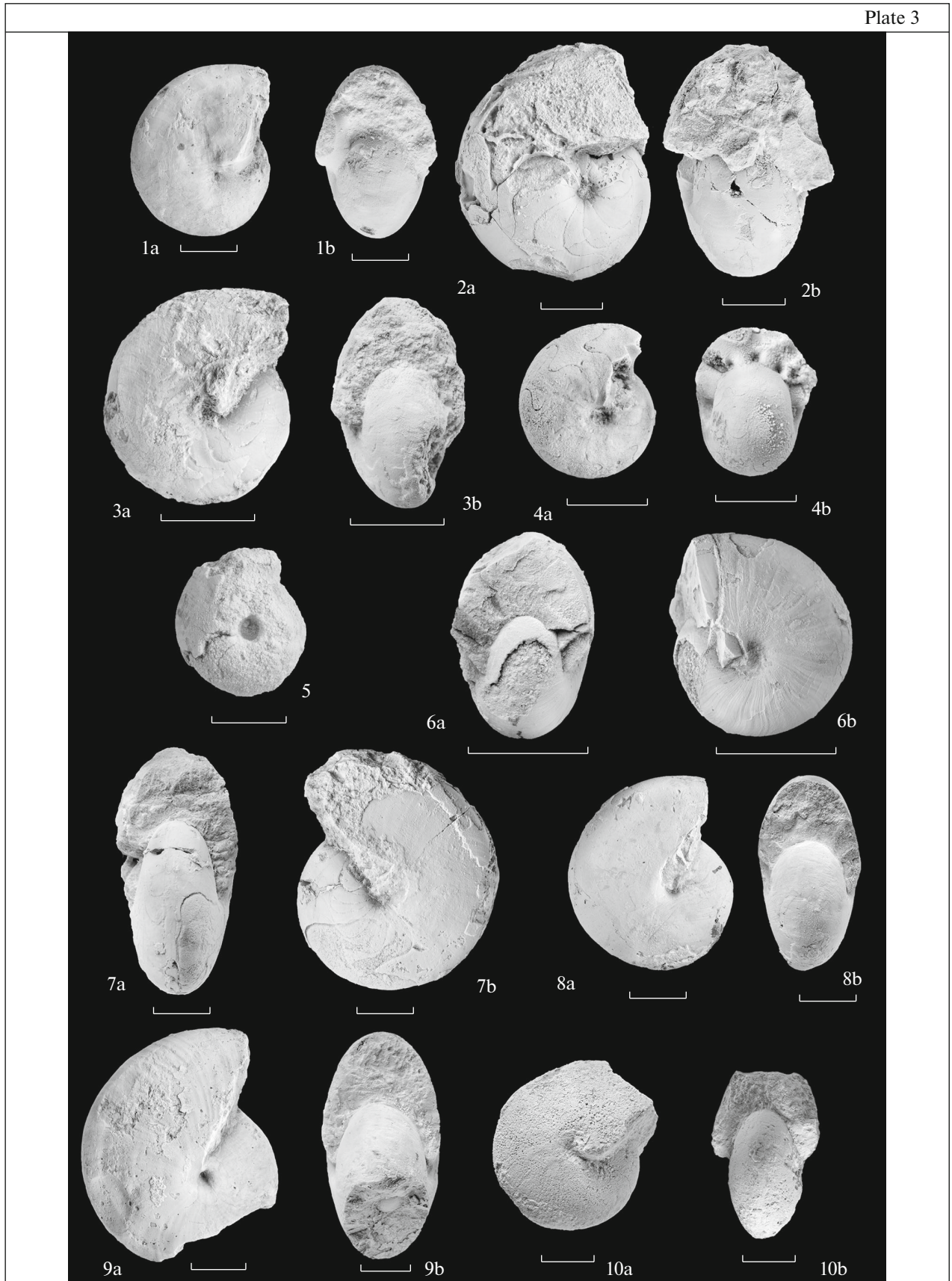
Explanation of Plate 3

All specimens from the Berchogur section (including loosely collected), from the Dzhangana Formation. Scale bars: (1–3, 6–10) 1 cm; (4, 5) 0.5 cm.

Figs. 1–6. *Acutimitoceras alabasense* sp. nov.: (1) holotype PIN, no. 4005/147; Member 3, Sample 1; (2) specimen PIN, no. 4005/122; Member 3, 834 near BS-2, loose; (3) specimen PIN, no. 4005/129 Member 3; (4) specimen PIN, no. 4005/115, Member 3; (5) specimen PIN, no. 5643/19; Member 3, loose; (6) specimen PIN, no. 4005/153, loose.

Figs. 7–10. *Acutimitoceras dzhanganense* sp. nov.: (7) specimen PIN, no. 4005/195, Member 3; (8) holotype PIN, no. 4005/126, Member 3, Sample 1; (9) specimen PIN, no. 4005/196, Member 3; (10) specimen PIN, no. 5643/1, Member 3.

Plate 3



Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
4005/122	39.8	20.9	26.8	1.0	0.53	0.67	0.03
4005/147 holotype	33.7	19.8	22.6	—	0.59	0.67	—
4005/129	25.8	13.6	16.6	—	0.53	0.64	—
4005/124	21.3	10.7	16.1	—	0.50	0.76	—
4005/150	20.5	12.6	13.5	—	0.61	0.66	—
4005/123	18.6	9.4	14	—	0.51	0.75	—
4005/117	12.7	7.0	8.4	—	0.55	0.66	—
4005/115	9.3	4.2	7.4	1.0	0.45	0.80	0.11

Ornamentation. No ornamentation is preserved in adult shells. No constrictions are present. Young shells show lamellae (in specimen no. 4005/124, at Dm = 14.5 mm, 4–5 lamellae are present per 1 mm of the flank), which extend more or less radially from the umbilicus then bend backwards to form a wide ventral sinus.

Suture (Figs. 3a, 3b; 4). The ventral lobe is narrow, lanceolate, with weakly convex sides. The external saddle is broadly rounded. The lateral lobe is relatively narrow, with weakly convex sides, noticeably shorter than the ventral lobe. The base of the lateral lobe is narrowly angular. The external side of the lateral lobe is more or less straight, and the inner side is weakly convex. The second external saddle is broad and as high as the first saddle.

Comparison. This species is similar in shell parameters to *?A. substriatum* (Münster, 1840) from Upper Franconia (Bavaria, Germany), from which it is distinguished by the absence of constrictions at all growth stages. In addition, it differs from specimens of *A. intermedium* (Schindewolf, 1923), illustrated by Korn (1994, p. 47) from Stockum in the wider whorls of the adult shell (at Dm = 30 mm, WW/Dm = 0.67 versus 0.60). It differs from the paratype CE 1130/29 of *A. simile* (Vöhringer, 1960) from Bed 1 of the Gattendorf Limestone in Hönnetal (Germany) and specimens of *A. cf. simile* figured by Korn and Weyer (2003) from Bed 80 of Hasselbach, Germany, in the shape of the whorl-cross section. In specimens from Berchogur, the umbilicus is still relatively open in the fifth whorl, and the cross section is wider (WW/Dm = 0.77), whereas in the German specimens the cross-section is narrower (Vöhringer, 1960, text-fig. 7a; Korn and Weyer, 2003, text-fig. 14b).

Remarks. Balashova (1953) and Kusina (1985) described at least some specimens of this species as "*I. (A.) substriatum* (Münster, 1840)". They also indicated that their specimens lacked constrictions (on both the shell and the mold). Kusina also noted that she compared her specimens with specimens of *?A. substriatum* described by Vöhringer (1960) from Hönnetal (Germany), rather than with the type mate-

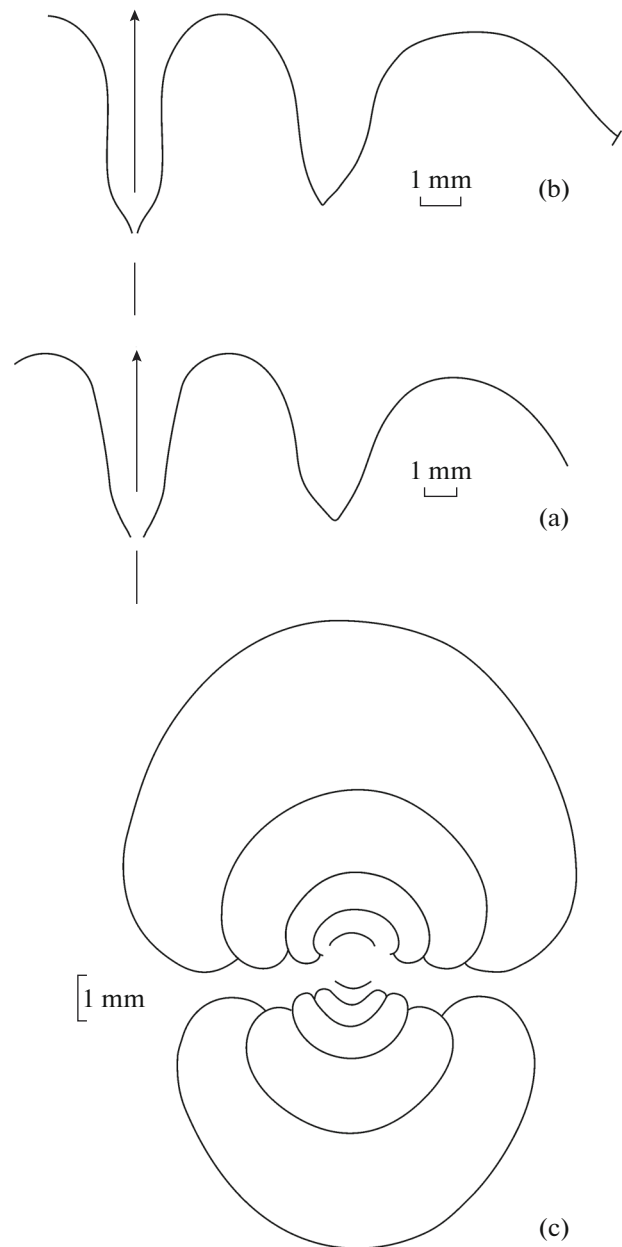


Fig. 3. Sutures and cross-section of *Acutimitoceras alabassense* sp. nov.: (a) holotype PIN, no. 4005/147, at WH = 11.2 mm, WW = 15.4 mm; (b) specimen PIN, no. 4005/122, at WH = 12.2 mm, WW = 19.6 mm; (c) specimen PIN, no. 4005/117, at Dm = 12.8; Berchogur section.

rial that was not then available to study. Korn (1994, p. 22, text-fig. 12D) published a photograph of the holotype of this species (Bayerische Staatssammlung für Paläontologie und Historische Geologie, München; BSP AS VII25) and gave its description. The holotype of *A. substriatum* is a shell ca. 25 mm in diameter, WW/Dm = 0.65, with constrictions on the shell and the mold. A small bulge is visible on the holotype next to the constrictions. The latter character is a diagnostic character of the genus *Mimimitoceras*,

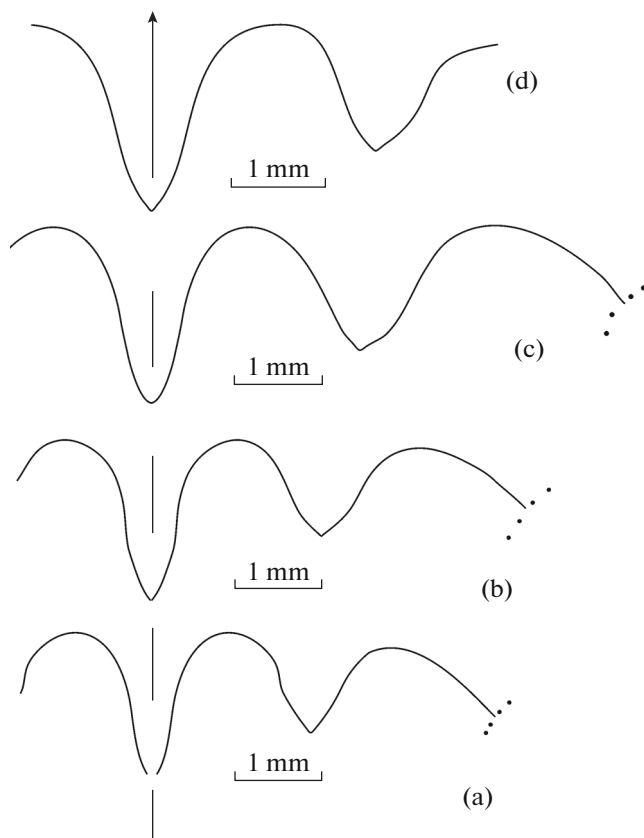


Fig. 4. Sutures of *Acutimitoceras alabasense* sp. nov., juvenile specimen PIN, no. 4005/115: (a) at WH = 3.8 mm, WW = 6.9 mm; (b) at WH = 4.0 mm, WW = 7.0 mm; (c) at WH = 4.1 mm, WW = 7.3 mm; (d) at WH = 4.2 mm, WW = 7.4 mm; Berchogur section.

and possibly because of this Korn (1994) provisionally assigned the species to *?Mimimitoceras*. Korn and Klug (2002) also assigned it to *?Mimimitoceras*. In the Berchogur specimens, the initial whorls are weakly evolute. Considering this and the absence of constrictions on the shells and molds of the Berchogur specimens, they are here assigned to *Acutimitoceras*.

Material. 10 specimens from the Berchogur section.

Acutimitoceras dzhanganense Nikolaeva, sp. nov.

Plate 3, figs. 7–10

Imitoceras subbilobatum (pars): Librovitch, 1940, p. 13, text-figs. 2–4, pl. 1, figs. 1–4; Balashova, 1953, p. 191, pl. 11, figs. 11–16.

Imitoceras (Acutimitoceras) subbilobatum (pars): Kusina, 1985, p. 43, pl. 3, fig. 5.

?Acutimitoceras subbilobatum: Sheng in Ji et al., 1989, p. 111, pl. 33, figs. 1, 2.

non *Goniatites subbilobatus* Münster, 1839.

Etymology. After the Dzhangana Formation.

Holotype. PIN, no. 4005/126; Kazakhstan, Aktobe Region, Shalkar District, northwest of the vil-

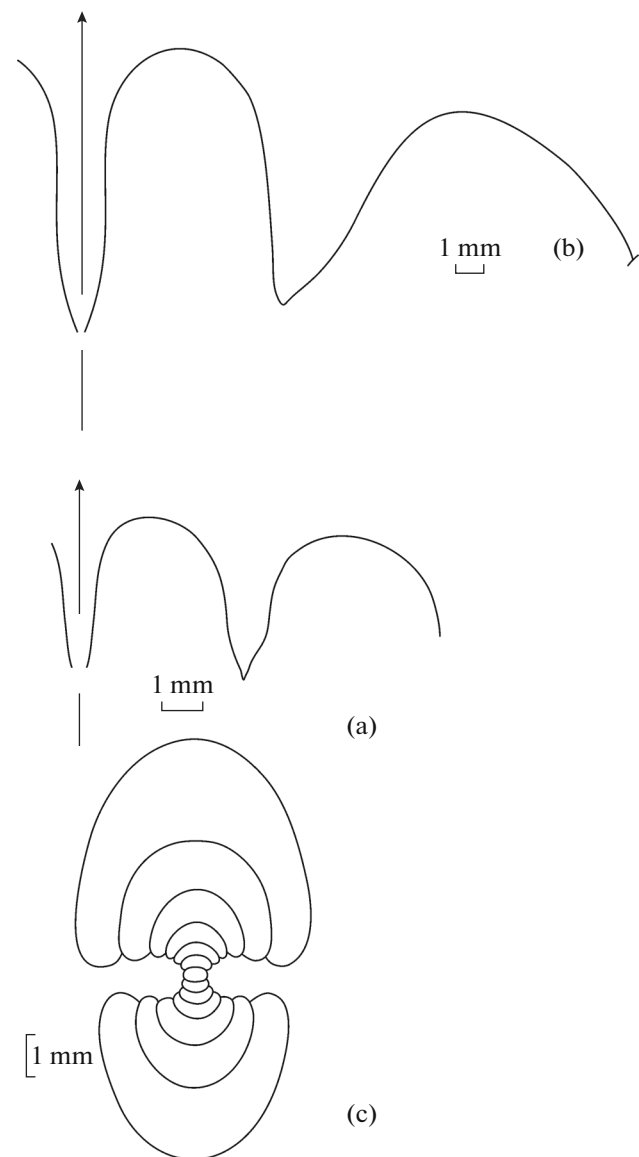


Fig. 5. Sutures and cross-section of *Acutimitoceras dzhanganense* sp. nov.: (a) specimen PIN, no. 5643/1, at WH = 10.5 mm, WW = 13.4 mm; (b) holotype PIN, no. 4005/126, at WH = 12.2 mm, WW = 13.4 mm; (c) specimen PIN, no. 4005/62, at Dm = 10.4 mm; Berchogur section.

lage of Berchogur (Birshogyr), left bank of the upper reaches of Burtybai dry creek, in its meridional portion, ca. 1 m north of the New Alabas Quarry, Berchogur Section; Dzhangana Formation; Lower Carboniferous, *Acutimitoceras* Genozone.

Description. Shape (Fig. 5c). The initial whorls are evolute (see Kusina, 1985, text-fig. 1). In the adult stages the shell is thickly discoidal, with relatively slowly expanding whorls ($W = 2.12$). The venter is narrowly rounded, the flanks are weakly convex, converging ventrally. The umbilicus is closed in adults.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm
4005/205	46.7	26.5	21.7	—	0.57	0.46
4005/126 holotype	45.8	26.1	23.6	—	0.57	0.52
4005/195	38.0	20.1	19.2	—	0.53	0.51
5643/1	34.2	18.6	19.2	—	0.54	0.56
4005/133	23.7	13.9	13.2	—	0.59	0.56
4005/58	21.5	12.4	11.7	—	0.58	0.54
4005/154	24.1	13.7	13.0	—	0.57	0.54

Ornamentation. No ornamentation is preserved on adult specimens. No constrictions are present. Young shells have growth lines, running straight on the flanks and forming a ventral sinus.

Suture (Figs. 5a, 5b). The ventral lobe is narrow with parallel sides, the external saddle is rounded and wide. The lateral lobe is relatively narrow, with a concave external side and a weakly convex internal side, slightly shorter than the ventral lobe. The second external saddle is wide, and as high as the first.

Comparison. In the shape of the cross-section, this species is similar to *A. subbilobatum* (Münster, 1839), from which it primarily differs in the absence of constrictions. This is clearly observed, especially when comparing the Berchogur material with the specimens figured by Korn from Stockum (Korn, 1994, text-figs. 42a–42c) and Ober-Rödinghausen (Korn, 1994, text-figs. 44d–44f). In addition, in the Berchogur specimens, the lateral lobe is narrower (see Korn, 1994, text-fig. 39). Also, this species is distinguished from specimens of *A. intermedium* (Schindewolf, 1923), cited by Korn (1994, p. 47) from Stockum by the narrower whorls of the adult shells (at Dm = 30 mm, WW/Dm = 0.56 versus 0.60). It differs from the type specimens of *A. procedens* Korn (Korn, 1984, p. 80, pl. 4, figs. 24, 25, text-fig. 5B) from Müssenbergl (Germany) in the absence of constrictions (there are at least four constrictions in the German species) and the absence of a lateral sinus in the growth lines of young specimens. This species differs from *A. prorsum* (Schmidt, 1925) in the wider shell (at Dm = 20 mm, WW/Dm = 0.54 versus 0.50), absence of constrictions and less strongly curved growth lines.

Remarks. Librovtich (1940), Balashova (1953), and Kusina (1985) identified at least some specimens of this species as *A. subbilobatum* (Münster, 1839). However, all these authors noted that none of the Berchogur specimens exhibited constrictions. Their identification was largely hindered by the then poor knowledge of the type material of *A. subbilobatum*. In addition, the suture of the holotype of this species was incorrectly drawn at the first description (see Münster, 1839, pl. 17, fig. 1; Librovtich, 1940), it was not clear whether any constrictions were present on the shell and/or mold, or the shape of the young whorls. Additionally, there was confusion with the nomenclature of this species, which was also occasionally referred to as

“*Aganides guerichi* Frech” (see the history of this issue in Librovtich, 1940). Kusina (1985) mentioned that it is possible that the Berchogur specimens belong to a new species, rather than to *subbilobatum*, but in the absence of an adequate description and illustration of Münster’s lectotype she was not confident in recognizing a new species. At present there are descriptions of well-preserved specimens of *A. subbilobatum* (Münster, 1839) from the type locality in Gattendorf in Germany (Korn, 1984), and also from Stockum and Ober-Rödinghausen (Korn, 1994), Hasselbachtal (Germany) (Korn and Weyer, 2003), Mfis (Anti-Atlas, Morocco) (Bockwinkel and Ebbighausen, 2006) and other localities of Western Europe and North Africa, and nearly all of them have constrictions on the mold. Considering that none of the Berchogur specimens “similar to *Acutimitoceras subbilobatum*” have constrictions, it is reasonable to assign them to a new species. It is also probable that specimens from the Dapoushang Section (China) illustrated by Sheng (Sheng in Ji et al., 1989, pl. 33, figs. 1, 2) also belong to this new species.

Material. 11 specimens from the Berchogur section.

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