Dicoelitid belemnites from the Caucasian margin of the Tethys: new data from the Upper Bajocian–Lower Bathonian of Karachay-Cherkessia, southwest Russia

Oksana S. Dzyuba, Vasily V. Mitta & Mikhail P. Sherstyukov

Early representatives of the belemnite family Dicoelitidae (Belemnopseina) from the Northern Caucasus are reported from the Upper Member of the Djangura Formation of Karachay-Cherkessia. We document the first records of *Dicoelites* (s. str.) from the Upper Bajocian of Eastern Europe and introduce the new species *Dicoelites aprilis* Dzyuba sp. nov. and *Dicoelites octobris* Dzyuba sp. nov. Additionally, *Conodicoelites* sp. from the Upper Bajocian as well as a new record of *Conodicoelites exiguus* (Krimholz, 1953) from the Lower Bathonian are described. New belemnite records from Karachay-Cherkessia indicate the successive appearance of dicoelitid genera in the Caucasian margin of the Tethys during the Late Bajocian, i.e. *Dicoelites* in the late Niortense Chron and *Conodicoelites* in the early Garantiana Chron. Our data provide evidence supporting the presence of *Dicoelites* in the Bajocian deposits of the western Tethyan domain that was previously considered doubtful. • Key words: Dicoelitidae, Middle Jurassic, Bajocian, Bathonian, Northern Caucasus, western Tethys, palaeobiogeography.

Dzyuba, O.S., Mitta, V.V. & Sherstyukov, M.P. 2019. Dicoelitid belemnites from the Caucasian margin of the Tethys: new data from the Upper Bajocian–Lower Bathonian of Karachay-Cherkessia, southwest Russia. *Bulletin of Geosciences 94(4)*, 409–424 (5 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received May 14, 2019; accepted in revised form September 8, 2019; published online December 10, 2019; issued December 31, 2019.

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Belemnite distribution patterns in the Middle Jurassic seas are still under investigation, with many scientific surprises for both the Boreal and Tethyan domains (*e.g.* Dzyuba *et al.* 2015, 2016, 2019; Weis *et al.* 2015b, 2017; Challinor & Hudson 2017; Dzyuba & de Lagausie 2018; Ippolitov 2018a, b, c; Ippolitov & Desai 2019). Among the early representatives of the suborder Belemnopseina Jeletzky, 1965, belemnites possessing long ventral and short dorsal alveolar grooves on the rostrum, *i.e.* members of the Tethyan family Dicoelitidae Sachs & Nalnjaeva, 1967, are the least studied group, especially in the Mediterranean-Caucasian Tethys (western Tethys). This family includes only two genera, elongate and hastate *Dicoelites* Boehm, 1906 and more robust, cylindriconical to conical *Conodicoelites* Stevens, 1965a.

Apart from ?*Dicoelites* sp. A described from the Lower Bajocian of Morocco (Weis *et al.* 2017, p. 221, fig. 7a, b) and "*Belemnites*" *jacquoti* Terquem & Jourdy (1869, p. 41, pl. 1, figs 6–9) from the Upper Bajocian of north-eastern France, which is presumably a dicoelitid (Weis *et al.* 2017), all known western Tethyan representatives of the family Dicoelitidae belong to the genus *Conodicoelites* (see below). The only dicoelitid belemnite described and illustrated from the Northern Caucasus is *Dicoelites exiguus* Krimholz (1953, p. 54, pl. 4, fig. 5). It comes from the "Upper Bajocian or Lower Bathonian" (Krimholz 1953, p. 56) of the former southern part of Stavropol Krai (5 km to the northeast of Zelenchukskaya Village), which is now a part of the Karachay-Cherkess Republic. This belemnite was later attributed to the genus *Conodicoelites* by Krimholz & Repin (1989).

During fieldwork (2014 to 2018), two of us (VVM and MPSh) conducted a palaeontological-stratigraphic study of the Upper Bajocian–Lower Bathonian in Karachay-Cherkessia. In the course of this study, cephalopod fossil material was collected containing not only ammonites, nautilids and dicoelitid belemnites but also specimens of belemnopseid (*Belemnopsis* Bayle, *Conobelemnopsis* Riegraf, *Longibelemnopsis* Riegraf, *Hibolithes* Montfort) and megateuthidid (*Megateuthis* Bayle, ?*Paramegateuthis* Gustomesov) rostra. The current state of the art in ammonite investigations allowed us to date belemnite occurrences with the chronostratigraphic units. In this report, we describe dicoelitids, introduce two new species, and discuss their palaeobiogeographic implications. The belemnites were studied by OSD and the geological setting including ammonite biostratigraphy were outlined by VVM.

Geological setting and material

All belemnites described herein come from natural outcrops located in the western part of the Northern Caucasus in Karachay-Cherkessia in the territory of the Kuban–Urup interfluve (Fig. 1). This territory was recognized as a typical area for the Djangura Formation, which is Bajocian–Lower Bathonian in age (Besnosov 1967). The Upper Bajocian and Lower Bathonian are represented here by terrigenous, predominantly clayey deposits with subordinate silt interlayers and are assigned to the Upper Djangura Member, which is approximately 700 m thick (Rostovtsev *et al.* 1992). The sedimentary environment is interpreted as a low energy marine setting, presumably distal shelf (Polyansky 1989). That area was situated very close to a zone of the so-called "Large Caucasus deep-water basin" located along the northern Tethyan margin between the Scythian Platform in the north and numerous terranes in the south (Rostovtsev *et al.* 1992, Ruban 2006, Adamia *et al.* 2011, Nikishin *et al.* 2012).

The standard Western European ammonite zones have been recognized for the Upper Member of the Djangura Formation, namely the Upper Bajocian *Strenoceras niortense*, *Garantiana garantiana* and *Parkinsonia parkinsoni* zones, and the Lower Bathonian *Zigzagiceras zigzag* Zone (Rostovtsev *et al.* 1992, Mitta & Sherstyukov 2014). Nevertheless, despite the similarity of the north Caucasian ammonite assemblages to those of the western part of the western Tethys, there are also endemic taxa (or not found so far in Western Europe?), primarily at the rank of species. In addition, some taxa that are widespread in Europe are unknown in the Northern Caucasus, for example, *Zigzagiceras*, which is a characteristic genus of the Lower Bathonian in Western Europe. Such differences are the reason why infrazonal units in the Northern Caucasus correspond only rarely in range to the units of the Western European ammonite scale. As a result, the most characteristic ammonite taxa have been used for infrazonal subdivision of each particular interval, regardless of whether they are endemic or widespread species (Fig. 2).

A characteristic feature of the Djangura Formation outcrops in the studied area is their large extent and rarity of condensed layers that allows us to observe gradual changes in the composition of fossil assemblages. Another feature is the inaccessibility of some particular parts of the formation, owing to riverside landslides and the continuous river channel migrations. The latter

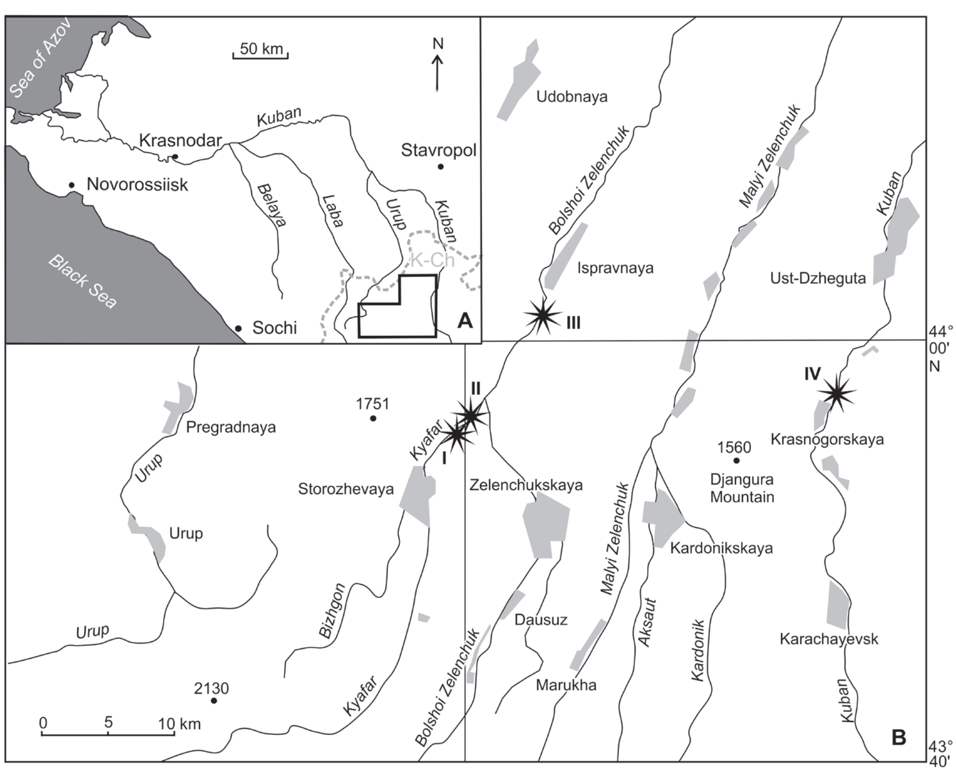


Figure 1. Location of the studied outcrops in the Kuban–Urup interfluve, Karachay-Cherkessia (K-Ch): I – localities 0-4, 5(10), 17, 30; II – locality 25; III – locality 8; IV – localities 19, 23.

often makes it difficult to study the boundaries between biostratigraphic units and makes it necessary to show the uncertain placement of these boundaries on the stratigraphic scheme by dotted lines (Fig. 2). According to the Stratigraphic Code of Russia (Zhamoida 2006), such newly defined biostratigraphic units with an uncertain lower or upper boundary are referred to as "beds with ... [fossil name]" or "... [fossil name] beds". In some cases, faunal horizons as the lesser units can be recognized in the Kuban–Urup interfluve. They fit the concept of faunal horizons *sensu* Callomon (1964, 1985).

The *Strenoceras niortense* Zone is represented in the Bolshoi Zelenchuk River Basin by dark grey sandy clays, with interlayers of siltstones (0.2–0.4 m) and scattered carbonate nodules. The lower and middle parts of the section are assigned to the two local biostratons, *Keppleritiana rostovtsevi* beds and *Keppleritiana graebensteini* beds (Mitta 2017c), but belemnites were not found in either of these units. Several rostra were collected from the uppermost part (about 25 m thick) of the *S. niortense* Zone on the Kyafar River (left tributary of the Bolshoi Zelenchuk River), below the Storozhevaya Village on the left bank (locality 30), and down the river on the right bank (locality 17). Ammonites recorded from this interval are quite typical for the standard *Baculatoceras baculatum* Subzone: *Baculatoceras* spp., *Spiroceras annulatum* (Deshayes), *Spir. bispinatum* (Baugier & Sauzé), *Spir.* aff. *fourneti* Roman & Pétouraud, *Sphaeroceras* cf. *tutthum* S. Buckman, *Calliphylloceras* cf. *disputabile* (Zittel), *Holcophylloceras zignodianum* (d'Orbigny), *Pseudophylloceras* cf. *kudernatschi* (Hauer), *Adabofoloceras belinskji* (Besnosov), *Megalytoceras* sp. (Mitta & Schweigert 2016, Mitta 2017b).

The rocks of the *Garantiana garantiana* Zone are exposed down the Kyafar River [*e.g.* locality 5(10)], but the contact with the *S. niortense* Zone is not observed here. The *G. garantiana* Zone is characterized by strata of grey argillite-like clays with scattered calcareous siltstone nodules, which sometimes compose nodular horizons; it is approximately 50 m thick. In the middle part of the strata, a horizon of clayey limestone nodules with a peculiar sedimentary structure (syneresis cracks, cone-in-cone) was recorded. This horizon appears to indicate a short interruption in sedimentation (Mitta 2019). Ammonite finds mostly come from the lower half of this zone; these are *Djanaliparkinsonia alanica* Mitta, *Vermisphinctes martiusii* (d'Orbigny), ?*Garantiana* sp., *Holcophylloceras* sp., *Adabofoloceras* sp., and *Phylloceras* sp. (Mitta 2018, 2019). The interval under discussion is defined as the *D. alanica* beds and is considered to correspond to the Dichotoma Chronosubzone (Mitta 2019). Single specimens of *Garantiana subgaranti* Wetzel and *Pseudogarantiana minima* (Wetzel) were found in the middle part of the upper half of the *G. garantiana* Zone, whereas

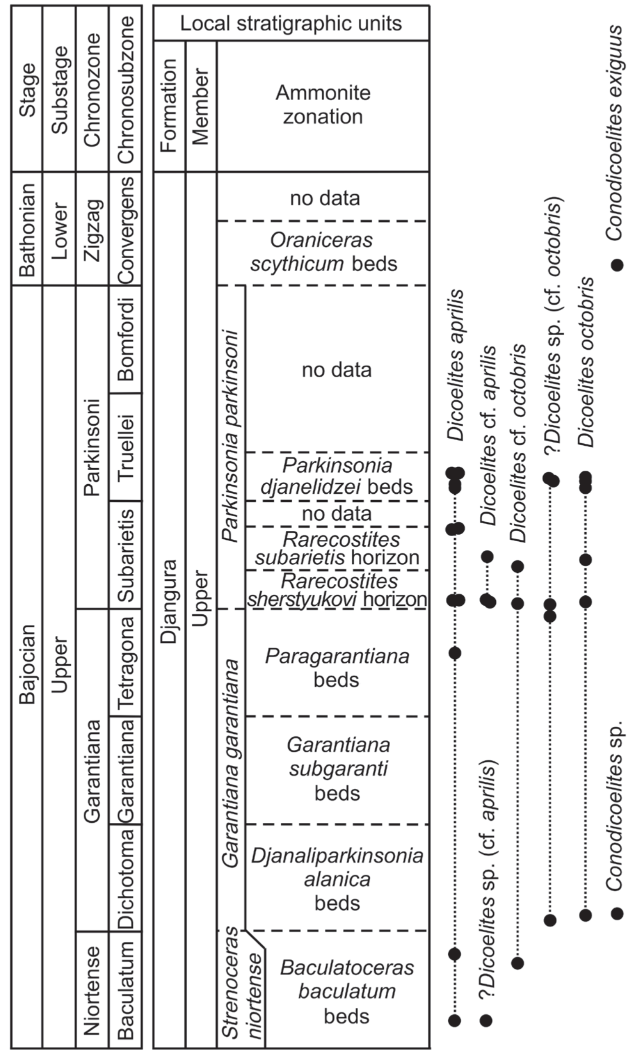


Figure 2. Stratigraphical position of dicoelitid records from the Kuban–Urup interfluve. Ammonite biostratigraphy is given after Mitta (2017a, 2018) and Mitta *et al.* (2017, 2018).

single specimens of *Garantiana* sp. and *Paragarantiana* sp. (sp. nov.?) were found in the topmost part of the zone. Regarding the local biostratigraphic scale, these findings are the reason to establish the *G. subgaranti* beds and the *Paragarantiana* beds, corresponding to the Garantiana (= Subgaranti) and Tetragona chronosubzones, respectively (Mitta 2019).

One more outcrop of the *G. garantiana* Zone (localities 19, 23) is located on the left bank of the Kuban River, below the Krasnogorskaya Village. At low water, grey clays with calcareous siltstone nodular horizons are exposed here. These clay strata overlap sandstones of the *S. niortense* Zone that contain numerous *Zoophycos* and rare *Baculatoceras* sp. In the lower 2–2.5 m of the clay strata, *Djanaliparkinsonia alanica*, *Vermisphinctes martiusii*, *Holcophylloceras* sp., *Dinolytoceras* sp. were found (Mitta 2018). Apparently, this is the lowermost part of the *D. alanica* beds, which are basal for the *G. garantiana* Zone in the territory of the Kuban–Urup interfluve. Lithologically similar clays crop out down the Kuban River (upward in the section), but macrofossils were not found in them.

The lower part of the *Parkinsonia parkinsoni* Zone in the valley of the Kyafar River is represented by dark grey claystones with interlayers and lenses of clayey limestone; siderite nodules are scattered in the strata or form the horizons (localities 0–4 on the right bank of the river). The total thickness of these strata exceeds 40 m. Numerous *Rarecostites* have been found here: *R. sherstyukovi* Mitta, *R. kyafarensis* Mitta, *R. subarietis* (Wetzel), *R. mutabilis* (Nicolesco). Single specimens of *Lissoceras haugi* Sturani, *Spir. obliquecostatum* (Quenstedt), *Patrulia karachaica* Mitta, as well as transitional *garantiana/parkinsoni* representatives of the genera *Holcophylloceras*, *Calliphylloceras*, *Adabofoloceras*, *Pseudophylloceras*, *Dinolytoceras* and *Nannolytoceras* were also recorded (Mitta 2017a, Mitta *et al.* 2018, Mitta & Sherstyukov 2018). The ammonite faunal horizons *R. sherstyukovi* and *R. subarietis* that correspond to the lower and middle parts of the Subarietis (= Acris) Chronosubzone, respectively, were established in the studied localities (Mitta 2017a). The contact between the *P. parkinsoni* and the *G. garantiana* zones is covered by Quaternary deposits (pebbles) and therefore cannot be studied on the Kyafar River.

Down the Kyafar River (upward in the section), very thin beds of siltstones occasionally crop out from under Quaternary alluvial deposits, but macrofauna was not found in these beds. The next outcrop revealing fossils of the *Parkinsonia parkinsoni* Zone was studied 1.5 km down the river from the end of the group of localities 0–4, on the left bank (locality 25). Grey to dark grey clays are exposed in this locality with carbonate nodules (5–7 cm in diameter) scattered throughout the strata or forming the horizons. The thickness of exposed strata is about 5 m. The ammonites *Parkinsonia djanelidzei* Kakhadze, rare *Rarecostites donezianus* (Borissjak), and numerous *Dinolytoceras zhivagoi* Besnosov allowed to assign this interval of the section to the *P. djanelidzei* beds (Mitta *et al.* 2017). Taking the presence of the last *Rarecostites* and the first *Parkinsonia* into account, these beds are considered to correspond approximately to the lowermost Truellei Chronosubzone; however, the possibility that they range up to the uppermost Subarietis Chronosubzone cannot be entirely excluded.

The Lower Bathonian part of the section is exposed on the right bank of the Bolshoi Zelenchuk River, 6.8 km below the mouth of the Kyafar River (*e.g.* locality 8). Bluish-dark grey calcareous clays with the exposed thickness not less than 7 m crop out here. They contain carbonate nodules, usually spherical, up to 5–15 cm in diameter. Macrofossils were found *in situ* only in the lower half of the section: frequent *Oraniceras scythicum* Mitta, rare *Oxycerites* sp., *Calliphylloceras* sp., *Phylloceras* sp., *Dinolytoceras* sp., and *Megalytoceras* sp. Very rare *Cadomites* sp., *Polyplectites* sp. and large body chambers of Perisphinctidae gen. et sp. indet. were found *ex situ* (Mitta 2015, Mitta *et al.* 2017). This interval is designated as the *O. scythicum* beds (Mitta *et al.* 2017). By the presence of a representative of the genus *Oraniceras*, these beds are assigned to the Lower Bathonian Zigzag Chronozone. Judging by the archaic nature of the index species, they should be correlated with the basal part of this chronozone, with the lower part of the Convergens Chronosubzone.

Thus, despite these correlations and the wealth of stratigraphic data, there are still many gaps in the infrazonal ammonite scale of the Upper Bajocian–Lower Bathonian of the Kuban–Urup interfluve. A correlation of the local stratigraphic units with the chronostratigraphic scale is shown in Fig. 2.

The 31 dicoelitid specimens examined here were collected *in situ*. Belemnites are relatively rare in the Upper Djangura Member. Moreover, different stratigraphic intervals are characterized by fossils in varying degrees, despite the lithological similarity of the host rocks. Most dicoelitid specimens come from the lower part of the *Parkinsonia parkinsoni* Zone exposed on the Kyafar River (21 specimens). Additionally, we collected four specimens from the *Baculatoceras baculatum* beds of the *S. niortense* Zone and two specimens from the *Paragarantiana* beds of the *G. garantiana* Zone of the Kyafar River, three specimens from the *Djanaliparkinsonia alanica* beds of the *G. garantiana* Zone of the Kuban River, and one specimen from the *Oraniceras scythicum* beds of the Bolshoi Zelenchuk River.

All illustrated specimens are stored in the Centre for Collective Use «Collection GEOCHRON» at the Trofimuk Institute of Petroleum Geology and Geophysics, Siberian Branch, Russian Academy of Sciences, Novosibirsk, Russia (collection no. 2069).

Systematic palaeontology

Belemnite terminology and abbreviations in the descriptions follow Doyle & Kelly (1988): L – total preserved length; l – length from apex to tip of alveolus; Dv – dorso-ventral diameter at the tip of the alveolus; Dl – lateral diameter at the tip of the alveolus; Dv_{max} – maximum dorso-ventral diameter; Dl_{max} – maximum lateral diameter; x – length from apex to maximum diameter. The degree of rostrum elongation (l/Dv, × 100%) and compression (Dl/Dv, × 100%; Dl_{max}/Dv_{max}, × 100%) were also calculated. In cases where it was possible, we measured the apical angle (in the lateral plane), the alveolar angle (in the dorso-ventral plane), and the ratio of the ventral radius at the tip of the alveolus to Dv, × 100%. The internal characters of the rostrum (ontogeny, position of the apical line and the alveolus, the alveolar angle) were studied in longitudinal sections. Approximate size (length) ranges are given by the terms small (<60 mm), medium (60–100 mm) and large (>100 mm). In most cases, rostra were coated with magnesium oxide prior to photography.

Subclass Coleoidea Bather, 1888
Order Belemnitida von Zittel, 1895
Suborder Belemnopseina Jeletzky, 1965
Family Dicoelitidae Sachs & Nalnjaeva, 1967

Genus *Dicoelites* Boehm, 1906

Type species. – *Belemnites dicoelus* Rothpletz, 1892 by monotypy.

Occurrence. – Upper Bajocian of eastern Europe (Northern Caucasus); Bathonian–Kimmeridgian of eastern Africa, southern and south-eastern Asia, Oceania, and West Antarctica; possibly the middle Toarcian–Aalenian of north-western North America, Toarcian (?) of eastern Asia (Tibet), Bajocian and Upper Jurassic of south-western South America, Lower Bajocian of northern Africa, Upper Bajocian of Western Europe.

***Dicoelites aprilis* Dzyuba sp. nov.**
Figure 3A–K

Holotype. – GEOCHRON 2069/5, complete rostrum, Fig. 3A.

Type horizon and locality. – Upper Bajocian, *Strenoceras niortense* Zone, *Baculatoceras baculatum* beds; Djangura Formation, Upper Member; locality 30 on the Kyafar River, Northern Caucasus, Russia.

Material. – Holotype specimen GEOCHRON 2069/5.

Paratypes: GEOCHRON 2069/6, rostrum lacking the apical part, locality 17 on the Kyafar River, from type horizon; GEOCHRON 2069/7, subcomplete, slightly deformed rostrum, locality 5 on the Kyafar River, *Garantiana garantiana* Zone, *Paragarantiana* beds; GEOCHRON 2069/8, complete rostrum; GEOCHRON 2069/9, rostrum lacking the apical region, locality 4 on the Kyafar River, *Parkinsonia parkinsoni* Zone, *Rarecostites sherstyukovi* horizon; GEOCHRON 2069/10, subcomplete rostrum, locality 1 on the Kyafar River; GEOCHRON 2069/11, subcomplete rostrum, locality 0 on the Kyafar River, *P. parkinsoni* Zone, *Rarecostites subarietis* horizon; GEOCHRON 2069/12–2069/15, four complete or subcomplete rostra, the two of them (2069/13 and 2069/15) in combination with a phragmocone, locality 25 on the Kyafar River, *P. parkinsoni* Zone, *Parkinsonia djanelidzei* beds.

Dicoelites cf. *aprilis* sp. nov.: GEOCHRON 2069/16, fragment of the rostrum with partly preserved alveolar and stem regions, locality 4 on the Kyafar River, *P. parkinsoni* Zone, *R. sherstyukovi* horizon, and two similar specimens from localities 3 (*R. subarietis* horizon) and 4 on the Kyafar River.

?*Dicoelites* sp. (cf. *aprilis* sp. nov.): GEOCHRON 2069/17, rostrum lacking the alveolar region and the anterior part of the stem region, from type horizon and locality. All from the Djangura Formation, Upper Member.

Etymology. – Referring to the discovery of the holotype in April.

Diagnosis. – Medium-sized, elongate, weakly hastate rostrum. Dl_{max} located slightly posterior to the mid-point. Apex acute, dorsally displaced. Long and deeply incised ventral alveolar groove. Short dorsal alveolar groove. Cross section subcircular. Alveolus occupying approximately one fourth of the rostrum.

Description. – Medium-sized, elongate rostrum (Tab. 1). The outline is symmetrical and weakly hastate. Dl_{max} is located slightly posteriorly of the mid-point of the rostrum. The profile is slightly asymmetrical and weakly hastate. The apex is acute (*c*. 20–22°) and is more or less dorsally displaced. A deeply incised, "v-shaped" ventral alveolar groove extends to the anterior apical region. This groove is combined with a splitting surface. In the alveolar region, there is commonly a shallow and "u-shaped" dorsal groove, which is faint in some individuals. The lateral lines are generally indistinct but may be represented by a wide depression in the alveolar and anterior stem regions of adult forms (Fig. 3G_2). The cross section is subcircular, more compressed in the anterior portion of the rostrum. The alveolus is ventrally displaced (the ventral radius is *c*. 42% of Dv) and occupies approximately one-fourth of the rostrum (Fig. 3H). The alveolar angle is *c*. 24°. The apical line is weakly cyrtolineate. The earliest juvenile stages are subcylindrical to hastate. The phragmocone with visible siphuncle is also preserved, indicating that the position of the longest alveolar groove is ventral (Fig. 3K_1).

Remarks. – *D. aprilis* sp. nov. resembles representatives of the genus *Belemnopsis* Bayle, 1878 (Belemnopseidae) in overall shape, cross section and in the possession of a long ventral alveolar groove. Moreover, a very short and shallow dorsal alveolar groove sometimes may be developed in *Belemnopsis*, but this feature is not recognized as a stable character for belemnopseid species. In some cases, both the ventral and dorsal alveolar grooves may be present on the rostrum of representatives of the genus *Pseudodicoelites* Sachs *in* Sachs & Nalnjaeva, 1967 (Pseudodicoelitidae), but this genus is characterized by a more deeply incised and longer dorsal alveolar groove, while its ventral alveolar groove is indistinct to absent.

The new species most closely resembles ?*Dicoelites jacquoti* (Terquem & Jourdy, 1869) and *D. paraohangaensis* Challinor & Hudson, 2017, but is well distinguished from both these species by its less depressed cross section in the stem and apical regions, its longer ventral alveolar groove, and its dorsally displaced apex. The species differs from *D. spellmanorum* Challinor & Hudson, 2017 by the latter two features and additionally by its larger size, its less hastate shape, and its less compressed cross section. It is also distinguished from *D. paraohangaensis* and *D. spellmanorum* by the better developed dorsal alveolar groove.

Some rostra in our collection represented by small fragments are not distinguishable from the species described. In case they show two alveolar grooves, these rostra are referred to as *D.* cf. *aprilis* sp. nov. (Tab. 1, Fig. 3L). The fragment of the rostrum with preserved posterior portion only is assigned to ?*Dicoelites* sp. (cf. *aprilis* sp. nov.) (Tab. 1, Fig. 3M).

Occurrence. – Upper Bajocian (*Baculatoceras baculatum* beds to *Parkinsonia djanelidzei* beds) of the Northern Caucasus (Karachay-Cherkessia).

***Dicoelites octobris* Dzyuba sp. nov.**
Figure 4A–F

Holotype. – GEOCHRON 2069/18, complete rostrum, Fig. 4A.

Type horizon and locality. – Upper Bajocian, *Parkinsonia parkinsoni* Zone, *Rarecostites subarietis* horizon; Djangura Formation, Upper Member; locality 2 on the Kyafar River, Northern Caucasus, Russia.

Material. – Holotype specimen GEOCHRON 2069/18.

Paratypes: GEOCHRON 2069/19, complete rostrum, locality 23 on the Kuban River, *Garantiana garantiana* Zone, *Djanaliparkinsonia alanica* beds; GEOCHRON 2069/20, subcomplete rostrum, locality 4 on the Kyafar River, *Parkinsonia parkinsoni* Zone, *Rarecostites sherstyukovi* horizon; GEOCHRON 2069/21–2069/23, three complete or subcomplete rostra, locality 25 on the Kyafar River, *P. parkinsoni* Zone, *Parkinsonia djanelidzei* beds.

Dicoelites cf. *octobris* sp. nov.: GEOCHRON 2069/24, fragment of the rostrum with partly preserved stem region, locality 4 on the Kyafar River, *P. parkinsoni* Zone, *R. sherstyukovi* horizon, and one similar specimen from locality 3 (*Rarecostites subarietis* horizon) on the Kyafar River, GEOCHRON 2069/25, rostrum lacking the alveolar region and the anterior stem region, locality 17 on the Kyafar River, *Strenoceras niortense* Zone, *Baculatoceras baculatum* beds.

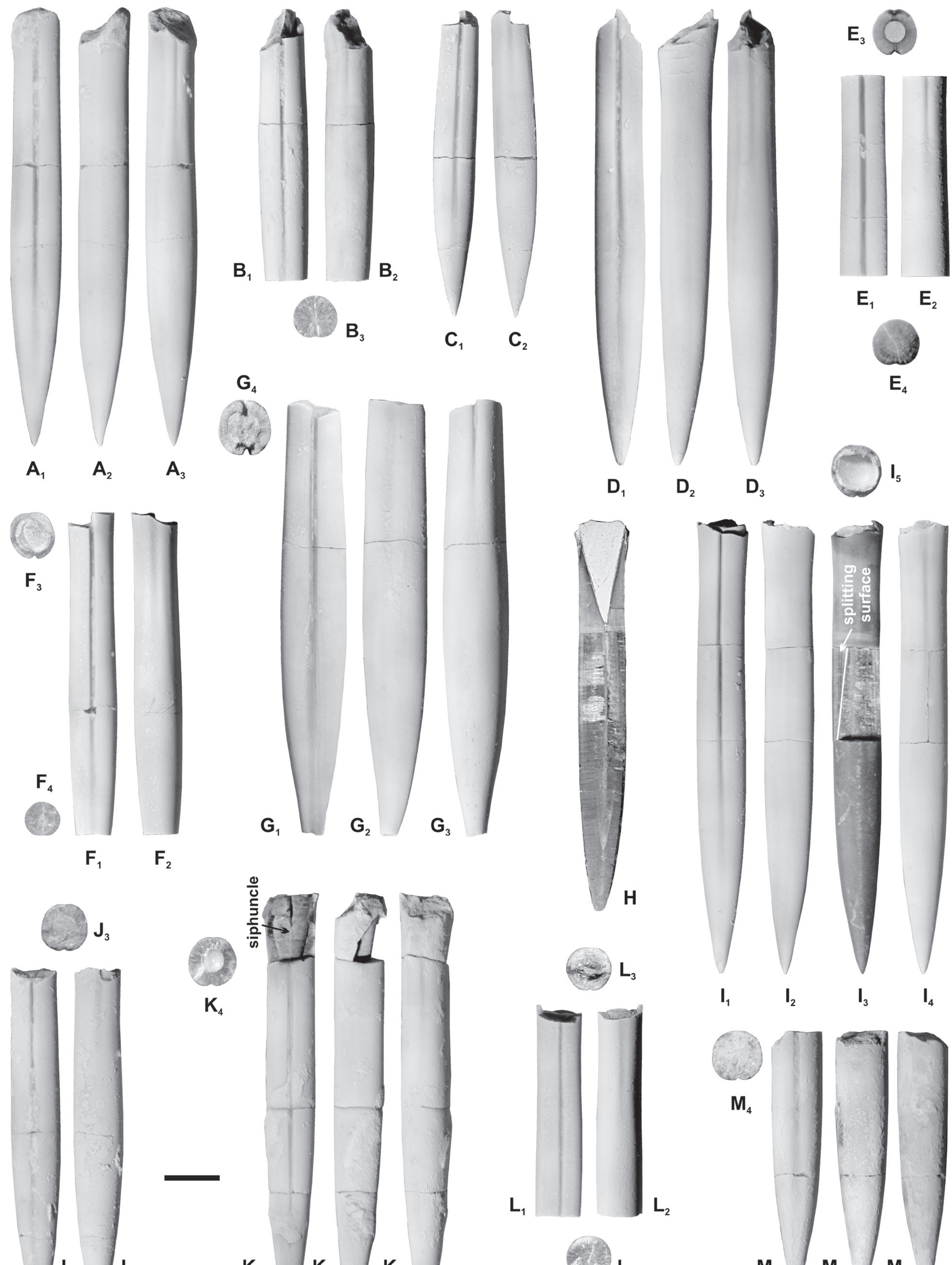
?*Dicoelites* sp. (cf. *octobris* sp. nov.): GEOCHRON 2069/26, fragment of the rostrum in the rock sample, locality 19 on the Kuban River, *G. garantiana* Zone, *D. alanica* beds, and four rostra consisting of fragments from localities 5 (*G. garantiana* Zone), 4 and 25 (*P. parkinsoni* Zone) on the Kyafar River. All from the Djangura Formation, Upper Member.

Etymology. – Due to the discovery of the holotype in October.

Diagnosis. – Medium-sized, slender, hastate rostrum. Dl_{max} located in the posterior portion. Apex acute, nearly centrally located. Moderately long, deeply incised ventral alveolar groove. Short, often faint dorsal alveolar groove. Cross section compressed, pyriform. Alveolus occupying approximately one-fifth of the rostrum.

Description. – Medium-sized, slender elongate rostrum (Tab. 1). The outline and profile are hastate, symmetrical or nearly symmetrical, with Dl_{max} located in the posterior portion of the rostrum. The apex is acute (*c.* 20–22°) and located nearly centrally. The apical line is closer to the aspect with a long alveolar groove, which consequently is considered the ventral groove. A deeply incised,

Figure 3. *Dicoelites* from the Upper Bajocian of Karachay-Cherkessia. • A–K – *Dicoelites aprilis* Dzyuba sp. nov.; A – holotype, GEOCHRON 2069/5, ventral (A_1), right lateral (A_2) and dorsal (A_3) views; B – GEOCHRON 2069/6, ventral (B_1), dorsal (B_2) views, and cross section at the posterior end (B_3); C – GEOCHRON 2069/7, ventral (C_1) and dorsal (C_2) views; D – GEOCHRON 2069/8, ventral (D_1), right lateral (D_2) and dorsal (D_3) views; E – GEOCHRON 2069/9, ventral (E_1), dorsal (E_2) views, and cross sections in the alveolar region (E_3) and near the point of maximum diameter (E_4); F – GEOCHRON 2069/10, ventral (F_1), dorsal (F_2) views, and cross sections at the anterior end (F_3) and at the posterior end (F_4); G – GEOCHRON 2069/11, ventral (G_1), right lateral (G_2), dorsal (G_3) views, and cross section at the anterior end (G_4); H – GEOCHRON 2069/12, longitudinal section; I – GEOCHRON 2069/13, ventral (I_1), right lateral (I_2), left lateral, with removed fragment (I_3), dorsal (I_4) views, and cross section at the anterior end (I_5); J – GEOCHRON 2069/14, ventral (J_1), dorsal (J_2) views, and cross section at the anterior end (J_3); K – GEOCHRON 2069/15, ventral (K_1), right lateral (K_2), dorsal (K_3) views, and cross section in the alveolar region (K_4). • L – *Dicoelites* cf. *aprilis* Dzyuba sp. nov.; GEOCHRON 2069/16, ventral (L_1), dorsal (L_2) views, and cross sections at the anterior end (L_3) and at the posterior end (L_4). • M – ?*Dicoelites* sp. (cf. *aprilis* Dzyuba sp. nov.); GEOCHRON 2069/17, ventral (M_1), right lateral (M_2), dorsal (M_3) views, and cross section at the anterior end (M_4). Scale bar is 10 mm.


A1
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F2
F3
F4
G1
G2
G3
G4
H
I1
I2
I3
I4
I5
splitting surface
J1
J2
J3
K1
K2
K3
K4
siphuncle
L1
L2
L3
L4
M1
M2
M3
M4

"v-shaped" ventral groove is developed in the alveolar and stem regions; posteriorly, the groove widens and shallows considerably. A ventral splitting surface is present. The dorsal alveolar groove is relatively short, "u-shaped" and often faint. The lateral lines may be slightly prominent. The cross section is compressed and pyriform. The alveolus is ventrally displaced (the ventral radius is *c*. 43% of Dv) and occupies approximately one-fifth of the rostrum (Fig. 4D). The alveolar angle is *c*. 27°. The apical line is weakly cyrtolineate to almost goniolineate. The earliest juvenile stages are hastate.

Remarks. – In general shape and cross section, *D. octobris* sp. nov. is close to representatives of the genus *Hibolithes* Montfort, 1808 (Belemnopseidae), but differs by its longer ventral alveolar groove and by having a dorsal alveolar groove as a stable character (at least in the rostra studied). The new species is similar to *D. spellmanorum* Challinor & Hudson, 2017 in having a slender hastate rostrum with a compressed cross section, but differs in its somewhat larger size, its better developed alveolar grooves, and the fact that its maximum diameter is located closer to the apex. The species is distinguished from *D. aprilis* sp. nov. by the latter feature and additionally by its somewhat smaller size, its more slender shape, its compressed cross section, its shorter ventral alveolar groove, and its almost non-eccentric apex. The new species is less elongate than *D. aviasi* Challinor & Grant-Mackie, 1989 and some other closely related species.

The fragments of the compressed rostra showing two alveolar grooves are referred to as *D.* cf. *octobris* sp. nov. (Tab. 1, Fig. 4G, H). More questionable fragments are assigned to ?*Dicoelites* sp. (cf. *octobris* sp. nov.) (Tab. 1, Fig. 4I).

Occurrence. – Upper Bajocian (*Djanaliparkinsonia alanica* beds to *Parkinsonia djanelidzei* beds, possibly the *Baculatoceras baculatum* beds) of the Northern Caucasus (Karachay-Cherkessia).

Genus *Conodicoelites* Stevens, 1965a

Type species. – *Dicoelites keeuwensis* Boehm, 1912 by original designation.

Occurrence. – Toarcian of north-western North America; Upper Bajocian–Callovian, as well as possibly Toarcian and Portlandian of Europe (with the exception of Northern Europe); Bathonian–Lower Kimmeridgian of south-western, southern and south-eastern Asia, Oceania, and West Antarctica.

***Conodicoelites exiguus* (Krimholz, 1953)**
Figure 4J–L

1953 *Dicoelites exiguus* sp. n.; Krimholz, p. 54, pl. 4, fig. 5.
1961 *Dicoelites exiguus* Krimholz. – Sibiryakova, p. 53, pl. 6, fig. 6.
1989 *Conodicoelites repini* Krimholz, sp. nov. – Krimholz & Repin, p. 92, pl. 1, fig. 3.

Types. – Two specimens, 210/21 and 210/22, from the same collection and locality, St. Petersburg University, Paleontological and Stratigraphic Museum (SPbU PSM), Russia; Djangura Formation, Upper Member; 5 km to the northeast of Zelenchukskaya Village, Northern Caucasus, Russia. Krimholz (1953) did not designate a holotype. The subcomplete rostrum, specimen no. 210/21, illustrated and described by Krimholz (1953, p. 54, pl. 4, fig. 5), is hereby designated as the lectotype and re-illustrated (Fig. 4J). A fragment of a rostrum represents another specimen of a former syntype series. This specimen, no. 210/22, is hereby designated as the paralectotype and is illustrated herein for the first time (Fig. 4K).

Material. – GEOCHRON 2069/27, complete rostrum, locality 8 on the Bolshoi Zelenchuk River, *Oraniceras scythicum* beds, Djangura Formation, Upper Member.

Diagnosis. – Medium-sized, moderately robust, cylindriconical to conical rostrum. Apex acute, dorsally displaced. Long and deeply incised ventral alveolar groove. Short and deeply incised dorsal alveolar groove. Cross section subcircular. Alveolus occupying one-third to two-fifths of the rostrum.

Description. – Medium-sized, moderately robust rostrum (Tab. 1). The outline is symmetrical and cylindriconical. The profile is asymmetrical, cylindriconical to conical. By analogy with the lectotype and paralectotype, the aspect with the longest alveolar groove is considered by us the venter. The venter is significantly inflated in the apical region, and the dorsum is only slightly inflated. The apex is acute (*c*. 26°) and dorsally displaced. A deeply incised, "v-shaped" ventral alveolar groove extends up to the anterior apical region, where it gradually widens and shallows. A deeply incised, "v-shaped" dorsal groove is well developed throughout the alveolar region. Both ventral and dorsal splitting surfaces may be present but not visible. The lateral lines are indistinct. The cross section is subcircular and almost equidimensional in the stem and apical regions, but slightly compressed in the alveolar region. The alveolus occupies approximately one-third of the rostrum.

Remarks. – The species strongly resembles *C. meyrati* (Ooster, 1857) but differs by having a shorter dorsal alveolar groove and a less compressed cross section. The

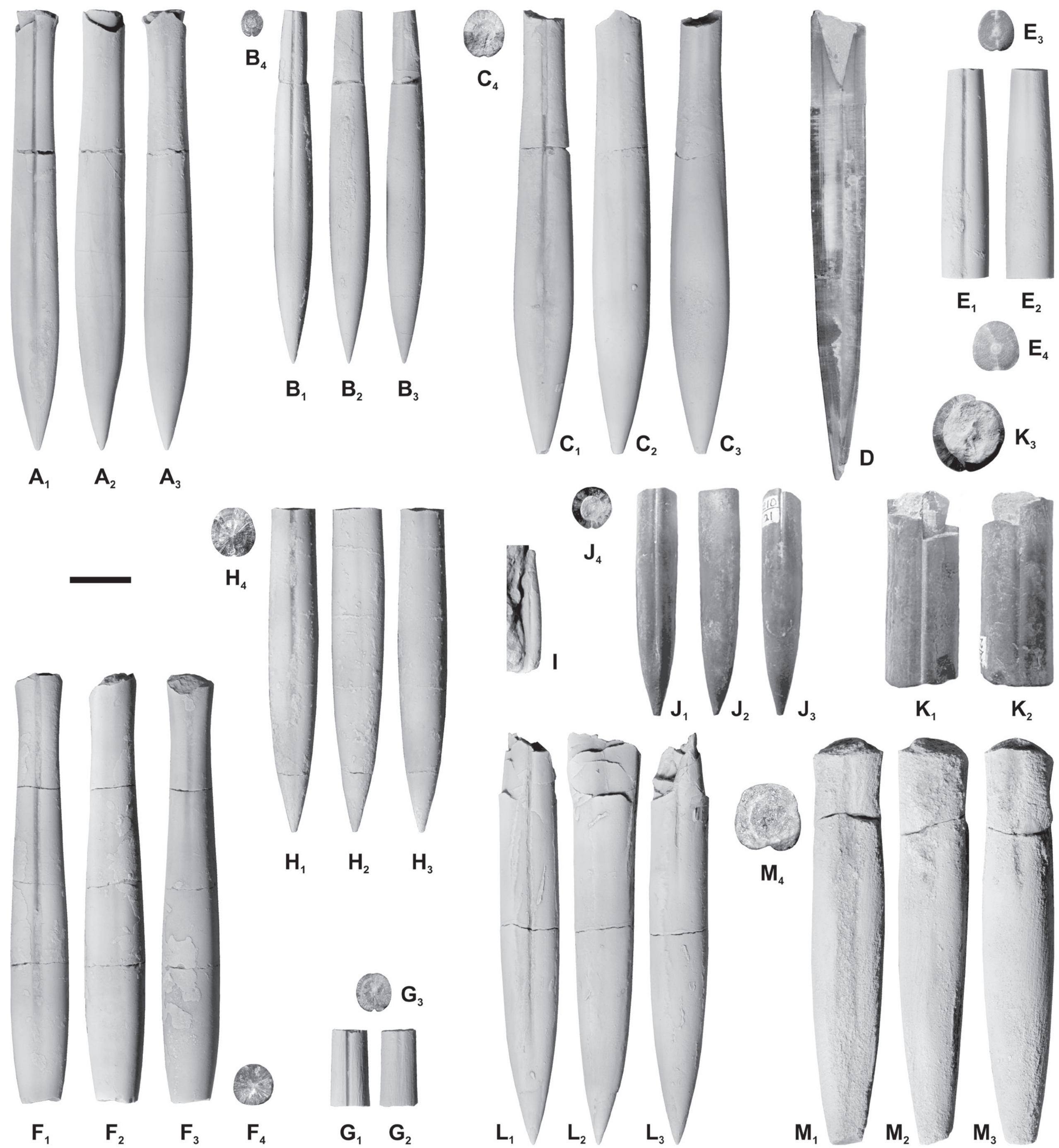

Figure 4. *Dicoelites* and *Conodicoelites* from the Upper Bajocian (A–I, M) and Lower Bathonian (J–L) of Karachay-Cherkessia. • A–F – *Dicoelites octobris* Dzyuba sp. nov.; A – holotype, GEOCHRON 2069/18, ventral (A_1), right lateral (A_2) and dorsal (A_3) views; B – GEOCHRON 2069/19, ventral (B_1), right lateral (B_2), dorsal (B_3) views, and cross section at the anterior end (B_4); C – GEOCHRON 2069/20, ventral (C_1), right lateral (C_2), dorsal (C_3) views, and cross section at the anterior end (C_4); D – GEOCHRON 2069/21, longitudinal section not ideally prepared; E –GEOCHRON 2069/22, ventral (E_1), dorsal (E_2) views, and cross sections near the tip of the alveolus (E_3) and near the point of maximum diameter (E_4); F – GEOCHRON 2069/23, ventral (F_1), right lateral (F_2), dorsal (F_3) views, and cross section at the posterior end (F_4). • G, H – *Dicoelites* cf. *octobris* Dzyuba sp. nov.; G – GEOCHRON 2069/24, ventral (G_1), dorsal (G_2) views, and cross section near the tip of the alveolus (G_3); H – GEOCHRON 2069/25, ventral (H_1), right lateral (H_2), dorsal (H_3) views, and cross section at the anterior end (H_4). • I – ?*Dicoelites* sp. (cf. *octobris* Dzyuba sp. nov.); GEOCHRON 2069/26, fragment of the rostrum (ventral view) in the rock sample. • J–L – *Conodicoelites exiguus* (Krimholz, 1953); J – lectotype, SPbU PSM 210/21, ventral (J_1), right lateral (J_2), dorsal (J_3) views, and cross section at the anterior end (J_4); K – paralectotype, SPbU PSM 210/22, ventral (K_1), dorsal (K_2) views, and cross section at the anterior end (K_3); L – GEOCHRON 2069/27, ventral (L_1), right lateral (L_2) and dorsal (L_3) views. • M – *Conodicoelites* sp.; GEOCHRON 2069/28, ventral (M_1), right lateral (M_2), dorsal (M_3) views, and cross section in the alveolar region (M_4). Scale bar is 10 mm.

specimen described was found approximately 15 km to the north of Zelenchukskaya Village that is not far from the type locality indicated by Krimholz (1953) for the species. Taking this new record as well as the record of *C. exiguus* from Turkmenistan (Sibiryakova 1961) into account, we conclude that the lectotype and paralectotype come from the Lower Bathonian rather than from the Upper Bajocian. The species *C. repini* Krimholz *in* Krimholz & Repin, 1989 is based on a single rostrum lacking the apex, which can be assigned to *C. exiguus*. This rostrum was found in the Lower–Middle Bathonian transition beds of Iran; in our opinion, it fulfils the diagnostic criteria for *C. exiguus*. Therefore, the name *C. repini* is included here in the synonymy of *C. exiguus*.

Occurrence. – Lower Bathonian of the Northern Caucasus (Karachay-Cherkessia) and Turkmenistan; Lower–Middle Bathonian transition of Iran.

***Conodicoelites* sp.**
Figure 4M

Material. – GEOCHRON 2069/28, rostrum lacking the apex, locality 19 on the Kuban River, *Garantiana garantiana* Zone, *Djanaliparkinsonia alanica* beds, Djangura Formation, Upper Member.

Description. – Medium-sized, moderately robust rostrum (Tab. 1). The outline is symmetrical and weakly hastate. The profile is asymmetrical, cylindriconical to conical. By analogy with *C. exiguus*, the aspect with the longest alveolar groove is considered to be the venter. The venter is flattened and the dorsum is slightly inflated. The apex is acute. Since our material comprises only one single rostrum, which is only incompletely preserved, we cannot examine and describe the alveolar grooves in detail. Nevertheless, it is clear that the ventral groove extends to the apical region, while the dorsal groove is confined to the alveolar region. The specimen shows no evidence of splitting surfaces associated with grooves although they may be present. The lateral lines are represented by a narrow groove-like depression in the alveolar region. The cross section is subquadrate, being slightly compressed in the anterior alveolar region and slightly depressed at the tip of the alveolus; the degree of rostrum depression increases toward the apex. The alveolus occupies approximately one-third of the rostrum.

Remarks. – The specimen somewhat resembles *C. exiguus* but is weakly hastate in outline, less asymmetrical in profile, and has a flattened venter. We abstain from describing a new species based on a single specimen. The specimen is close to *C. waageni* (Neumayr, 1871), but this species differs by its longer dorsal alveolar groove. The same concern applies to the morphologically closest species *C. riljensis* Gaković & Stoyanova-Vergilova, 1978 and *C. nishavaensis* Stoyanova-Vergilova, 1979; additionally, the former species is distinguished by its depressed cross section in the anterior alveolar region, while the latter is compressed on the entire length of its rostrum and has a more cylindrical rostrum shape with an inflated venter.

Occurrence. – Upper Bajocian (*Djanaliparkinsonia alanica* beds) of the Northern Caucasus (Karachay-Cherkessia).

Discussion

Dicoelitid belemnites of the western Tethys

New belemnite records from the Northern Caucasus (Karachay-Cherkessia) contribute to the palaeontological characteristics of the Mediterranean belemnite province of the Tethyan Realm *sensu* Challinor *et al.* (1992) or the Mediterranean-Caucasian faunal Subrealm of the Tethyan Realm *sensu* Westermann (2000) in Bajocian time. Our data provide evidence supporting the presence of *Dicoelites* in the Bajocian deposits of the western Tethyan domain. Two new species, *D. aprilis* Dzyuba sp. nov. and *D. octobris* Dzyuba sp. nov., are recorded from the Upper Bajocian of the southern part of eastern Europe. These new data significantly increase the possibility that ?*Dicoelites* sp. A from the Lower Bajocian (Laeviuscula Chronozone) of Morocco (Weis *et al.* 2017) and "*Belemnites*" *jacquoti* Terquem & Jourdy, 1869 from the Upper Bajocian of north-eastern France belong to the genus *Dicoelites*. The latter two taxa, both characterized by a rostrum with alveolar grooves of different length and depth in ventral and dorsal positions, were identified based on limited material. It cannot be excluded that these rostra are of individuals with developed dorsal groove and belong to one of the belemnopseid genera, *Belemnopsis* or *Hibolithes*. This possibility precludes us from assigning them to *Dicoelites* with certainty. Although the position of the alveolar grooves on the rostra (dorsal *vs*. ventral) was not precisely defined, we have major doubts about the relevance of their assignment to the genus *Pseudodicoelites* (Pseudodicoelitidae), which is characterized by a long dorso-alveolar groove and some-times by a short ventro-alveolar groove but is an exclusively boreal taxon (Sachs & Nalnjaeva 1975, Jeletzky 1980).

The single rostrum identified herein as *Conodicoelites* sp., which probably belongs to the new unknown species, is reported from the Upper Bajocian (Garantiana Chronozone) of the Northern Caucasus. The species *C. exiguus* (Krimholz, 1953) is recorded herein from the Lower Bathonian (Zigzag Chronozone) with certainty, being previously known in the Northern Caucasus as

Table 1. Measurements of the studied belemnites. Abbreviations: * – measured at the anterior end; L – total preserved length; l – length from apex to tip of alveolus; Dv – dorso-ventral diameter at the tip of the alveolus; Dl – lateral diameter at the tip of the alveolus; Dv_{max} – maximum dorso-ventral diameter; Dl_{max} – maximum lateral diameter; x – length from apex to maximum diameter; (l/Dv, × 100%) – degree of rostrum elongation; (Dl/Dv, × 100%; Dl_{max}/Dv_{max}, × 100%) – compression.

Specimen no.	L, mm	l, mm	Dv, mm	Dl, mm	Dv_{max}, mm	Dl_{max}, mm	x, mm	l/Dv, × 100%	Dl/Dv, × 100%	Dl_{max}/Dv_{max}, × 100%
Dicoelites aprilis Dzyuba sp. nov.										
GEOCHRON 2069/5	79.6	53.0	8.6	8.7	9.0	9.3	36.0	616	101	103
GEOCHRON 2069/6	49.3	–	8.7	8.7	8.8	8.9	–	–	100	101
GEOCHRON 2069/7	55.6	53.0	7.1	6.8	7.2	7.5	29.0	746	96	104
GEOCHRON 2069/8	82.8	55.5	9.2	8.6	9.1	9.2	38.5	603	93	101
GEOCHRON 2069/9	36.3	–	8.3	7.8	8.4	8.6	–	–	94	102
GEOCHRON 2069/10	58.5	–	8.1	7.8	8.4	8.6	–	–	96	102
GEOCHRON 2069/11	79.2	~66.0	10.9	10.6	11.5	11.7	~38.0	606	97	102
GEOCHRON 2069/12	71.0	51.9	8.4	8.2	8.7	9.0	34.0	618	98	103
GEOCHRON 2069/13	82.3	59.7	8.7	8.4	8.9	8.8	42.5	686	97	99
GEOCHRON 2069/14	56.2	–	8.5	8.2	8.7	9.0	–	–	96	103
GEOCHRON 2069/15	69.8	–	8.6	8.5	8.8	8.8	–	–	99	100
Dicoelites cf. *aprilis* Dzyuba sp. nov.										
GEOCHRON 2069/16	38.6	–	7.7	7.8	7.9	8.2	–	–	101	104
?*Dicoelites* sp. (cf. *aprilis* Dzyuba sp. nov.)										
GEOCHRON 2069/17	44.6	–	–	–	9.0	9.1	39.0	–	–	101
Dicoelites octobris Dzyuba sp. nov.										
GEOCHRON 2069/18	71.8	56.7	6.8	6.2	8.0	7.8	25.0	834	91	98
GEOCHRON 2069/19	57.7	56.0	4.3	3.7	6.6	6.4	23.0	1302	86	97
GEOCHRON 2069/20	72.4	65.0	7.6	6.7	9.4	9.6	24.0	855	88	102
GEOCHRON 2069/21	76.6	64.1	9.1	8.0	–	–	–	704	88	–
GEOCHRON 2069/22	34.3	–	6.8	5.9	8.2	7.6	–	–	87	93
GEOCHRON 2069/23	70.2	–	6.9	6.5	9.9	9.4	–	–	94	95
Dicoelites cf. *octobris* Dzyuba sp. nov.										
GEOCHRON 2069/24	12.8	–	6.3	5.8	–	–	–	–	92	–
GEOCHRON 2069/25	52.9	–	7.9*	7.1*	8.1	7.9	25.5	–	90*	98
?*Dicoelites* sp. (cf. *octobris* Dzyuba sp. nov.)										
GEOCHRON 2069/26	20.0	–	–	–	–	–	–	–	–	–
Conodicoelites exiguus (Krimholz, 1953)										
GEOCHRON 2069/27	67.2	46.9	9.5	9.3	–	–	–	494	98	–
Conodicoelites sp.										
GEOCHRON 2069/28	64.7	–	11.1	11.5	–	–	–	–	104	–

originating from the "Upper Bajocian or Lower Bathonian". The representatives of this species were also illustrated and described from southwestern Asia, where they were found in the Lower Bathonian of Turkmenistan (Sibiryakova 1961) and the Lower–Middle Bathonian transition beds of Iran (Krimholz & Repin 1989, as *C. repini* Krimholz, sp. nov.). Besides *C. exiguus*, some other species of the genus *Conodicoelites* are known from the western Tethyan domain. In southeastern Europe, *C. riljensis* Gaković & Stoyanova-Vergilova (1978, p. 419, pl. 1, fig. 1) was discovered in Bosnia and Herzegovina, being recorded from the "upper part of Domerian", which is currently assigned to the Lower Toarcian Tenuicostatum Chronozone (for discussion see Weis *et al.* 2015a). The two

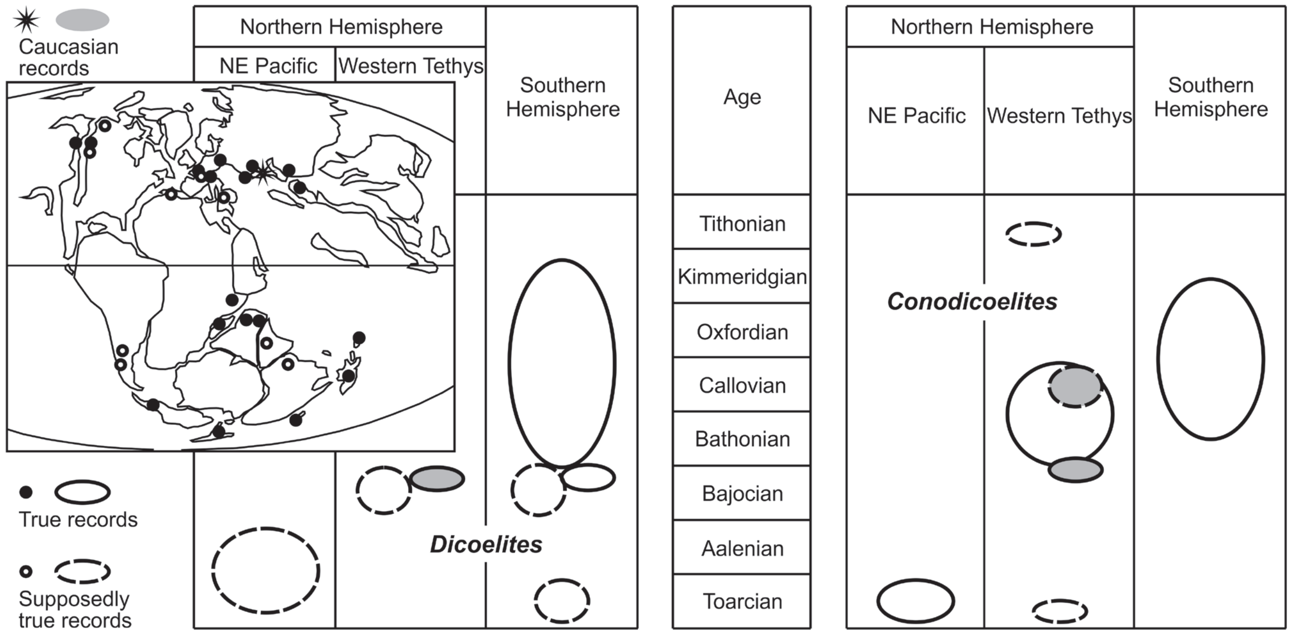

Figure 5. Dicoelitid distribution pattern. Compiled from numerous sources (see text). Generalized plate tectonic map of Jurassic is based on Scotese (2004) and Golonka (2011).

species *C. glojenensis* Stoyanova-Vergilova (1979, p. 55, pl. 3, fig. 2) and *C. nishavaensis* Stoyanova-Vergilova (1979, p. 55, pl. 3, fig. 1) were reported from the Bathonian of Bulgaria. However, the western Tethyan representatives of *Conodicoelites* are more common in the Callovian; they were recognized in France, Switzerland, Poland, and the Crimea (*e.g.* Bülow-Trummer 1920, Krimholz 1931, Pugaczewska 1961) under the generic name *Dicoelites* prior to the publication of the generic name *Conodicoelites* proposed by Stevens (1965a). *Conodicoelites keeuwensis* (Boehm, 1912) was mentioned but not illustrated for the Callovian of western Abkhazia, the Southern Caucasus (Krimholz *in* Rostovtsev *et al.* 1992). The species "*Belemnites*" *pellati* de Loriol *in* Loriol & Pellat (1874, p. 14, pl. 1, fig. 10) recorded from the middle Portlandian of France is also similar to *Conodicoelites* in having a robust rostrum with two alveolar grooves in ventral and dorsal positions, although its affiliation to Dicoelitidae is usually questioned (*e.g.* Bülow-Trummer 1920, Stevens 1965a). According to Weis *et al.* (2015b), the Aalenian–Lower Bajocian west-Tethyan species "*Belemnites*" *avena* Dumortier *in* Mayer 1866, previously considered as a representative of *Dicoelites* (*e.g.* Boehm 1912, Bülow-Trummer 1920), belongs to the genus *Rhabdobelus* Naef, 1922 of the family Hastitidae (Belemnitina).

In the Late Aalenian–Early Bajocian, the Caucasian belemnite communities were represented by a mixed belemnitin–belemnopsein fauna that was characteristic for the area from southern England to northern Iran (Weis *et al.* 2017). In the Late Bajocian, however, the communities were dominated by belemnopseins in the area of Karachay-Cherkessia (herein and unpublished data). This change in the taxonomic structure of the belemnite fauna displays a gradual displacement of belemnitins by belemnopseins, distinctive for the Tethyan seas during Bajocian–Bathonian times (*e.g.* Doyle & Bennet 1995, Weis *et al.* 2017). New data described herein indicate the successive appearance of dicoelitid genera in the Caucasian margin of the Tethys during the Late Bajocian, i.e. *Dicoelites* in the late Niortense Chron and *Conodicoelites* in the early Garantiana Chron, both before mid-Late Bajocian time.

Dicoelitid distribution pattern

Reliable records of the earliest Dicoelitidae were reported from the Toarcian of western Canada in North America, where *Conodicoelites* has been well documented (Jeletzky 1980). This dicoelitid represents a component of the earliest belemnite fauna known from the north-eastern Pacific (*e.g.* Jeletzky 1980, Dzyuba *et al.* 2019). Other Toarcian records of dicoelitids elsewhere are less certain (Fig. 5). The presence of *Conodicoelites* in the Toarcian of southeastern Europe (Bosnia and Herzegovina) requires confirmation by new reliable data (*cf.* Weis *et al.* 2015a). Supposedly true records of *Dicoelites* are known from the middle Toarcian–Aalenian of western and northern Canada in North America (Jeletzky 1980) and from the Toarcian (?) of China (southern Tibet) in eastern Asia (Wu 1982; for discussion see Iba *et al.* 2015). Therefore, the earliest distribution pattern of the dicoelitid genera *Dicoelites* and *Conodicoelites* is considered uncertain so far (*e.g.* Iba *et al.* 2015, Challinor & Hudson 2017, Weis *et al.* 2017). It is not clear what area or even hemisphere was the centre of origin of the Dicoelitidae, the Northern Hemisphere [north-eastern Pacific (?), western Tethys (?)] or the Southern Hemisphere (*e.g.* southern Tethys where southern Tibet was located in Jurassic times).

Whatever it was, prior to the appearance of dicoelitid belemnites in the Caucasian margin of the Tethys, they apparently had already existed in the west Tethyan seas and beyond (Fig. 5). *Dicoelites* is also known from the Bajocian of Argentina (Neuquén Basin) but was never illustrated (Doyle *et al.* 1997), whereas *Dicoelites* sp. A from the Upper Bajocian of Indonesia (Sula Islands) has been figured (Challinor *et al.* 1992). However, most of the reliable records of *Dicoelites* and *Conodicoelites* in the Southern Hemisphere come from the Bathonian–Kimmeridgian from Somaliland, Madagascar, the Himalayas, Indonesia, Papua New Guinea, New Caledonia, New Zealand, and West Antarctica (for a summary see Stevens 1965a, Combémorel 1988, Challinor 1991, Doyle *et al.* 1997, Challinor & Hikuroa 2007, Challinor & Hudson 2017). According to Challinor (1991), some specimens of *Belemnopsis* described from the Middle Jurassic of Western Australia by Whitehouse (1924) could belong to *Dicoelites*, but Stevens (1965a) regarded them as *Belemnopsis* variants with a slightly developed dorsal groove. A few poorly preserved *Dicoelites* rostra were mentioned from the Upper Jurassic of Argentina and Chile (Stevens 1965b).

Taking into account that dicoelitids became relatively widespread and abundant in post-Bajocian times before their disappearance by the end of the Jurassic, we can conclude that our records from the Northern Caucasus contributes new data to the study of the early history of the distribution of this family.

Conclusions

Our study of dicoelitid belemnite specimens collected from the Upper Bajocian–Lower Bathonian of Karachay-Cherkessia (Northern Caucasus, southwest Russia) has revealed *Dicoelites aprilis* Dzyuba sp. nov., *Dicoelites octobris* Dzyuba sp. nov., *Conodicoelites* sp., and *Conodicoelites exiguus* (Krimholz, 1953). Both new species of *Dicoelites* have been established within the Upper Bajocian, indicating the range for the genus in the Northern Caucasus from the Baculatum Chronosubzone of the Niortense Chronozone up to the Parkinsoni Chronozone. They represent the first records of *Dicoelites* (s. str.) from the Upper Bajocian of Eastern Europe. *Conodicoelites* sp. is documented for the Upper Bajocian (Garantiana Chronozone), while the species *C. exiguus* is recorded from the Lower Bathonian (Zigzag Chronozone).

Dicoelites aprilis sp. nov. resembles members of the genus *Belemnopsis* (Belemnopseidae), while *Dicoelites octobris* sp. nov. resembles members of the genus *Hibolithes* (Belemnopseidae), but these new species possess a ventral alveolar groove in stable combination with a dorsal alveolar groove, which is a characteristic feature of the Dicoelitidae. New belemnite records from Karachay-Cherkessia contribute to a dicoelitid distribution pattern in the Middle Jurassic. Here, we provide evidence that the first appearance of *Dicoelites* in the European marginal seas of the Tethys Ocean and *Conodicoelites* in the Caucasian area of these seas occurred before mid-Late Bajocian time.

Acknowledgements

We are grateful to Vladimir V. Arkadiev (St. Petersburg) for photographs and information about the type series of *Conodicoelites exiguus* (Krimholz, 1953) and to Cynthia D. Schraer (Anchorage) for reading and English language editing of the manuscript. We thank the reviewers, Martin Košťák (Prague) and Robert Weis (Luxembourg) for their helpful comments and valuable suggestions. This is a contribution to the RFBR (Russian Foundation for Basic Research) project no. 19-05-00130.

References

Adamia, Sh., Alania, V., Habukiani, A., Kutelia, Z. & Sadradze, N. 2011. Great Caucasus (Cavcasioni): a long-lived North-Tethyan Back-Arc Basin. *Turkish Journal of Earth Sciences 20*, 611–628.

Bather, F.A. 1888. Shell growth in Cephalopoda (Siphonopoda). *Annals and Magazine of Natural History 6(1)*, 298–310. DOI 10.1080/00222938809460727

Bayle, E. 1878. Fossiles principaux des terrains de la France. Atlas, 1–176. *In* Bayle, E. & Zeiller, R. (eds) *Explication de la carte géologique de France 4. Atlas. Part 1*. Imprimerie Nationale, Paris.

Besnosov, N.V. 1967. *Bajocian and Bathonian deposits of the Northern Caucasus*. 179 pp. Nauka, Moscow. [in Russian]

Boehm, G. 1906. Geologische Mitteilungen aus dem Indo-Australischen Archipel. 1: Neues aus dem Indo-Australischen Archipel. *Neues Jahrbuch für Mineralogie etc 22*, 385–412.

Boehm, G. 1912. Beiträge zur Geologie von Niederländisch-Indien. 1. Die Südküsten der Sula-Inseln Taliabu und Mangoli. 4. Unteres Callovien. *Palaeontographica 3*, 121–179.

Bülow-Trummer, E. von 1920. *Fossilium catalogus 1. Animalia. Pars 11. Cephalopoda Dibranchiata*. 313 pp. Junk, Berlin.

Callomon, J.H. 1964. Notes on the Callovian and Oxfordian

Stages, 269–291. *In* Maubege, P.L. (ed.) *Colloque du Jurassique à Luxembourg, 1962: comptes rendus et mémoires*. Institut grand-ducal, Section des sciences naturelles, physiques et mathématiques, Luxembourg.

Callomon, J.H. 1985. The evolution of the Jurassic ammonite family Cardioceratidae. *Special Papers in Palaeontology 33*, 49–90.

Challinor, A.B. 1991. Belemnite successions and faunal provinces in the southwest Pacific, and the belemnites of Gondwana. *BMR Journal of Australian Geology & Geophysics 12*, 301–325.

Challinor, A.B. & Grant-Mackie, J.A. 1989. Jurassic Coleoidea of New Caledonia. *Alcheringa 13(4)*, 269–304. DOI 10.1080/03115518908619051

Challinor, A.B. & Hikuroa, D.C.H. 2007. New Middle and Upper Jurassic belemnite assemblages from West Antarctica (Latady Group, Ellsworth Land): taxonomy and paleobiogeography. *Palaeontologia Electronica 10(1)*, 1–29. *http://palaeo-electronica.org*

Challinor, A.B. & Hudson, N. 2017. Early and Middle Jurassic belemnites of New Zealand. *Australasian Palaeontological Memoirs 50*, 1–69.

Challinor, A.B., Doyle, P., Howlett, P.J. & Nalnjaeva, T.I. 1992. Belemnites of the circum-Pacific region, 334–341, 636–645. *In* Westermann, G.E.G. (ed.) *The Jurassic of the Circum-Pacific*. Cambridge University press, Cambridge. DOI 10.1017/CBO9780511529375.025

Combémorel, R. 1988. Les bélemnites de Madagascar. *Documents de la Laboratoire de Géologie de la Faculté des Sciences de Lyon 104*, 1–239.

Doyle, P. & Bennett, M.R. 1995. Belemnites in biostratigraphy. *Palaeontology 38(4)*, 815–829.

Doyle, P. & Kelly, S.R.A. 1988. *The Jurassic and Cretaceous belemnites of Kong Karls Land, Svalbard*. 77 pp. Norsk Polarinstitutt, Oslo.

Doyle, P., Kelly, S.R.A., Pirrie, D. & Riccardi, A.C. 1997. Jurassic belemnite distribution patterns: implications of new data from Antarctica and Argentina. *Alcheringa: An Australasian Journal of Palaeontology 21*, 219–228. DOI 10.1080/03115519708619175

Dzyuba, O.S. & Lagausie, B. de 2018. New belemnites (Megateuthididae, Cylindroteuthididae) from the Bajocian and Bathonian of the Yuryung-Tumus Peninsula, northern Siberia, Russia and their palaeobiogeographic implications. *Paläontologische Zeitschrift 92*, 87–105. DOI 10.1007/s12542-017-0380-6

Dzyuba, O.S., Weis, R., Nalnjaeva, T.I. & Riegraf, W. 2015. *Rarobelus* nom. nov. from the Boreal Toarcian–Aalenian and its systematic position (Belemnitida, Belemnitina, Megateuthididae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 275*, 305–315. DOI 10.1127/njgpa/2015/0465

Dzyuba, O.S., Goryacheva, A.A., Ruban, D.A., Gnezdilova, V.V. & Zayats, P.P. 2016. New data on Callovian (Middle Jurassic) belemnites and palynomorphs from the Northern Caucasus, southwest Russia. *Geologos 22(1)*, 49–59. DOI 10.1515/logos-2016-0004

Dzyuba, O.S., Schraer, C.D., Hults, C.P., Blodgett, R.B. & Schraer, D.J. 2019. Early Bajocian belemnites of South-central Alaska: new data and new perspectives on mid-Middle Jurassic Megateuthididae and Belemnopseidae biogeography. *Journal of Systematic Palaeontology 17(11)*, 911–935. DOI 10.1080/14772019.2018.1486335

Gaković, M. & Stoyanova-Vergilova, M. 1978. *Conodicoelites riljensis* spec. nov. (Belemnitida) from the Domerian in the Dinarides. *Geoloshki Anali Balkanskoga Poluostrva 42*, 413–420. [in Bulgarian with English summary]

Golonka, J. 2011. Phanerozoic palaeoenvironment and palaeolithofacies maps of the Arctic region. *Geological Society of London, Memoirs 35*, 79–129. DOI 10.1144/M35.6

Iba, Y., Sano, S., Rao, X., Fuchs, D., Chenc, T., Weis, R. & Sha, J. 2015. Early Jurassic belemnites from the Gondwana margin of the Southern Hemisphere – Sinemurian record from South Tibet. *Gondwana Research 28*, 882–887. DOI 10.1016/j.gr.2014.06.007

Ippolitov, A.P. 2018a. Lower Bathonian belemnites and biostratigraphy of the central and southern parts of the East European Platform: Part 1. Megateuthididae. *Stratigraphy and Geological Correlation 26(2)*, 179–205. DOI 10.1134/S0869593818020041

Ippolitov, A.P. 2018b. Lower Bathonian belemnites and biostratigraphy of the central and southern parts of the East European Platform: Part 2. Cylindroteuthididae and Belemnotheutididae. *Stratigraphy and Geological Correlation 26(4)*, 433–458. DOI 10.1134/S0869593818040020

Ippolitov, A.P. 2018c. Marine Early Bajocian deposits of the Lower Volga Region (Volgograd region) and their belemnite-based stratigraphy. *Stratigraphy and Geological Correlation 26(3)*, 298–332. DOI 10.1134/S0869593818030073

Ippolitov, A.P. & Desai, B.G. 2019. Dwarf megateuthidid belemnites from the Bathonian of Kachchh (India: Gujarat) and their significance for palaeobiogeography. *Journal of Systematic Palaeontology 17(8)*, 613–634. DOI 10.1080/14772019.2018.1448471

Jeletzky, J.A. 1965. Taxonomy and phylogeny of fossil Coleoidea (= Dibranchiata). *Geological Survey of Canada, Paper 65(2)*, 72–76. DOI 10.4095/121441

Jeletzky, J.A. 1980. Dicoelitid belemnites from the Toarcian–Middle Bajocian of western and Arctic Canada. *Geological Survey of Canada, Bulletin 338*, i–vii, 1–71. DOI 10.4095/109531

Krimholz, G.Ya. 1931. Jurassic belemnites of the Crimea and Caucasus. *Transactions of the Geological and Prospecting Service of U.S.S.R. 76*, 1–52.

Krimholz, G.Ya. 1953. Materials to the stratigraphy and fauna of the Lower and Middle Jurassic of the Caucasus. *Uchenye Zapiski Leningradskogo Gosudarstvennogo Universiteta 159*, 25–58. [in Russian]

Krimholz, G.Ya. & Repin, Yu.S. 1989. About few Jurassic guards from Iran and belemnitid's commissure, 86–93. *In* Soloviev, V.A. (ed.) *Stage and zonal scales of the Boreal Mesozoic of the USSR*. Nauka, Moscow. [in Russian]

Loriol, P. de & Pellat, E. 1874. Monographie paléontologique des étages supérieurs de la formation Jurassique des environs de Boulogne-sur-Mer. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 24*, 1–292.

Mayer, K. 1866. Diagnoses de bélemnites nouvelles. *Journal of Conchology 3(6)*, 358–369.

Mitta, V.V. 2015. Genus *Oraniceras* (Parkinsoniidae, Ammonoidea) from the Lower Bathonian of southern European Russia. *Paleontological Journal 49(6)*, 595–601. DOI 10.1134/S0031030115060088

Mitta, V.V. 2017a. On some *Rarecostites* (Parkinsoniidae, Ammonoidea) from the Upper Bajocian Parkinsoni zone of the Northern Caucasus. *Paleontological Journal 51(5)*, 464–479. DOI 10.1134/S0031030117050057

Mitta, V.V. 2017b. The ammonoid genus *Spiroceras* (Spiroceratidae, Ammonoidea) from the Upper Bajocian of the Northern Caucasus. *Paleontological Journal 51(2)*, 133–142. DOI 10.1134/S0031030117020101

Mitta, V.V. 2017c. The genus *Keppleritiana* gen. nov. (Stephanoceratidae, Ammonoidea) from the Upper Bajocian of the Northern Caucasus. *Paleontological Journal 51(3)*, 247–257. DOI 10.1134/S0031030117030066

Mitta, V.V. 2018. On the first finds of the genus *Djanaliparkinsonia* (Stephanoceratidae, Ammonoidea) in the Upper Bajocian of the Northern Caucasus. *Paleontological Journal 52(4)*, 379–388. DOI 10.1134/S0031030118040093

Mitta, V.V. 2019. Ammonites and stratigraphy of the Upper Bajocian *Garantiana garantiana* Zone in the interfluve between the Kuban and Urup rivers (Northern Caucasus). *Paleontological Journal 53(11)*, 72–86. DOI 10.1134/S0031030119110066

Mitta, V.V. & Schweigert, G. 2016. A new morphotype of lower jaw associated with *Calliphylloceras* (Cephalopoda: Ammonoidea) from the Middle Jurassic of the Northern Caucasus. *Paläontologische Zeitschrift 90(2)*, 293–297. DOI 10.1007/s12542-016-0288-6

Mitta, V.V. & Sherstyukov, M.P. 2014. On the Bajocian and Bathonian of Bolshoy Zelenchuk River Basin (Northern Caucasus), 74–81. *In* Ivanov, A.V. (ed.) *Problems of paleoecology and historical geoecology*. Saratov State Technical University, Saratov. [in Russian]

Mitta, V.V. & Sherstyukov, M.P. 2018. First record of *Patrulia* (Ammonoidea: Stephanoceratidae) in the Upper Bajocian of the Northern Caucasus, Russia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 288(3)*, 251–254. DOI 10.1127/njgpa/2018/0739

Mitta, V.V., Savelieva, Ju.N., Fedorova, A.A. & Shurekova, O.V. 2017. Biostratigraphy of the Bajocian–Bathonian boundary beds in the basin of the Bolshoi Zelenchuk River (Northern Caucasus). *Stratigraphy and Geological Correlation 25(6)*, 607–626. DOI 10.1134/S0869593817060065

Mitta, V.V., Savelieva, Ju.N., Fedorova, A.A. & Shurekova, O.V. 2018. Ammonites, microfauna and palynomorphs from the lower part of the Upper Bajocian Parkinsoni Zone of the basin of the Bolshoi Zelenchuk River, Northern Caucasus. *Stratigraphy and Geological Correlation 26(5)*, 552–570. DOI 10.1134/S0869593818050040

Montfort, P.D. de. 1808. *Conchyliologie systématique, et classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Tome 1*. 409 pp. F. Schoell, Paris.

Naef, A. 1922. *Die fossilen Tintenfische. Eine paläozoologische Monographie*. 322 pp. Gustav Fischer, Jena. DOI 10.5962/bhl.title.2082

Neumayr, M. 1871. Die Cephalopoden-Fauna der Oolith von Balin bei Krakau. *Abhandlungen der Kaiserlich-königlichen Geologischen Reichanstalt 5(2)*, 19–54.

Nikishin, A.M., Ziegler, P.A., Bolotov, S.N. & Fokin, P.A. 2012. Late Palaeozoic to Cenozoic evolution of the Black Sea–southern Eastern Europe region: a view from the Russian Platform. *Turkish Journal of Earth Sciences 21(5)*, 571–634.

Ooster, W.A. 1857. *Catalogue des Céphalopodes fossiles des alpes suisses: avec la description et les figures des espèces remarquables 1: Céphalopodes acétabulifères*. 32 pp. Imprimerie de Zurcher et Furrer, Zurich.

Polyansky, B.V. 1989. *Mesozoic coal-bearing formations of the Mesotethys northern margin*. 192 pp. Nauka, Moscow. [in Russian]

Pugaczewska, H. 1961. Belemnoids from the Jurassic of Poland. *Acta Paleontologica Polonica 6*, 105–236.

Rostovtsev, K.O., Agaev, V.B., Azarian, N.R., Babaev, R.G., Besnosov, N.V., Hassanov, N.A. *et al.* 1992. *Jurassic of the Caucasus*. 192 pp. Nauka, St. Petersburg. [in Russian]

Rothpletz, A. 1892. Die Perm-, Trias- und Jura-Formation auf Timor und Rotti im Indischen Archipel. *Palaeontographica 39(2–3)*, 57–106.

Ruban, D.A. 2006. The palaeogeographic outlines of the Caucasus in the Jurassic: the Caucasian Sea and the Neotethys Ocean. *Geološki Anali Balkanskoga Poluostrva 67*, 1–11. DOI 10.2298/GABP0667001R

Sachs, V.N. & Nalnjaeva, T.I. 1967. Recognition of the superfamily Passaloteuthaceae in the suborder Belemnoidea (Cephalopoda, Dibranchia, Decapoda). *Doklady Akademii Nauk SSSR 173(2)*, 438–441. [in Russian]

Sachs, V.N. & Nalnjaeva, T.I. 1975. *Early and Middle Jurassic belemnites of the northern USSR. Megateuthinae and Pseudodicoelitinae*. 192 pp. Nauka, Moscow. [in Russian]

Scotese, C.R. 2004. A Continental Drift Flipbook. *The Journal of Geology 112*, 729–741. DOI 10.1086/424867

Sibiryakova, L.V. 1961. *The problem of oil-and-gas-bearing capacity of Central Asia 5: Middle Jurassic molluscan fauna of the Great Balkhan and its stratigraphic value*. 233 pp. Gostoptekhizdat, Leningrad. [in Russian]

Stevens, G.R. 1965a. The belemnite genera *Dicoelites* Boehm and *Prodicoelites* Stolley. *Palaeontology 7(4)*, 606–620.

Stevens, G.R. 1965b. The Jurassic and Cretaceous belemnites of New Zealand and a review of the Jurassic and Cretaceous belemnites of the Indo-Pacific Region. *New Zealand Geological Survey, Paleontological Bulletin 36*, 1–283.

Stoyanova-Vergilova, M. 1979. Bathonian belemnites from Bulgaria. *Geologica Balcanica 9(4)*, 47–58.

Terquem, O. & Jourdy, E. 1869. Monographie de l'étage Bathonien dans le département de la Moselle. *Mémoires de la Société Géologique de France (2), 9(1)*, 1–175. DOI 10.5962/bhl.title.11874

Weis, R., Mariotti, N. & Di Cencio, A. 2015a. Systematics and evolutionary implications of Early Jurassic belemnites from the Peri-Mediterranean Tethys. *Paläontologische Zeitschrift 89(4)*, 729–747. DOI 10.1007/s12542-015-0265-5

Weis, R., Mariotti, N. & Wendt, J. 2015b. The belemnite genus *Rhabdobelus* from Middle Jurassic Tethyan sediments of central Italy and Sicily, with a systematic review. *Paläontologische Zeitschrift 89(2)*, 133–146. DOI 10.1007/s12542-014-0223-7

Weis, R., Sadki, D. & Mariotti, N. 2017. Aalenian–Bajocian belemnites from the Middle and High Atlas, Morocco: taxonomy, biostratigraphy and palaeobiogeographical affinities. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 284(2)*, 215–240. DOI 10.1127/njgpa/2017/0659

Westermann, G.E.G. 2000. Marine faunal realms of the Mesozoic: review and revision under the new guidelines for biogeographic classification and nomenclature. *Palaeogeography, Palaeoclimatology, Palaeoecology 163*, 49–68. DOI 10.1016/S0031-0182(00)00142-5

Whitehouse, F.W. 1924. Some Jurassic fossils from Western Australia. *Journal of the Royal Society of Western Australia 11*, 1–13. DOI 10.5694/j.1326-5377.1924.tb65604.x

Wu, S. 1982. Characteristics of Early Jurassic–Early Cretaceous belemnoid assemblages from southern Xizang (Tibet). *Contribution to the Geology of the Qinghai-Xizang (Tibet) Plateau 10*, 113–121. [in Chinese]

Zhamoida, A.I. (ed.) 2006. *Stratigraphic Code of Russia. Third edition*. 96 pp. VSEGEI Press, St. Petersburg. [in Russian]

Zittel, K.A. von 1895. *Grundzüge der Palaeontologie (Palaeozoologie)*. 971 pp. Oldenbourg, München-Leipzig.