

New belemnites (Megateuthididae, Cylandroteuthididae) from the Bajocian and Bathonian of the Yuryung-Tumus Peninsula, northern Siberia, Russia and their palaeobiogeographic implications

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Abstract New species of *Paramegateuthis* (Megateuthididae) and *Cylindroteuthis* (Cylandroteuthididae) are described from the Bajocian–Bathonian boundary interval of the Yuryung-Tumus Peninsula, northern Siberia, Russia. Additionally, *Paramegateuthis subishmensis* Stoyanova-Vergilova, 1983, first documented from the Sub-Mediterranean region, is described herein from the Arctic. We propose the presence of a temporary passage between the Boreal and Tethyan seas in the European part of Russia during the Early Bajocian Humphriesianum Chronozone as an explanation of the migration of *P. subishmensis*. New belemnite records from the Yuryung-Tumus section contribute to the palaeontological characteristics of the Arctic domain.

Keywords Belemnites · Bajocian · Bathonian · Northern Siberia · Taxonomy · Palaeobiogeography

Kurzfassung Neue Arten von *Paramegateuthis* (Megateuthididae) und *Cylindroteuthis* (Cylandroteuthididae) aus dem Bajocium–Bathonium-Grenzintervall der Yuryung-Tumus-Halbinsel in Nordsibirien (Russland) werden beschrieben. Desweiteren wird *Paramegateuthis*

subishmensis Stoyanova-Vergilova, 1983, zuvorderst submediterran nachgewiesen, aus der Arktis nachgewiesen. Deshalb schlagen wir, zur Erklärung für die Migration von *P. subishmensis*, die Anwesenheit einer temporären Passage (im europäischen Teil von Russland) zwischen dem Boreal- und dem Tethys- Meer im frühen Bajocium (Humphriesianum Chronozone) vor. Die neuen Belemnitenbelege aus dem Yuryung-Tumus-Profil erbringen einen wesentlichen Beitrag zur Paläontologie der Arktis.

Schlüsselwörter Belemniten · Bajocium · Bathonium · Nordsibirien · Taxonomie · Paläobiogeographie

Introduction

In the Middle Jurassic, a belemnite fauna was essentially reorganised in the Boreal seas. From Siberian data, it follows that abundant and highly diverse Toarcian–Early Aalenian belemnite assemblages were transformed into quantitatively and taxonomically poor faunas in latest Aalenian–Bathonian times, with an especially dramatic diversity drop during the time interval from the beds with *Normannites* to the *Boreiocephalites borealis* Zone (e.g., Sachs and Nalnjaeva 1975; Shurygin et al. 2000; Meledina et al. 2005), i.e., during the mid-Early Bajocian (cf. Meledina 2014; de Lagausie and Dzyuba 2017). In the Bajocian, soon after the extinction of the Hastitidae, the Cylandroteuthididae appeared and began to replace the last representatives of Megateuthididae and Pseudodicoelitidae. This event is considered as the beginning of a new stage in the evolution of Boreal belemnites (Meledina et al. 2005). Up to the first half of the Bathonian, only *Paramegateuthis* (Megateuthididae) and probably *Lenobelus* (Pseudodicoelitidae) co-existed with cylandroteuthidids in the high-

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latitude Boreal seas (Sachs and Nalnjaeva 1975; Doyle and Kelly 1988; Meledina et al. 2005; Mitta et al. 2015; for age interpretation see de Lagausie and Dzyuba 2017). Since the end of the Bathonian, the *Cylindroteuthididae* were the only belemnites, developing in the Arctic basin during the Jurassic (e.g., Sachs and Nalnjaeva 1979; Doyle 1987; Dzyuba 2004; Meledina et al. 2005). In northern Siberia, *Megateuthididae* and *Cylindroteuthididae* co-occur in strata embracing the interval from the *Cranocephalites gracilis* ammonite Zone to the so-called ‘beds without ammonites’ located between the *Arcticoceras ishmae* and *Arcticoceras cranocephaloide* ammonite zones, i.e., in the interval from the uppermost Lower Bajocian to the lowermost Middle Bathonian (de Lagausie and Dzyuba 2017).

The first belemnite described from the Bajocian–Bathonian boundary deposits of northern Siberia is *Cylindroteuthis spathi* Sachs and Nalnjaeva, 1964 (*Cylindroteuthididae*). Subsequently, Sachs and Nalnjaeva (1966, 1975) described several belemnite taxa belonging to *Cylindroteuthididae* and *Megateuthididae* from the Yuryung-Tumus Peninsula, Anabar Bay, Anabar River, Olenyok River, and the Lena River Basin (see Appendix). The problematic *Pseudodicoelites* sp. (*Pseudodicoelitidae*), which may belong to *Lenobelus*, has been reported from Anabar Bay (Sachs and Nalnjaeva 1975).

One of the Boreal key sections for the Lower–Middle Jurassic interval is situated on the Yuryung-Tumus Peninsula, where an Upper Pliensbachian to Middle Bathonian succession is very well exposed (Meledina et al. 1987; de Lagausie and Dzyuba 2017). A recent study of a new collection of belemnites from the peninsula made it possible to (1) define the precise vertical ranges of several key belemnites in the Bajocian–Bathonian boundary interval, (2) establish interregionally correlatable belemnite zones, and, finally, (3) refine the biostratigraphy across the Bajocian–Bathonian boundary in northern Siberia (de Lagausie and Dzyuba 2017).

In this paper, we describe new belemnite species belonging to *Megateuthididae* and *Cylindroteuthididae* from the Bajocian–Bathonian boundary interval of the Yuryung-Tumus Peninsula. Furthermore, we provide a palaeontological description of the Yuryung-Tumus specimens of *Paramegateuthis subishmensis* Stoyanova-Vergilova, 1983, which is the index species of the Siberian *P. subishmensis* belemnite zone traceable to Bulgaria, and we illustrate this species in full. Previously, only a single Arctic (Siberian) specimen, assigned to *P. subishmensis*, has been illustrated in the literature (de Lagausie and Dzyuba 2017). The palaeobiogeographic implications of the new belemnite data are also considered here.

Geological setting

The studied outcrops are located on the Yuryung-Tumus Peninsula between Khatanga Gulf and Nordvik Bay, northern Siberia, Russia (Fig. 1). The uppermost Lower Bajocian to Middle Bathonian strata are generally well-exposed in a number of coastal cliffs along the eastern edge of the peninsula. The belemnite remains were collected from the upper two-thirds of the stratotype section of the Yuryung-Tumus Formation (outcrops 17“Z”, 17“I”, 19“G”, and 20“G” sensu Meledina et al. 1987), which predominantly consists of siltstone and claystone, and contains numerous subglobular calcareous concretions, pyrite nodules, and glendonite aggregates (Figs. 2, 3). The examined interval of the section (members XVII to XXI) is approximately 100.5 m thick. Belemnites (*Paramegateuthis*, *Cylindroteuthis*, and *Pachyteuthis*) are rare throughout the section. Ammonites, bivalves, foraminifers, ostracods, crinoids, and plant fossils have also been reported from the section (e.g., Meledina et al. 1987; Nikitenko et al. 2013).

The sedimentary environment is interpreted as a moderately shallow marine setting, from the middle sublittoral zone to the outer part of the upper sublittoral zone (Nikitenko et al. 2013). According to Smith et al. (1994) and Scotese (2014), this basin was located at the palaeolatitude of $\sim 75^\circ\text{N}$ in the Middle Jurassic.

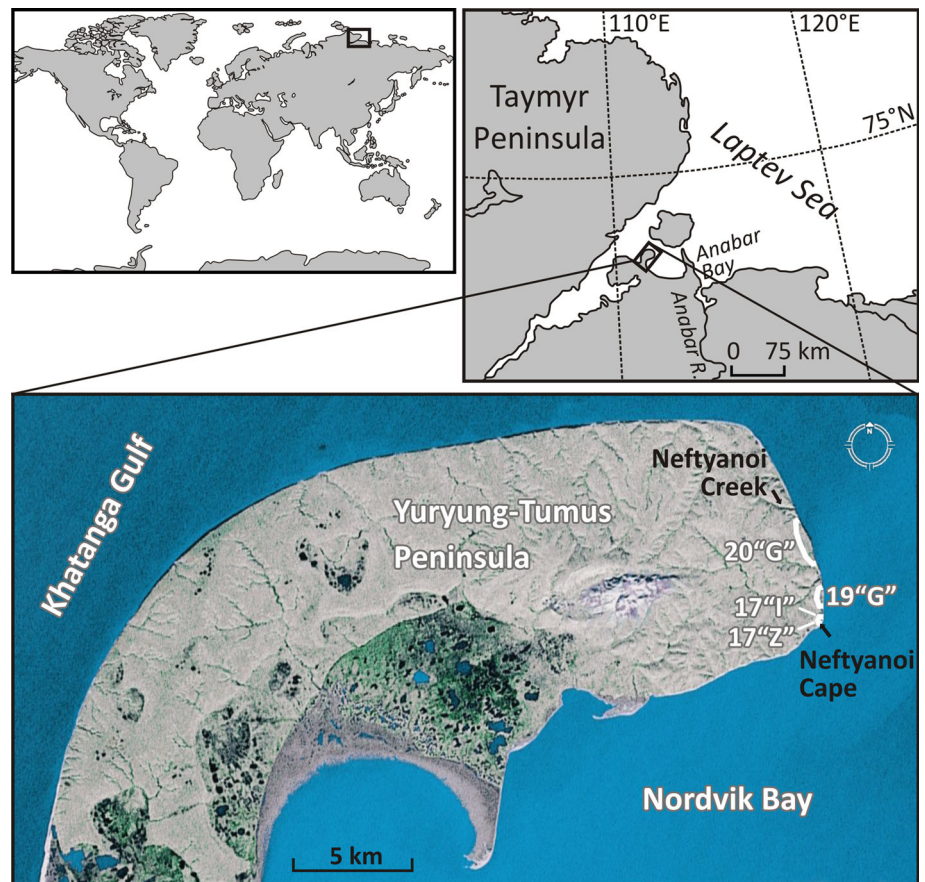
The zonal scales based on ammonites, belemnites, bivalves, foraminifers, and ostracods follow the biostratigraphic scheme proposed by Nikitenko et al. (2013) and recently revised by us in the belemnite part and in the age interpretation of all faunal successions (de Lagausie and Dzyuba 2017).

Materials and methods

The belemnite specimens, CSGM2070/9–20, are stored in the Central Siberian Geological Museum (CSGM), Novosibirsk, Russia. All these specimens were collected in 2009 from the Yuryung-Tumus section. This collection continues the earlier illustrated collection, CSGM2070/1–8 (de Lagausie and Dzyuba 2017), which contained biostratigraphically important belemnites (CSGM2070/1–7) and ammonite (CSGM2070/8) from the Bajocian–Bathonian transition beds of the Yuryung-Tumus Peninsula. Belemnite collections CSGM83, 84, 87–89, 91 of Sachs and Nalnjaeva (Sachs and Nalnjaeva 1964, 1966, 1975; Efremova et al. 1983; Nalnjaeva 1986, 1989; Meledina et al. 1998; Repin et al. 2006; Nalnjaeva et al. 2011) were also studied for comparative analysis of new belemnite material.

Belemnite terminology mainly follows that of Doyle and Kelly (1988). The measurements (in mm) were as follows: *L*, total preserved length; *l*, length from apex to tip of alveolus;

Fig. 1 Location of the studied outcrops on the Yuryung-Tumus Peninsula, northern Siberia



D_v , dorso-ventral diameter at the tip of the alveolus; D_l , lateral diameter at the tip of the alveolus. Additionally, following Sachs and Nalnjaeva (1964), we calculated the degree of rostrum elongation ($l/D_v, \times 100\%$) and compression ($D_l/D_v, \times 100\%$). Approximate size (length) ranges are given by the terms small (<60 mm), medium (60–100 mm) and large (>100 mm). Rostra were coated with magnesium oxide prior to photography.

Systematic palaeontology

We use the classification system adopted by Dzyuba (2011) for Cylindroteuthididae and Dzyuba et al. (2015) for Megateuthididae. The main characters, distinguishing these belemnite families, include the number and position of rostrum grooves and the shape of juvenile rostrum. The Early–Middle Jurassic family Megateuthididae possesses more or less developed dorsolateral apical grooves, sometimes in combination with a ventral apical groove. The Middle Jurassic to Early Cretaceous family Cylindroteuthididae is characterised by a ventral apical groove. Juveniles of Megateuthididae are generally conical to cylindrical, whereas juveniles of Cylindroteuthididae are cylindrical to slightly subhastate (spindle-like).

Subclass **Coleoidea** Bather, 1888

Order **Belemnitida** von Zittel, 1895

Suborder **Belemnitina** von Zittel, 1895

Family **Megateuthididae** Sachs and Nalnjaeva, 1967

(= Mesoteuthidae Gustomesov, 1977; = Acrocoelitidae Riegraf, 1980, nom. transl. Riegraf 1995)

Genus **Paramegateuthis** Gustomesov, 1960

1958 *Paramegateuthis* Gustomesov: p. 158, nom. nud.

Type species. *Megateuthis (Paramegateuthis) ishmensis* Gustomesov, 1960.

Other species included. *P. manifesta* Nalnjaeva in Sachs and Nalnjaeva, 1975, *P. nescia* Nalnjaeva in Sachs and Nalnjaeva, 1975, *P. ovata* de Lagausie and Dzyuba sp. nov., *P. schurygini* Dzyuba sp. nov., *P. subishmensis* Stoyanova-Vergilova, 1983, and *P. zimevizensis* Stoyanova-Vergilova, 1983 (composed the group with elongated rostrum, along with the type species); *P. bella* (Barskov in Mitta et al. 2004), *P. gustomesovi* Stoyanova-Vergilova, 1983, *P. nalnyaevae* Doyle in Doyle and Kelly, 1988, *P. parabajosicus* Nalnjaeva in Sachs and Nalnjaeva, 1975, *P. parabella* (Barskov in Mitta et al., 2004), *P. pressa* Nalnjaeva in Sachs and Nalnjaeva, 1975, *P. timanensis* (Gustomesov, 1960), and probably *P. bajosicus*

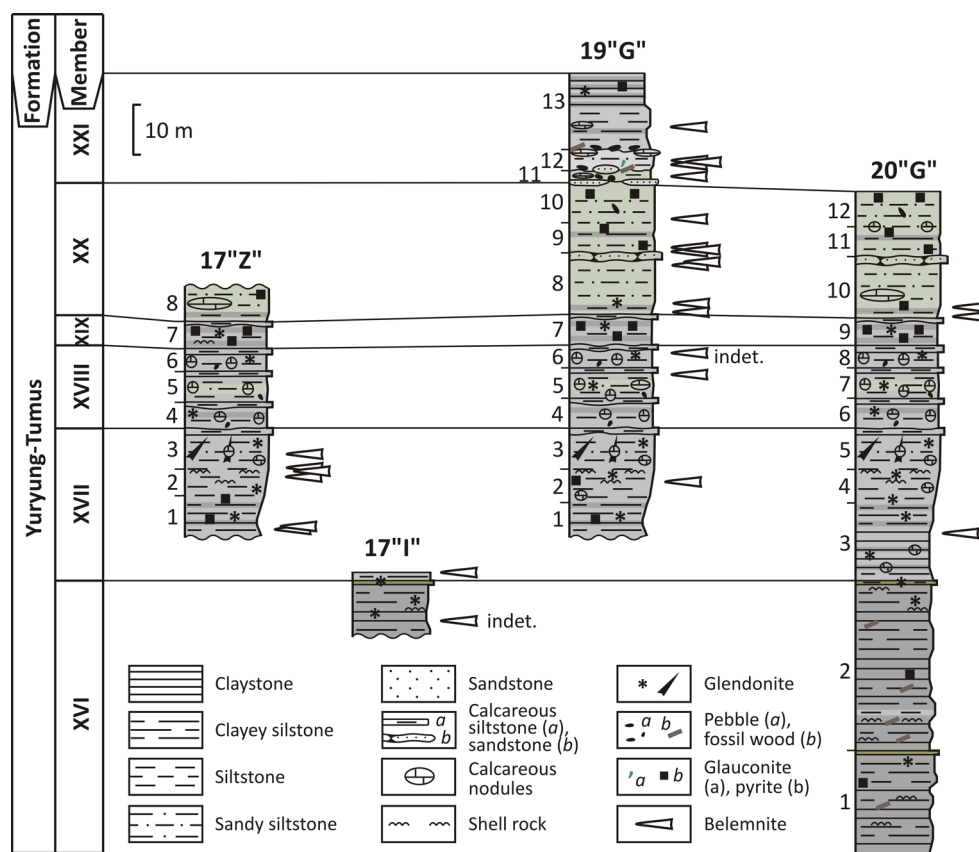


Fig. 2 Correlation of the studied outcrops at the Yuryung-Tumus Peninsula, modified after Meledina et al. (1987), and levels from which the belemnites were collected

(Ivanova, 1959) (composed the group with relatively short rostrum).

Remarks. The genus is represented by the compressed, conical to cylindrical, commonly small to medium sized species of Megateuthidae, with elongated dorsolateral apical grooves, a goniolineate apical line, and a nearly central alveolus with an acute alveolar angle. *Paramegateuthis* most closely resembles *Megateuthis* Bayle, 1878, but the latter differs in its larger and stouter rostrum with short dorsolateral apical grooves. Moreover, some *Megateuthis* develop an epirostrum.

Stratigraphic and geographic distribution. Middle Aalenian (Bradfordensis Chronozone) to Middle Bathonian of northern and eastern Europe, northern and northeastern Asia, and (?) northern North America.

Paramegateuthis ovata de Lagausie and Dzyuba sp. nov. Figure 4a, b

1968 *Mesoteuthis inornata* (Phillips)—Moskalenko: p. 30, pl. 5, fig. 2.

1968 *Mesoteuthis* aff. *rhenana* (Opper)—Moskalenko: p. 31, pl. 6, figs. 1–6.

1988 *Paramegateuthis nescia* Nal'nyaeva [Nalnjaeva]—Doyle and Kelly: p. 24, pl. 4, figs. 1–7.

Etymology. From *ovata* (Latin) meaning oval, egg-shaped, in reference to a shape of the rostrum cross-section.

Holotype. CSGM2070/9, a subcomplete rostrum (Fig. 4a).

Paratype. CSGM2070/10, a rostrum lacking the apex (Fig. 4b).

Locality and Horizon. Outcrop 17“Z”, bed 2, 150 cm below the top (CSGM2070/10), and near Outcrop 20“A”, the analogue of the base of bed 3 in Outcrop 17“Z” (the holotype), Yuryung-Tumus Peninsula, northern Siberia; *Boreiocephalites borealis* Zone, member XVII, Yuryung-Tumus Formation, Lower Bajocian, Middle Jurassic.

Diagnosis. Large-sized, moderately elongated, conical to cylindrical rostrum. Cross-section strongly compressed, elliptical. Dorsolateral apical grooves elongated and shallow, but may be weakly incised. Alveolus occupying approximately one-third of the rostrum.

Description. Medium to large sized, moderately elongated rostrum (Table 1). The outline is symmetrical and conical to cylindrical. The profile is nearly symmetrical and

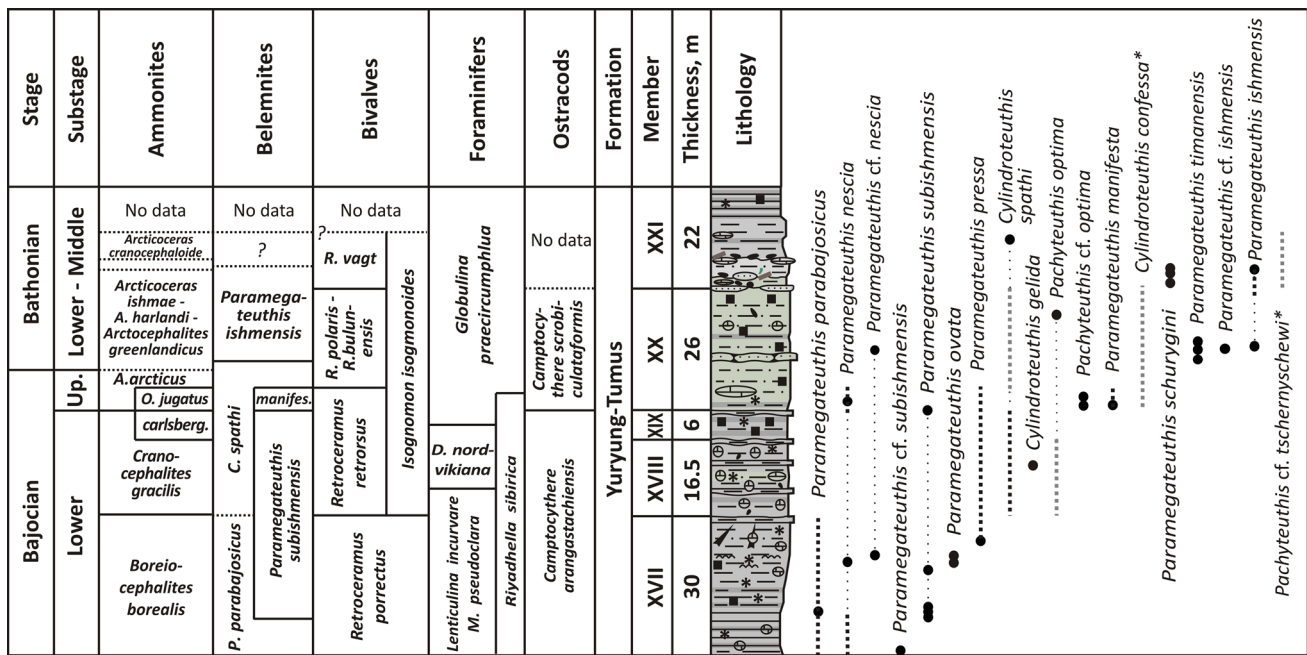


Fig. 3 Biostratigraphy and distribution of belemnites throughout the Bajocian–Bathonian boundary deposits at the eastern edge of the Yuryung-Tumus Peninsula modified after de Lagausie and Dzyuba (2017), with the addition of records of new belemnite species (for legend see Fig. 2). The approximate position of previous records

(Sachs and Nalnjaeva 1975; Nalnjaeva 1986; Meledina et al. 1987) is shown by the *dotted line*: not illustrated records are displayed in *grey colour*, and records that are not found in situ are indicated with *asterisks*

conical to cylindrical. The lateral aspects are strongly flattened throughout the alveolar and stem regions. The apex is acute in outline and is slightly more obtuse in profile, and it is centrally located to slightly dorsally displaced. The cross-section is very compressed and elliptical, especially in the alveolar and stem regions. Dorsolateral apical grooves are developed as elongated and shallow to weakly incised depressions, and the apex may bear striae. Lateral lines are poorly defined. The alveolus is centrally located, slightly compressed and elliptical in the cross-section and occupies approximately one third of the rostrum. The alveolar angle is 22°. The earliest juvenile stages are elongated conical (Fig. 4a4).

Comparison. The species is very similar to *P. nescia* Nalnjaeva in size and in having the elongated and commonly shallow dorsolateral apical grooves, but is easily distinguished due to its well-developed lateral flattenings and strongly compressed cross-section (72–76 vs. 83–95% in *P. nescia*, according to Sachs and Nalnjaeva 1975). Moreover, unlike *P. nescia*, the new species is not slender, and its apex is more obtuse in profile. In the degree of rostrum compression, *P. ovata* sp. nov. is close to the two very compressed but extremely short species of *Paramegateuthis*, namely, *P. parabajosicus* Nalnjaeva and *P. pressa* Nalnjaeva. The new species differs from *P. zimevizensis* Stoyanova-Vergilova and *P. subishmensis* Stoyanova-Vergilova by its larger size, its more elongated

and less conical shape, and its more shallow dorsolateral apical grooves.

Remarks. The large-sized *Mesoteuthis inornata* and medium-sized *Mesoteuthis* aff. *rhenana*, both described by Moskalenko (1968) from the basal beds of the Oshurkova Formation on the Urkan River (upper reaches of the Amur River, the Russian Far East), share similar characteristics with *P. ovata* sp. nov. The compression rate is equivalent for the Siberian specimens and “*M. aff. rhenana*”, but the latter specimens are slightly more elongated, in all probability due to their lower maturity stage. According to Dzyuba and Nalnjaeva (2011), the basal beds of the Oshurkova Formation most likely correspond to the uppermost Lower Bajocian. The mid-Toarcian–earliest Aalenian *Megateuthis rhenana* (Oppel), including *Belemnites inornatus* Phillips as a synonym sensu (Doyle 1992), is larger in size and less compressed, and generally has shorter dorsolateral apical grooves.

The non-slender and strongly compressed *P. nescia*, described by Doyle and Kelly (1988) from the upper part of the Passet Member (Middle Jurassic, below the first records of *Arcticoceras*) of Kongsøya and the lower part of the Dunnérffjellet Member (Lower Bathonian, beds with *Arcticoceras* cf. *harlandi* Rawson) of Svenskøya (Kong Karls Land, Svalbard), is assigned herein to the new species. Both the Svalbard material and the Russian Far East material illustrate the uniform variation of a rostrum shape, which ranges from conical to almost cylindrical.

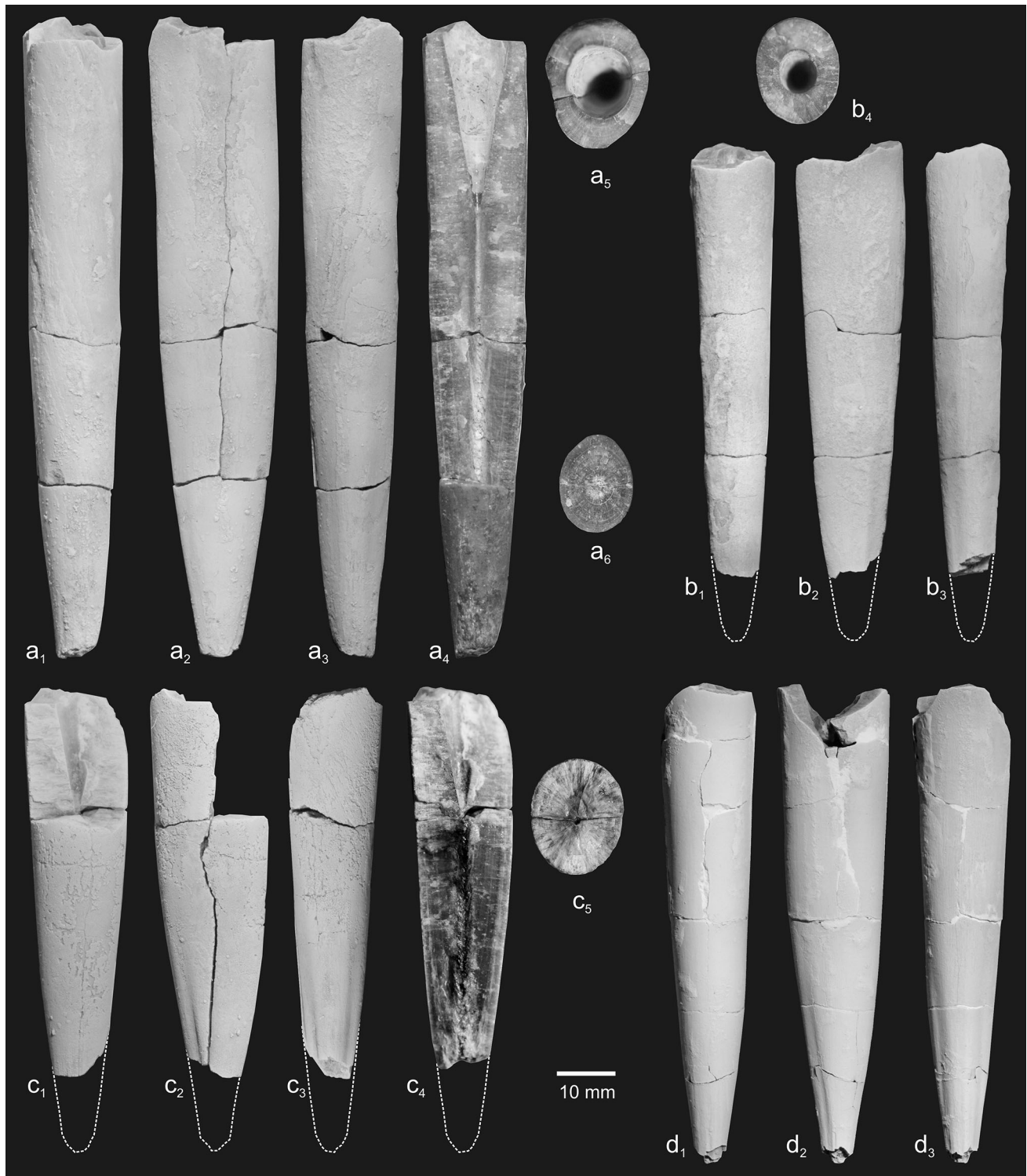


Fig. 4 Belemnites from the Lower Bajocian of the Yuryung-Tumus Peninsula (**a–c**) and Anabar Bay (**d**), northern Siberia. **a, b** *Paramegateuthis ovata* de Lagausie and Dzyuba sp. nov. **a** Specimen CSGM2070/9, the holotype: ventral (a_1), right lateral (a_2), dorsal (a_3) views, longitudinal section in view a_1 (a_4), and cross-sections near the anterior end (a_5) and in the apical region (a_6). **b** Specimen CSGM2070/10: ventral (b_1), left lateral (b_2), dorsal (b_3) views, and cross-section near the anterior end (b_4). **c** *Paramegateuthis* cf.

subishmensis Stoyanova-Vergilova, 1983, specimen CSGM2070/11: ventral (c_1), right lateral (c_2), dorsal (c_3) views, longitudinal section in view c_1 (c_4) and cross-section near the tip of the alveolus (c_5). **d** *Paramegateuthis subishmensis* Stoyanova-Vergilova, 1983, specimen CSGM87-121, originally assigned by Sachs and Nalnjaeva (1975) to *Paramegateuthis ishmensis* (Gustomesov): ventral (d_1), right lateral (d_2) and dorsal (d_3) views

Table 1 Measurements for *Paramegateuthis ovata* de Lagausie and Dzyuba sp. nov.

Specimen no.	<i>L</i> , mm	<i>l</i> , mm	<i>D_v</i> , mm	<i>D_l</i> , mm	<i>l/D_v</i> , ×100%	<i>D_l/D_v</i> , ×100%
CSGM2070/9	111.0	76.5	21.8	16.6	351	76
CSGM2070/10	74.5	–	18.0	12.9	–	72

Stratigraphic and geographic distribution. Lower Bajocian (*Boreiocephalites borealis* Zone) of northern Siberia (Yuryung-Tumus Peninsula), and the Russian Far East (Amur River Basin); Middle Jurassic (pre-Middle Bathonian strata, the general stratigraphic position in the strata is not specified) of Svalbard (Kong Karls Land).

Paramegateuthis schurygini Dzyuba sp. nov.

Figure 5f–h

2017 *Cylindroteuthis* cf. *confessa* Nalnjaeva—de Lagausie and Dzyuba: pl. 1, figs. 9–11.

Etymology. In honour of Prof. Boris N. Shurygin (Борис Н. Шурыгин), Russian geologist and palaeontologist, and an expert on the Arctic Jurassic.

Holotype. CSGM2070/18, a subcomplete rostrum (Fig. 5f).

Paratypes. CSGM2070/19, a subcomplete rostrum (Fig. 5g); CSGM2070/2, an incomplete rostrum partially showing the alveolar and stem regions (de Lagausie and Dzyuba 2017, pl. 1, Figs. 9–11; Fig. 5h).

Locality and Horizon. Outcrop 19“G”, bed 11, 100 cm above the bottom (the holotype), bed 12, 150 cm above the bottom (CSGM2070/19), and 230 cm below the top (CSGM2070/2), Yuryung-Tumus Peninsula, northern Siberia; uppermost *Paramegateuthis ishmensis* Zone, member XXI, Yuryung-Tumus Formation, Lower Bathonian to Middle Bathonian transition, Middle Jurassic.

Diagnosis. Large-sized, elongated, slender conical to cylindrical rostrum. Cross-section compressed, elliptical to weakly pyriform with a broader dorsum than venter. Long tiny dorsolateral apical grooves. Apex striated. Alveolus occupying one fourth of the rostrum.

Description. Large-sized, elongated, slender rostrum (Table 2). The outline is symmetrical and conical to cylindrical. The profile is asymmetrical and cylindrical, with a more inflated venter than dorsum. The apex is very acute and nearly centrally located. The cross-section is compressed, elliptical to weakly pyriform (dorsum is broader than venter) in the alveolar region, and elliptical in the stem and apical regions. The dorsolateral apical grooves are elongated but tiny, and apical striae may be well-developed. Lateral lines are present as a broad almost central depression, visible mainly in an anterior half of the rostrum. The alveolus is centrally located to slightly dorsally displaced and subcircular in the cross-section, and it occupies one fourth of the rostrum. The alveolar angle is

25°–27°. The earliest juvenile stages are elongated cylindrical (Fig. 5h).

Comparison. The species most closely resembles *P. nescia* Nalnjaeva but is distinguished by its more cylindrical and elongated rostrum, the apex of which may bear numerous striae. This new species is the most elongated of *Paramegateuthis* (Fig. 6).

Remarks. A rostrum lacking the apical region can be easily confused with *Cylindroteuthis confessa* Nalnjaeva (Cylandroteuthidae). In such a case, ontogeny investigations are required to verify the taxon name. One incomplete rostrum, reported by us from the Yuryung-Tumus section as *C. cf. confessa* (de Lagausie and Dzyuba 2017), appears to have megateuthid ontogeny (Fig. 5h).

Paramegateuthis subishmensis Stoyanova-Vergilova, 1983

Figures 4d, 5a–e

pars 1975 *Paramegateuthis manifesta* Nalnjaeva—Sachs and Nalnjaeva: p. 62, pl. 9, figs. 6, 7.

pars 1975 *Paramegateuthis ishmensis* Gustomesov—Sachs and Nalnjaeva: p. 64, text-fig. 24.

1983 *Paramegateuthis subishmensis*—Stoyanova-Vergilova: p. 254, pl. 1, fig. 4; pl. 2, figs. 1, 2.

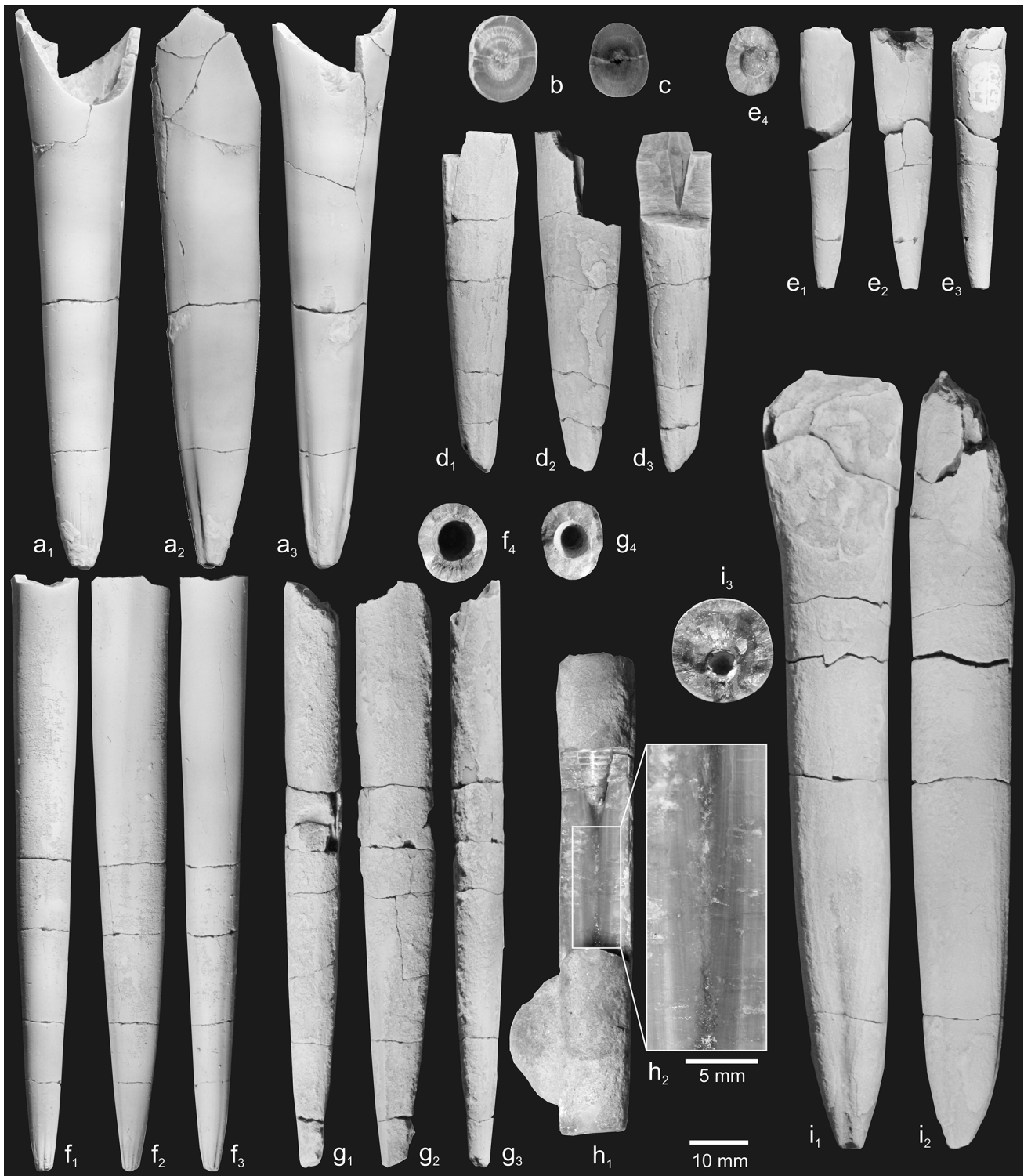
1990 *Paramegateuthis subishmensis* Stoyanova-Vergilova—Stoyanova-Vergilova: pl. 2, fig. 1.

1993 *Paramegateuthis subishmensis* Stoyanova-Vergilova—Stoyanova-Vergilova: p. 69, pl. 34, figs. 1–3.

2017 *Paramegateuthis subishmensis* Stoyanova-Vergilova—de Lagausie and Dzyuba: pl. 1, figs. 15–17.

Holotype. HIMG J₂ 1274, Sofia, Bulgaria; the core-drilling R₅ near the village of Dolni Lukovit, depth 2986.5 m, Bulgaria; *Stephanoceras humphriesianum* Zone, Lower Bajocian, Middle Jurassic. Designated by Stoyanova-Vergilova (1983, pl. 2, fig. 1).

Studied material. Two well-preserved rostra (CSGM2070/4, 12), three partially complete rostra (CSGM2070/13, 15, 16), and two incomplete rostra partially showing the alveolar and stem regions (CSGM2070/14, 17); all from the member XVII, with the exception of CSGM2070/4, found at the base of member XX, all from the Yuryung-Tumus Formation. CSGM2070/12: Outcrop 20“G”, bed 3; CSGM2070/13, 16, 17: Outcrop 17“Z”, bed 1; CSGM2070/14: Outcrop 19“G”, bed 2; CSGM2070/15: Outcrop 17“Z”, bed 1, 150 cm above the bottom; CSGM2070/4: Outcrop 20“G”, bed 10, near the bottom.



Description. Medium-sized, moderately elongated rostrum (Table 3). The outline is symmetrical and conical. The profile is symmetrical to slightly asymmetrical due to the slightly inflated venter, and conical. The apex is acute to very acute and attenuated. The cross-section is subcircular in the anterior part of the alveolar region but is compressed

and elliptical to weakly pyriform near the tip of the alveolus, in the stem and apical regions. Dorsolateral apical grooves may be strongly incised, especially in the apical region; anteriorly, they can be transformed into depressions, visible up to the alveolar region. In general, lateral lines are poorly defined. Striae are commonly not observed

Fig. 5 Belemnites from the Lower Bajocian (a–e, i) and Lower–Middle Bathonian (f–h) of the Yuryung-Tumus Peninsula, northern Siberia. **a–e** *Paramegateuthis subishmensis* Stoyanova-Vergilova, 1983. **a** Specimen CSGM2070/12: ventral (a_1), right lateral (a_2) and dorsal (a_3) views. **b, c** Specimens CSGM2070/13, 14: cross section at the tip of the alveolus. **d** Specimen CSGM2070/15: ventral (d_1), left lateral (d_2) and dorsal (d_3) views. **e** Specimen CSGM2070/16: ventral (e_1), left lateral (e_2), dorsal (e_3) views, and cross-section near the anterior end (e_4). **f–h** *Paramegateuthis schurygini* Dzyuba sp. nov. **f** Specimen CSGM2070/18, the holotype: ventral (f_1), right lateral (f_2), dorsal (f_3) views, and cross-section near the anterior end (f_4). **g** Specimen CSGM2070/19: ventral (g_1), right lateral (g_2), dorsal (g_3) views, and cross-section near the anterior end (g_4). **h** Specimen CSGM2070/2: ventral view (h_1) and fragment of longitudinal section (h_2). **i** *Cylindroteuthis gelida* de Lagausie sp. nov., specimen CSGM2070/20, the holotype: ventral (i_1), right lateral (i_2) views, and cross-section in the alveolar region (i_3)

at the apex and the ventral apical groove is absent, but one specimen (CSGM2070/12) bears clearly defined three ventral striae (Fig. 5a₁). The alveolus is centrally located, subcircular to compressed elliptical in cross-section and occupies approximately two fifths of the rostrum. The alveolar angle is 23°–25°.

Comparison. The species somewhat resembles *P. nescia* Nalnjaeva but is distinguished by a less elongated and more conical rostrum, with a less asymmetrical profile and possessing more developed dorsolateral apical grooves. *P. subishmensis* is close to *P. manifesta* Nalnjaeva in the acutely conical shape of its rostrum. However, it differs from the latter by its slightly less elongated form and by the dorsolateral apical grooves, which are not closely spaced and commonly shorter. *P. subishmensis* is similar to *P. zimevizensis* Stoyanova-Vergilova in general shape and in having the incised dorsolateral apical grooves, but is more elongated and possesses a more attenuated apex. *P. subishmensis* may be confused with *P. ishmensis* (Gustomesov), but the former species is greater in size, more conical, and its apex tends to be attenuated.

Remarks. A single specimen, CSGM2070/4, recorded from the base of the Upper Bajocian at the Yuryung-Tumus section, was illustrated by us earlier (de Lagausie and Dzyuba 2017, pl. 1, figs. 15–17). Here, we illustrate several specimens from the Early Bajocian *Boreiocephalites borealis* Zone.

The representatives of *P. manifesta* recorded by Sachs and Nalnjaeva (1975) from the *Boreiocephalites* “*pseudoborealis*” (= *borealis*) Zone of Siberia, in our opinion, can be

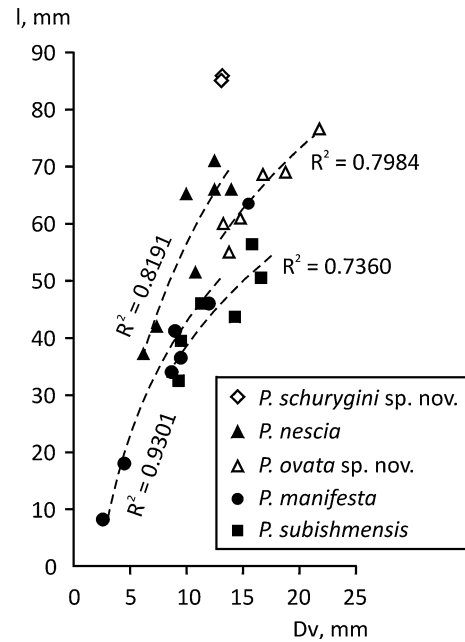


Fig. 6 Scatter plot of length from rostrum apex to tip of alveolus (l) to dorso-ventral diameter at the tip of the alveolus (D_v) for some species of *Paramegateuthis*. Data from literary sources (Moskalenko 1968; Sachs and Nalnjaeva 1975; Doyle and Kelly 1988) are also used. The logarithmic regression curves are shown by the dotted lines. R^2 coefficient of determination

classified as *P. subishmensis*. At least two illustrated specimens, CSGM87-150 and 151, collected on the Yuryung-Tumus Peninsula (Sachs and Nalnjaeva 1975, pl. 9, figs. 6, 7), are closer to juveniles of the considered species due to the degree of elongation of their rostrum and the development characteristics of the dorsolateral apical grooves, which are less closely spaced than those of true *P. manifesta* Nalnjaeva. Moreover, *P. ishmensis*, described by Sachs and Nalnjaeva (1975), may partly be assigned to *P. subishmensis*; for example, the specimen CSGM87-121 (see Fig. 4d of present paper) is characterised by conical shape with an attenuated apex. According to the museum label, this specimen is from the “Lower Bathonian” (=Lower Bajocian; cf. de Lagausie and Dzyuba 2017) of Anabar Bay.

Stratigraphic and geographic distribution. Lower Bajocian (*Stephanoceras humphriesianum* Zone) of Bulgaria. In northern Siberia, the uppermost Lower Bajocian up to the Lower–Upper Bajocian boundary (*Boreiocephalites borealis* Zone to the base of the *Arctocephalites arcticus* Zone) of the Yuryung-Tumus Peninsula and Anabar Bay.

Table 2 Measurements for *Paramegateuthis schurygini* Dzyuba sp. nov.

Specimen no.	L , mm	l , mm	D_v , mm	D_l , mm	$l/D_v, \times 100\%$	$D_l/D_v, \times 100\%$
CSGM2070/18	102.5	85.8	13.2	11.4	650	86
CSGM2070/19	100.2	85.0	13.1	10.7	649	82
CSGM2070/2	82	–	15.7	12.6	–	80

Table 3 Measurements for *Paramegateuthis subishmensis* Stoyanova-Vergilova

Specimen no.	<i>L</i> , mm	<i>l</i> , mm	<i>D_v</i> , mm	<i>D_l</i> , mm	<i>l/D_v</i> , ×100%	<i>D_l/D_v</i> , ×100%
CSGM2070/4	80.1	~46	11.3	10.1	~407	89
CSGM2070/12	96.1	50.5	16.6	13.8	304	83
CSGM2070/13	67.0	–	15.1	11.9	–	79
CSGM2070/14	–	–	12.8	10.4	–	81
CSGM2070/15	58.1	>43.7	14.3	12.0	>306	84
CSGM2070/16	44.5	–	9.9	8.7	–	88
CSGM2070/17	–	–	11.4	9.8	–	86

Paramegateuthis cf. *subishmensis* Stoyanova-Vergilova, 1983

Figure 4c

Studied material. CSGM2070/11, a rostrum partially lacking the alveolar and apical regions from Outcrop 17“I”, at the top of the outcrop; member XVII, Yuryung-Tumus Formation.

Description. Medium-sized, moderately elongated rostrum. The outline is symmetrical and conical. The profile is nearly symmetrical and cylindrical. The apical region shows a tendency to be attenuated. The cross-section is compressed and elliptical (Table 4). The dorsolateral apical grooves are well-developed and strongly incised in the apical region. Lateral lines are not defined. The tip of the alveolus is centrally located.

Remarks. The specimen is closest to *P. subishmensis* Stoyanova-Vergilova in general shape, development characteristics of the dorsolateral apical grooves, and in tendency of the apical region to be attenuated. However, the incomplete preservation of the rostrum does not allow us to assign this specimen to *P. subishmensis* with certainty.

Stratigraphic and geographic distribution. Lower Bajocian (*Boreiocephalites borealis* Zone) of northern Siberia (Yuryung-Tumus Peninsula).

Family **Cylindroteuthididae** Stolley, 1919

(= Pachyteuthidae Stolley, 1919)

Subfamily **Cylindroteuthidinae** Stolley, 1919

Genus **Cylindroteuthis** Bayle, 1878

Type species. *Belemnites puzosianus* d’Orbigny, 1842.

Other species included. *C. confessa* Nalnjaeva in Sachs and Nalnjaeva 1975, *C. gelida* de Lagausie sp. nov., *C. spathi*

Sachs and Nalnjaeva 1964, and numerous Callovian to Early Valanginian species.

Remarks. The genus contains the compressed, elongated cylindrical to cylindrical, large-sized species of Cylindroteuthidae, with a generally inflated venter, a more or less developed ventral apical groove, a weakly cyrtolineate apical line, and a slightly excentric alveolus with an acute to very acute alveolar angle. *Cylindroteuthis* is easily distinguished from the related genus *Arctoteuthis*, Sachs and Nalnjaeva 1964 (Cylindroteuthidinae) which possesses a more flattened venter and uncompressed cross-section. *Cylindroteuthis* resembles *Pachyteuthis* Bayle, 1878 (Pachyteuthidinae) in its similar compression and inflated venter, but the latter is robust and has a more excentric alveolus and a strongly cyrtolineate apical line.

Stratigraphic and geographic distribution. Uppermost Lower Bajocian to Lower Valanginian of northern, western and eastern Europe, northern and northeastern Asia, and North America.

Cylindroteuthis gelida de Lagausie sp. nov.

Figure 5i

Etymology. From *gelida* (Latin) meaning frozen, in reference to a cold climate in the Arctic.

Holotype. CSGM2070/20, a well-preserved rostrum (Fig. 5i).

Locality and Horizon. Outcrop 19“G”, bed 5, near the top, just under the calcareous bed, Yuryung-Tumus Peninsula, northern Siberia; *Cranocephalites gracilis* Zone, member XVIII, Yuryung-Tumus Formation, Lower Bajocian, Middle Jurassic.

Diagnosis. Large-sized, moderately elongated, cylindrical to subcylindrical rostrum. Cross-section rounded

Table 4 Measurements for *Paramegateuthis* cf. *subishmensis* Stoyanova-Vergilova

Specimen no.	<i>L</i> , mm	<i>l</i> , mm	<i>D_v</i> , mm	<i>D_l</i> , mm	<i>l/D_v</i> , ×100%	<i>D_l/D_v</i> , ×100%
CSGM2070/11	66.0	–	19.8	15.8	–	80

subquadrate. Ventral apical groove short but well-developed. Alveolus occupying two fifths of the rostrum.

Description. Large-sized, moderately elongated rostrum (Table 5). The outline is symmetrical and cylindrical to subcylindrical. The profile is symmetrical and cylindrical to subcylindrical. The apex is centrally located, moderately acute and devoid of striae. The cross-section is rounded subquadrate. The ventral apical groove is well-developed, deeply incised in the apical region, and then expanded and flattened in the posterior part of the stem region. Lateral lines are poorly defined. The alveolus is ventrally displaced, circular in cross-section and occupies two fifths of the rostrum.

Comparison. The morphologically closest species is *C. spathi* Sachs and Nalnjaeva, but the new species differs by its larger and notably less elongated rostrum (Fig. 7). Additionally, the alveolus of the new species is more displaced towards the venter.

Remarks. Both *C. gelida* sp. nov. and *C. spathi* are the earliest known species among *Cylindroteuthis*, which is believed to have appeared soon after the appearance of the first *Pachyteuthis* (e.g., Dzyuba and Nalnjaeva 2011). It should be noted that in the rostrum morphology the genus *Pachyteuthis* shows more similarity with the new species than with *C. spathi*. *C. gelida* sp. nov., representing moderately elongated species of the genus *Cylindroteuthis*, like *Pachyteuthis* is characterised by a rather excentric alveolus.

An incomplete rostrum, reported as *Cylindroteuthis* (*Cylindroteuthis*) sp. (Doyle and Kelly 1988, pl. 4, figs. 15–17) from Kong Karls Land (Svalbard), is closest to *C. gelida* sp. nov., but its species affiliation requires further investigation.

Palaeobiogeographic implications

Boreal and Tethyan belemnite realms can be recognised in the Bajocian and Bathonian (e.g., Sachs and Nalnjaeva 1975; Doyle 1987; Challinor et al. 1992). According to Challinor et al. (1992), the Arctic and Boreal-Pacific provinces are defined within the Boreal Realm for this time interval, whereas the Tethyan Realm can be subdivided into the Mediterranean, Himalayan and South Pacific provinces. New records from the Yuryung-Tumus section contribute to the belemnite palaeontological characteristics of the Arctic province (Fig. 8). In the mid-Middle Jurassic, Megateuthididae was represented in this province by the only genus

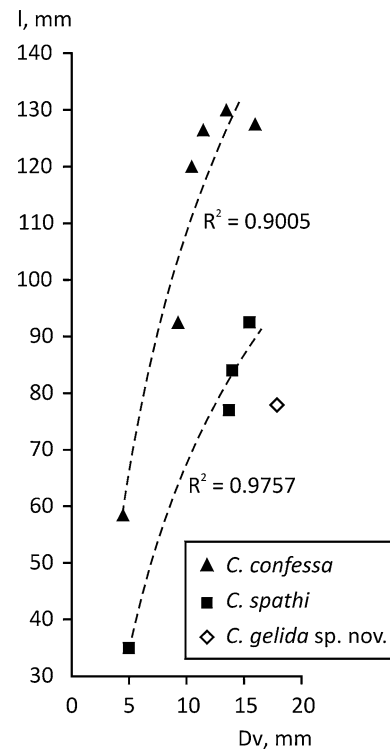


Fig. 7 Scatter plot of length from rostrum apex to tip of alveolus (l) to dorso-ventral diameter at the tip of the alveolus (D_v) for some species of *Cylindroteuthis*. Data from literary sources (Sachs and Nalnjaeva 1964, 1975) are also used. The logarithmic regression curves are shown by the dotted lines. R^2 coefficient of determination

Paramegateuthis, whereas *Cylindroteuthididae* was represented by *Cylindroteuthis*, *Microbelus* and *Pachyteuthis*.

The earliest records of the genus *Paramegateuthis* are known from the Aalenian–Bajocian transition interval of Bulgaria (Stoyanova-Vergilova 1983, 1990), Dagestan in Northern Caucasus (Ippolitov et al. 2015), and tentatively also Svalbard (Doyle and Kelly 1988). The first appearance of *Paramegateuthis* in Siberia was recorded from the Bajocian beds lacking ammonites and referred to as “beds without ammonites” (Sachs and Nalnjaeva 1975) or *Retroceramus clinatus* bivalve Zone (Meledina et al. 1987). These beds are now assigned to the *Chondroceras marshalli* ammonite beds (cf. Shurygin et al. 2011) corresponding to the basal part of the Humphriesianum Chronozone (cf. Meledina 2014). However, Nalnjaeva (1986) also supposed the presence of *Paramegateuthis* in the preceding *Retroceramus lucifer* bivalve Zone, which embraces the upper part of the *Arkelloceras tozeri* ammonite Zone (cf. Shurygin et al. 2011); the locality remains unknown.

Table 5 Measurements for *Cylindroteuthis gelida* de Lagausie sp. nov.

Specimen no.	L , mm	l , mm	D_v , mm	D_1 , mm	l/D_v , ×100%	D_1/D_v , ×100%
CSGM2070/20	131.4	77.9	17.9	17.2	435	96

Age		East Greenland	Svalbard	Franz Josef Land	Pechora Basin	Northern Siberia
Bajocian	Early	—	—	—	—	—
	Late	—	—	—	—	—
Bathonian	Early	—	—	—	—	—
	Middle	—	—	—	—	—
not considered herein						

Fig. 8 Stratigraphic ranges of belemnites at the Bajocian–Bathonian boundary in the Arctic province compiled from numerous sources (see Appendix). Age interpretation is after de Lagausie and Dzyuba (2017), with application of information on East Greenland (Callomon et al. 2015), Svalbard (Dallmann 1999), Franz Josef Land (Dibner

1998), Pechora Basin (Mitta et al. 2015), and northern Siberia (Shurygin et al. 2000; Nikitenko et al. 2013). The *solid line* refers to the indubitable records; the *dotted line* shows records that require verification with respect to the age interpretation (*black colour*) or taxonomic affinity (*grey colour*)

During the latest Early Bajocian to Middle Bathonian, *Paramegateuthis* became a typical faunal component of the Arctic province, but there are some records outside the Arctic, namely, *Paramegateuthis subishmensis* Stoyanova-Vergilova in Bulgaria (e.g., Stoyanova-Vergilova 1983), “*Paramegateuthis*” *bajosicus* (Ivanova), *Paramegateuthis bella* (Barskov) and *Paramegateuthis parabella* (Barskov) near Saratov in Central Russia (Ivanova 1959; Dzyuba in Mitta et al. 2014b), and *Paramegateuthis “timanensis”* (Gustomesov) in the south of the Russian Far East (Nalnjaeva in Challinor et al. 1992). It is noteworthy that *Megateuthis* (= *Mesoteuthis*, fide Doyle 1992), from the predominant genus among Megateuthididae during the early Middle Jurassic, was present essentially in the Mediterranean province of the Tethyan Realm (Doyle 1987; Doyle and Bennett 1995) but is also known from the Russian Far East (Kinasov in Efimova et al. 1968; Moskalenko 1968; Dzyuba and Nalnjaeva 2011), i.e., from the Boreal-Pacific province of the Boreal Realm (Fig. 9). Elsewhere, this genus completely disappeared to the end of the Bajocian (e.g., Doyle and Bennett 1995; Weis and Mariotti 2008; Dzyuba and Weis 2015).

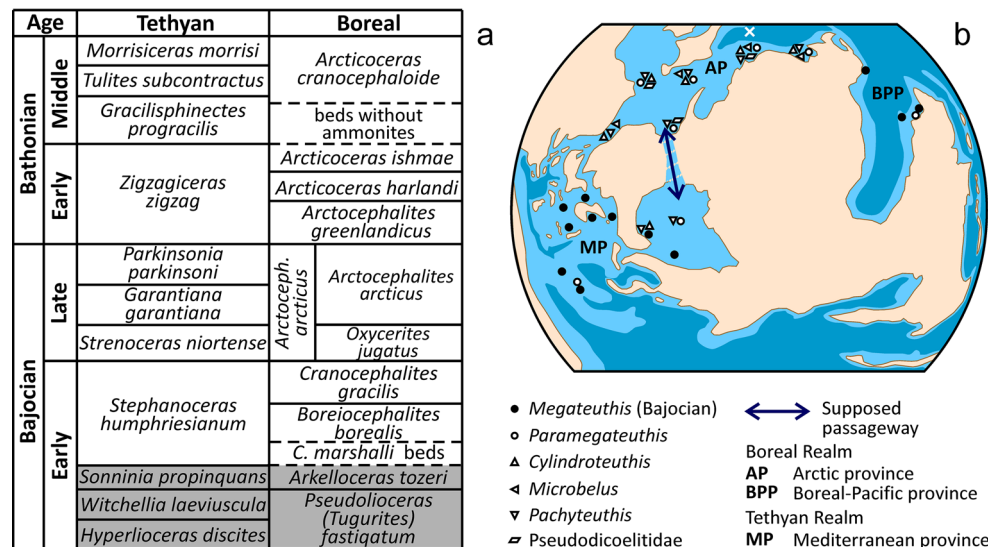
The genera *Cylindroteuthis*, *Microbelus* and *Pachyteuthis* show a similar distribution pattern within the Arctic province in the Bajocian–Bathonian transition time (Fig. 9). Additionally, *Pachyteuthis bodylevskii* Sachs and Nalnjaeva and *Pachyteuthis optima* Sachs and Nalnjaeva were recorded from the Lower Bathonian of the Saratov vicinity, Central Russia (e.g., Mitta et al. 2014b), and few rostra externally not distinguishable from *Cylindroteuthis* and *Pachyteuthis* (the ontogeny of the rostra remained unknown) were found together in the pre-Callovia deposits of Central Ukraine (Nikitin 1977). At the beginning of the Callovian, i.e., an interval of global sea-level rise (Hallam 2001; Ruban 2015), cylindroteuthidids became widespread in northwestern and eastern

Europe as well as on the north-western margin of North America, and at the end of the Bathonian or in the Callovian *Cylindroteuthis* also penetrated the northwestern Pacific up to the Tetori Basin, Central Japan (see Fig. 3 of Sano et al. 2010). The Early Bajocian genus *Eocylindroteuthis*, commonly considered as ‘early cylindroteuthidids’ of Europe, is currently assigned to Megateuthididae (Dzyuba et al. 2015).

The Bajocian–Bathonian megateuthidid and cylindroteuthidid taxa, reported from the northeastern Pacific region (southern Alaska, western Canada) and Arctic Canada (for summarised data see Stevens 1965: 160; Doyle and Kelly 1988: 40–44; Dzyuba 2004: 47, 56, 62–63), are still poorly investigated and need to be revised, and we did not include these data in this work. The concept considering the northeastern Pacific as a possible centre of origin of cylindroteuthidids in the mid-Bajocian time (Sachs and Nalnjaeva 1975; for a discussion see also Dzyuba and Nalnjaeva 2011) still requires confirmation by new reliable data.

The biogeographic distribution of *Paramegateuthis*, *Cylindroteuthis* and *Pachyteuthis* raises the question of the north–south (or south–north) migration pathways of these genera during the Bajocian–Bathonian. The first hypothesis is a migration by the Norway–Greenland pass (Viking Corridor, cf. Westermann 1993). However, palaeontological, tectonic, O and Nd isotope evidence suggest considerable restrictions of this seaway in Aalenian–Bathonian times (e.g., Meledina et al. 2005; Shurygin 2005; Dera et al. 2015; Korte et al. 2015). Moreover, all these belemnite genera were evidently absent in the Tethyan basins of Western Europe during the Bajocian–Bathonian (e.g., Doyle 1987). Since *Paramegateuthis subishmensis* Stoyanova-Vergilova was found only in the uppermost Lower Bajocian of Bulgaria (Stoyanova-Vergilova 1983, 1990) and northern Siberia (de Lagausie and Dzyuba 2017; present paper), supposed *Cylindroteuthis* and

Fig. 9 Accepted biostratigraphic correlation of the Tethyan and Boreal ammonite schemes in the studied interval (a) and global distribution of the mid-Middle Jurassic belemnites recognised in the Boreal Realm (b). Compiled from numerous sources (see text and Fig. 8). Palaeogeography (170 Ma) is modified after R. Blakey (<http://jan.ucc.nau.edu/rcb7/mollglobe.html>; <https://deeptimemaps.com>); the position of the North Pole is marked by white cross



Pachyteuthis were recorded in Central Ukraine (Nikitin 1977) in the “Bathonian” beds, which also contain *Holcobelus* (an Aalenian–Early Bajocian belemnite genus sensu Weis et al. 2012), and the genera *Paramegateuthis* and *Pachyteuthis* were found together with Tethyan ammonites in the Lower Bathonian of the Middle Volga region in Central Russia (Mitta et al. 2014b); thus, we can imagine the presence of a passageway (or temporary passageways) between the Boreal and Tethyan seas in the European part of Russia during the Bajocian–Bathonian transition (Fig. 9). Recently, the earliest existence of an East European passageway in the Jurassic was argued for the end of the Late Bajocian on the basis of the co-occurrence of Tethyan ammonites and Boreal foraminifers in Central Russia (Mitta et al. 2014b). Herein, we conclude that a passageway could have been temporarily opened in the Early Bajocian Humphriesianum Chronozone.

As follows from the above, the genus *Megateuthis* was not present in the Arctic province but can be recognised in the Boreal-Pacific province of the Boreal Realm. The main hypothesis that we can make about the migration of *Megateuthis* from a dispersal centre in the Tethys is via pathways marginal to Asian terranes. Unfortunately, information about belemnites from Southeast and East Asia is scant and must be improved to confirm this hypothesis.

Another possible explanation of the appearance of *Megateuthis* in the northwestern Pacific is that *Paramegateuthis* represents just a dwarf form of *Megateuthis*, being developed mainly in the Arctic. It is noteworthy that *Paramegateuthis nalnyaevae* Doyle, *Paramegateuthis nescia* Nalnjaeva, *Paramegateuthis ovata* de Lagausie and Dzyuba sp. nov., and *Paramegateuthis schurygini* Dzyuba sp. nov. represent atypically large forms of *Paramegateuthis*, close in length to the smallest *Megateuthis* (e.g., *Megateuthis beneckeii* Schwegler, the species without epirostrum), however, all of

these species are characterised by long dorsolateral apical grooves typical of the *Paramegateuthis*. The latest Early Bajocian species “*Mesoteuthis soloniensis* Nalnjaeva and Dzyuba known from the Russian Far East is very large and elongated, but simultaneously has very elongated dorsolateral apical grooves and apparently lacks an epirostrum (Dzyuba and Nalnjaeva 2011: p. 261, figs. 2a, b, c). In the Russian Far East, *Megateuthis* sp. indet., “*Mesoteuthis inornata* (Phillips)”, and “*Mesoteuthis aff. rhenana* (Opepel)” were also recorded by Moskalenko (1968) from the beds, which are currently considered as the latest Early Bajocian in age (Dzyuba and Nalnjaeva 2011). All specimens of “*M. aff. rhenana*” were referred by Sachs and Nalnjaeva (1975) to *Paramegateuthis ishmensis* (Gustomesov). In our opinion, these specimens and “*M. inornata*” actually belong to *Paramegateuthis* but are more similar to *P. ovata* sp. nov. However, *Megateuthis* sp. indet. (Moskalenko 1968: p. 29, pl. 5, fig. 4) as well as *Megateuthis “elliptica”* (Miller) from the Bajocian of the Artyk River in the Russian Far East (Kinasov in Efimova et al. 1968: p. 133, pl. 81, fig. 1) are closer to typical *Megateuthis*. Sachs and Nalnjaeva (1975) identified Far East *M. “elliptica”* with *P. nescia*; however, this identification seems unlikely considering the smaller rostrum of *P. nescia* and its longer dorso-lateral apical grooves.

Krimholz (1947), Tuchkov (1954), Voronets (1962), Kinasov (in Efimova et al. 1968), and Sachs and Nalnjaeva (1975) reported numerous “*Mesoteuthis*” taxa from the Toarcian and Aalenian of northern Siberia and northeastern Russia. Several of these taxa were recently assigned to *Rarobelus gigantoides* (Pavlov) (Dzyuba et al. 2015); many others are similar to *Acrocoelites* and *Odontobelus* and evidently need to be revised (Dzyuba and Weis 2015). Therefore, it cannot be excluded that *Megateuthis* may have penetrated the Boreal-Pacific province for the first time at the end of the

Early Bajocian. Considering the size of the rostrum and degree of elongation of the dorsolateral apical grooves as a product of intrageneric variability, the appearance of *Megateuthis* (?=*Paramegateuthis*) in the northwestern Pacific can be explained by a migration from the Arctic. However, this issue apparently requires further investigation.

Conclusions

The study of new material collected from the Bajocian–Bathonian transition beds of the Yuryung-Tumus Peninsula (northern Siberia) has revealed three new belemnite species: *Paramegateuthis ovata* de Lagausie and Dzyuba sp. nov., *Paramegateuthis schurygini* Dzyuba sp. nov. (Megateuthididae), and *Cylindroteuthis gelida* de Lagausie sp. nov. (Cylindroteuthididae). Siberian representatives of the species *Paramegateuthis subishmensis* Stoyanova-Vergilova, 1983, known from Bulgaria, are also described herein in detail. Additionally, *P.* cf. *subishmensis* is recorded very close to the base of the Lower Bajocian *Boreiocephalites borealis* ammonite Zone. These new findings provide evidence for a more diverse species composition of the mid-Middle Jurassic belemnite assemblages in the Arctic province than previously thought. *P. ovata* sp. nov. can also be considered as a faunal component of the Boreal-Pacific province in the latest Early Bajocian due to the “*Mesoteuthis*

inornata” and “*Mesoteuthis* aff. *rhenana*” records (Moskalenko 1968) assigned here to this new species.

There are still many questions concerning the cause and timing of the appearance of some Middle Jurassic belemnites in different parts of the Boreal Realm. However, to explain the migration path of *Paramegateuthis subishmensis*, it seems reasonable to conclude that a passage in the European part of Russia between the Boreal and Tethyan seas was opened (at least, temporarily) in the Early Bajocian Humphriesianum Chronozone.

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Appendix

see Table 6.

Table 6 List of the Arctic belemnites, illustrated in the literature, from the Bajocian–Bathonian boundary deposits

Original identification	Source	Accepted identification
East Greenland		
<i>Cylindroteuthis subextensa</i>	Spath (1932), pl. 1, fig. 5	<i>Microbelus parens</i> ^f
<i>Cylindroteuthis subextensa</i>	Spath (1932), pl. 17, fig. 2	Belemnitina ^f
<i>Cylindroteuthis subextensa</i>	Spath (1932), pl. 2, fig. 2; pl. 16, fig. 2	<i>Cylindroteuthis spathi</i> ^b
<i>Cylindroteuthis subrediviva</i>	Spath (1932), pl. 12, fig. 3; pl. 21, fig. 2, 3	<i>Pachyteuthis tschernyschewi</i> ^f
Svalbard		
<i>Lenobelus</i> cf. <i>viligaensis</i>	Doyle and Kelly (1988), pl. 1, figs. 1–10	<i>Lenobelus</i> cf. <i>viligaensis</i>
<i>Paramegateuthis nalnyaevae</i> , sp. nov.	Doyle and Kelly (1988), pl. 3, figs. 1–8	<i>Paramegateuthis nalnyaevae</i>
<i>Paramegateuthis</i> aff. <i>nalnyaevae</i>	Doyle and Kelly (1988), pl. 4, figs. 10, 11	<i>Paramegateuthis</i> ? aff. <i>nalnyaevae</i>
<i>Paramegateuthis nescia</i>	Doyle and Kelly (1988), pl. 4, fig. 1–7	<i>Paramegateuthis ovata</i> ^f
<i>Paramegateuthis</i> cf. <i>timanensis</i>	Nalnjaeva et al. (2011), pl. 3, fig. 6	<i>Paramegateuthis</i> cf. <i>timanensis</i>
<i>Paramegateuthis</i> sp. juv.	Doyle and Kelly (1988), pl. 4, figs. 8, 9	<i>Paramegateuthis</i> sp. juv.
<i>Paramegateuthis</i> ? sp.	Doyle and Kelly (1988), pl. 4, figs. 12–14	<i>Paramegateuthis</i> ? sp.
<i>Cylindroteuthis</i> (<i>Cylindroteuthis</i>) sp.	Doyle and Kelly (1988), pl. 4, figs. 15–17	<i>Cylindroteuthis</i> sp. (<i>C.</i> cf. <i>gelida</i>) ^f
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>bodylevskii</i>	Doyle and Kelly (1988), pl. 5, figs. 15–17	<i>Pachyteuthis bodylevskii</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>optima</i>	Doyle and Kelly (1988), pl. 6, figs. 1–8	<i>Pachyteuthis optima</i>
Franz Josef Land		

Table 6 continued

Original identification	Source	Accepted identification
<i>Belemnites</i> sp.	Newton and Teall (1898), pl. 29, fig. 5	<i>Paramegateuthis</i> cf. <i>nescia</i> ^f
<i>Paramegateuthis</i> cf. <i>nescia</i>	Efremova et al. (1983), pl. 11, fig. 3	<i>Paramegateuthis</i> cf. <i>nescia</i>
<i>Paramegateuthis</i> cf. <i>pressa</i>	Efremova et al. (1983), pl. 11, fig. 5	<i>Paramegateuthis</i> <i>pressa</i> ^f
<i>Belemnites borealis</i>	Samoilovich and Bodylevsky (1933), pl. 1, figs. 5, 6	<i>Paramegateuthis</i> sp. ^f
<i>Cylindroteuthis tornatilis</i>	Ognev (1933), pl. 2, figs. 1–2	<i>Cylindroteuthis</i> cf. <i>spathi</i> ^f
<i>Cylindroteuthis tschernyschewi</i>	Ognev (1933), pl. 1, figs. 1–12	<i>Pachyteuthis</i> cf. <i>bodylevskii</i> ^f
<i>Belemnites panderi</i>	Samoilovich and Bodylevsky (1933), pl. 1, fig. 7	<i>Pachyteuthis</i> cf. <i>bodylevskii</i> ^c
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>bodylevskii</i> , sp. nov.	Sachs and Nalnjaeva (1966), pl. 3, fig. 2	<i>Pachyteuthis</i> <i>bodylevskii</i>
<i>Pachyteuthis</i> cf. <i>panderi</i>	Ognev (1933), pl. 1, figs. 17, 18	<i>Pachyteuthis</i> cf. <i>tschernyschewi</i> ^f
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) cf. <i>parens</i>	Efremova et al. (1983), pl. 11, fig. 4	<i>Microbelus parens</i> ^d
Pechora Basin		
<i>Belemnopsis</i> sp. indet.	Meledina et al. (1998), plate-fig. 5; = Repin et al. (2006), pl. 52, fig. 2	<i>Lenobelus?</i> sp. ^e
<i>Megateuthis</i> (<i>Paramegateuthis</i>) <i>ishmensis</i> , sp. nov.	Gustomesov (1960), pl. 44, figs. 4, 5	<i>Paramegateuthis ishmensis</i>
<i>Paramegateuthis ishmensis</i>	Sachs and Nalnjaeva (1975), pl. 11, fig. 3	<i>Paramegateuthis ishmensis</i>
<i>Paramegateuthis ishmensis</i>	Meledina et al. (1998), plate-fig. 4; = Repin et al. (2006), pl. 53, fig. 3	<i>Paramegateuthis ishmensis</i>
<i>Paramegateuthis ishmensis</i>	Mitta et al. (2015), figs. 8.2, 8.3	<i>Paramegateuthis ishmensis</i>
<i>Megateuthis</i> (<i>Paramegateuthis</i>) <i>timanensis</i> , sp. nov.	Gustomesov (1960), pl. 44, fig. 6	<i>Paramegateuthis timanensis</i>
<i>Paramegateuthis timanensis</i>	Repin et al. (2006), pl. 54, fig. 3	<i>Paramegateuthis timanensis</i>
<i>Paramegateuthis timanensis</i>	Mitta et al. (2015), figs. 8.4, 8.5	<i>Paramegateuthis timanensis</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>optima</i> , sp. nov.	Sachs and Nalnjaeva (1966), pl. 1, fig. 2; pl. 2, fig. 1; text-fig. 2	<i>Pachyteuthis optima</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>optima</i>	Repin et al. (2006), pl. 54, fig. 2 (=Sachs and Nalnjaeva 1966, pl. 1, fig. 2)	<i>Pachyteuthis optima</i>
<i>Pachyteuthis optima</i>	Mitta et al. (2015), fig. 8.6	<i>Pachyteuthis optima</i>
<i>Cylindroteuthis tschernyschewi</i> , sp. nov.	Krimholz (1929), pl. 44, figs. 1–3, pl. 45, fig. 7	<i>Pachyteuthis</i> ^a <i>tschernyschewi</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>tschernyschewi</i>	Gustomesov (1964), pl. 15, figs. 1–5	<i>Pachyteuthis tschernyschewi</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>tschernyschewi</i>	Sachs and Nalnjaeva (1966), pl. 3, fig. 1; pl. 4, fig. 1; pl. 5, figs. 1, 2; (?) text-fig. 3	<i>Pachyteuthis tschernyschewi</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>tschernyschewi</i>	Nalnjaeva (1989), plate-figs. 5, 6	<i>Pachyteuthis tschernyschewi</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>tschernyschewi</i>	Meledina et al. (1998), plate-fig. 3; = Repin et al. (2006), pl. 54, fig. 1	<i>Pachyteuthis tschernyschewi</i>
<i>Pachyteuthis tschernyschewi</i>	Mitta et al. (2014a), fig. 1	<i>Pachyteuthis tschernyschewi</i>
<i>Pachyteuthis tschernyschewi</i>	Mitta et al. (2015), fig. 8.1	<i>Pachyteuthis tschernyschewi</i>
<i>Belemnopsis</i> sp. indet.	Meledina et al. (1998), plate-fig. 6; = Repin et al. (2006), pl. 52, fig. 3	<i>Pachyteuthis?</i> sp. ^e
Northern Siberia		
<i>Paramegateuthis ishmensis</i>	Nalnjaeva (1974), pl. 8, fig. 3; = Sachs and Nalnjaeva (1975), pl. 11, fig. 2	<i>Paramegateuthis ishmensis</i>
<i>Paramegateuthis ishmensis</i>	Sachs and Nalnjaeva (1975), pl. 11, figs. 2, 4	<i>Paramegateuthis ishmensis</i>
<i>Paramegateuthis ishmensis</i>	de Lagausie and Dzyuba (2017), pl. 1, figs. 18–20	<i>Paramegateuthis ishmensis</i>
<i>Paramegateuthis ishmensis</i>	Nalnjaeva (1974), pl. 8, fig. 4; = Sachs and Nalnjaeva (1975), pl. 11, fig. 1	<i>Paramegateuthis manifesta</i> ^e

Table 6 continued

Original identification	Source	Accepted identification
<i>Paramegateuthis manifesta</i> , sp. nov.	Sachs and Nalnjaeva (1975), pl. 9, figs. 5, 8; text-fig. 23	<i>Paramegateuthis manifesta</i>
<i>Paramegateuthis manifesta</i>	Nalnjaeva (1986), pl. 14, fig. 7 (= Sachs and Nalnjaeva 1975, pl. 9, fig. 5)	<i>Paramegateuthis manifesta</i>
<i>Paramegateuthis manifesta</i>	de Lagausie and Dzyuba (2017), pl. 1, figs. 22–24	<i>Paramegateuthis manifesta</i>
<i>Paramegateuthis nescia</i> , sp. nov.	Sachs and Nalnjaeva (1975) pl. 9, figs. 1–4; text-fig. 22	<i>Paramegateuthis nescia</i>
<i>Paramegateuthis ovata</i> , sp. nov.	Present paper, Fig. 4a, b	<i>Paramegateuthis ovata</i>
<i>Paramegateuthis parabajosicus</i> , sp. nov.	Sachs and Nalnjaeva (1975), pl. 10, figs. 7–10; text-fig. 26	<i>Paramegateuthis parabajosicus</i>
<i>Paramegateuthis parabajosicus</i>	Nalnjaeva (1986), pl. 14, fig. 8 (= Sachs and Nalnjaeva 1975, pl. 10, fig. 8)	<i>Paramegateuthis parabajosicus</i>
<i>Paramegateuthis parabajosicus</i>	de Lagausie and Dzyuba (2017), pl. 1, figs. 25–28	<i>Paramegateuthis parabajosicus</i>
<i>Paramegateuthis pressa</i> , sp. nov.	Sachs and Nalnjaeva (1975), pl. 10, figs. 4–6; text-fig. 27	<i>Paramegateuthis pressa</i>
<i>Cylindroteuthis</i> cf. <i>confessa</i>	de Lagausie and Dzyuba (2017), pl. 1, figs. 9–11	<i>Paramegateuthis schurygini</i> ^f
<i>Paramegateuthis schurygini</i> , sp. nov.	Present paper, Fig. 5f–h	<i>Paramegateuthis schurygini</i>
<i>Paramegateuthis ishmensis</i>	Sachs and Nalnjaeva (1975), text-fig. 24; +CSGM87-121, see Fig. 4d of present paper	<i>Paramegateuthis subishmensis</i> ^f
<i>Paramegateuthis manifesta</i>	Sachs and Nalnjaeva (1975), pl. 9, figs. 6, 7	<i>Paramegateuthis subishmensis</i> ^f
<i>Paramegateuthis subishmensis</i>	de Lagausie and Dzyuba (2017), pl. 1, figs. 15–17	<i>Paramegateuthis subishmensis</i>
<i>Paramegateuthis subishmensis</i>	Present paper, Figs. 4d, 5a–e	<i>Paramegateuthis subishmensis</i>
<i>Paramegateuthis</i> cf. <i>subishmensis</i>	Present paper, Fig. 4c	<i>Paramegateuthis</i> cf. <i>subishmensis</i>
<i>Paramegateuthis timanensis</i>	Nalnjaeva (1974), pl. 8, fig. 2; = Sachs and Nalnjaeva (1975), pl. 11, fig. 5; = Nalnjaeva (1986), pl. 14, fig. 6	<i>Paramegateuthis timanensis</i>
<i>Paramegateuthis timanensis</i>	Sachs and Nalnjaeva (1975), pl. 11, figs. 5–8; text-fig. 25	<i>Paramegateuthis timanensis</i>
<i>Paramegateuthis timanensis</i>	de Lagausie and Dzyuba (2017), pl. 1, figs. 12–14	<i>Paramegateuthis timanensis</i>
<i>Mesoteuthis inornata</i>	Sachs and Nalnjaeva (1975), pl. 13, fig. 5 (not fig. 6 as erroneously presented in the plate explanation): CSGM87-73	<i>Paramegateuthis?</i> sp. ^f
<i>Cylindroteuthis</i> (<i>Cylindroteuthis</i>) <i>confessa</i> , sp. nov.	Sachs and Nalnjaeva (1975), pl. 10, figs. 1–3; text-fig. 31	<i>Cylindroteuthis confessa</i>
<i>Cylindroteuthis gelida</i> , sp. nov.	Present paper, Fig. 5i	<i>Cylindroteuthis gelida</i>
<i>Cylindroteuthis</i> (<i>Cylindroteuthis</i>) <i>spathi</i> , sp. nov.	Sachs and Nalnjaeva (1964, 1966, 1975), pl. 1, figs. 1–3; text-fig. 4	<i>Cylindroteuthis spathi</i>
<i>Cylindroteuthis</i> (<i>Cylindroteuthis</i>) <i>spathi</i>	Nalnjaeva (1986), pl. 14, fig. 2	<i>Cylindroteuthis spathi</i>
<i>Cylindroteuthis spathi</i>	de Lagausie and Dzyuba (2017), pl. 1, figs. 1, 2 (=Nalnjaeva 1986, pl. 14, fig. 2), 3–5	<i>Cylindroteuthis spathi</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>optima</i> , sp. nov.	Sachs and Nalnjaeva (1966), pl. 2, fig. 2	<i>Pachyteuthis optima</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>subrediviva</i>	Sachs and Nalnjaeva (1966), pl. 1, figs. 4, 5; pl. 2, fig. 5; text-fig. 4	<i>Pachyteuthis subrediviva</i>
<i>Pachyteuthis</i> (<i>Pachyteuthis</i>) <i>parens</i> , sp. nov.	Sachs and Nalnjaeva (1966), pl. 1, fig. 3; text-fig. 1	<i>Microbelus</i> ^d <i>parens</i>
<i>Acroteuthis</i> (<i>Microbelus</i>) <i>pseudolateralis</i>	Sachs and Nalnjaeva (1966), pl. 34, figs. 1, 2; text-Fig. 46	<i>Microbelus pseudolateralis</i>

Authors of re-identification: ^aGustomesov (1964); ^bSachs and Nalnjaeva (1964); ^cSachs and Nalnjaeva (1966); ^dDzyuba (2004); ^eDzyuba in Mitter et al. (2015); ^fPresent paper

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