

# Lower Bathonian Belemnites and Biostratigraphy of the Central and Southern Parts of the East European Platform: Part 2. *Cylindroteuthididae* and *Belemnotheutididae*

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**Abstract**—Belemnites from the lower Bathonian deposits of the Russian Plate are revised and discussed on the basis of study of the two reference sections—Pletnyovka and Sokur quarries. This is the second part of the investigation dealing with representatives of the family *Cylindroteuthididae*, and “rostrum-less” belemnites of the family *Belemnotheutididae*, while members of the family *Megateuthididae* were discussed in detail in the first part (Ippolitov, 2018). The *cylindroteuthidids* are found only in the Sokur Quarry and comprise four species all assigned to the genus *Pachyteuthis*, including a new species, *Pachyteuthis mittai* sp. nov. For *Belemnotheutididae*, the presence of a single species *Acanthoteuthis foliostris* sp. nov. is recorded, which is the first confirmed record of the genus *Acanthoteuthis* in the pre-Callovian strata. The study of morphological changes within *Cylindroteuthididae* across the succession allowed two biohorizons to be recognized and the existing belemnite-based scheme for the lower Bathonian of the Volga Region and its correlation with sections in the Pechora River basin to be updated. As the result of the revision, a complex zonal and infrazonal belemnite-based stratigraphic scheme of the lower Bathonian of the Volga Region is introduced. The presence of an endemic genus deriving from Arctic-Boreal immigrants in the lower Bathonian of the Middle Russian Sea allows the belemnite fauna of this age to be interpreted as the first isolated episode of differentiation of the Boreal-Atlantic Province in belemnites. The study of the development of the cephalopod fauna in the early Bathonian of the Russian Plate indicates a biphasic formation of the meridional strait connecting the Middle Russian Sea with the Arctic basins and also supports the hypothesis of a short-term opening of a sub-latitudinal Pripyat Strait during the maximum highstand.

**Keywords:** belemnites, *Pachyteuthis*, *Acanthoteuthis*, lower Bathonian, European Russia, stratigraphy

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## INTRODUCTION

The lower Bathonian occurrences of the family *Cylindroteuthididae* in the Russian Plate are confirmed from a single locality—the Sokur Quarry in the Saratov suburbs, from where they were originally described by I.S. Barskov (Mitta et al., 2004). All figured specimens are represented by a single genus *Pachyteuthis* Bayle, 1878, although some occurrences had previously been mentioned under the generic names *Cylindroteuthis* (Mitta et al., 2011) and *Megateuthis* (Mitta and Seltzer, 2002; Seltzer and Ivanov, 1997). There is also a record of a single *cylindroteuthidid* find from the northern part of Volgograd region (Saltykov, 2008: “*Cylindroteuthis* cf. *spathi* Sak.”), although it was not described or figured, and it is not possible to judge its assignment to the family *Cylindroteuthididae*.

Although *cylindroteuthidids* from the Sokur Quarry were repeatedly studied by different authors (Barskov in Mitta et al., 2004, 2011; Nalnjaeva in Meledina et al.,

2009; Dzyuba in Mitta et al., 2012, 2014b), their classification at the species level still remains problematic, which is clearly evident from differences in definitions of the same taxa by all the authors mentioned above and sometimes even in papers published in different years by the same author (see a review in Mitta et al., 2014b, table 1). The objective problems with *cylindroteuthidid* classification are due to the high morphological plasticity of this group and also due to a complex and in part self-contradictory classification of Bathonian—Callovian representatives of the genus *Pachyteuthis* at the species level (see discussion in Gustomesov, 1990, p. 68; Mitta et al., 2011, p. 41).

By its geographic origin, the family *Cylindroteuthididae* is Boreal (Dzyuba, 2004; Dzyuba and Nalnjaeva, 2011; Sachs and Nalnjaeva, 1966). Its presence in the lower Bathonian deposits of the Volga Region along with the ammonites *Arcticoceras* and *Greencephalites* is a result of immigration from the Pechora Basin via a meridional strait that was opened up across the

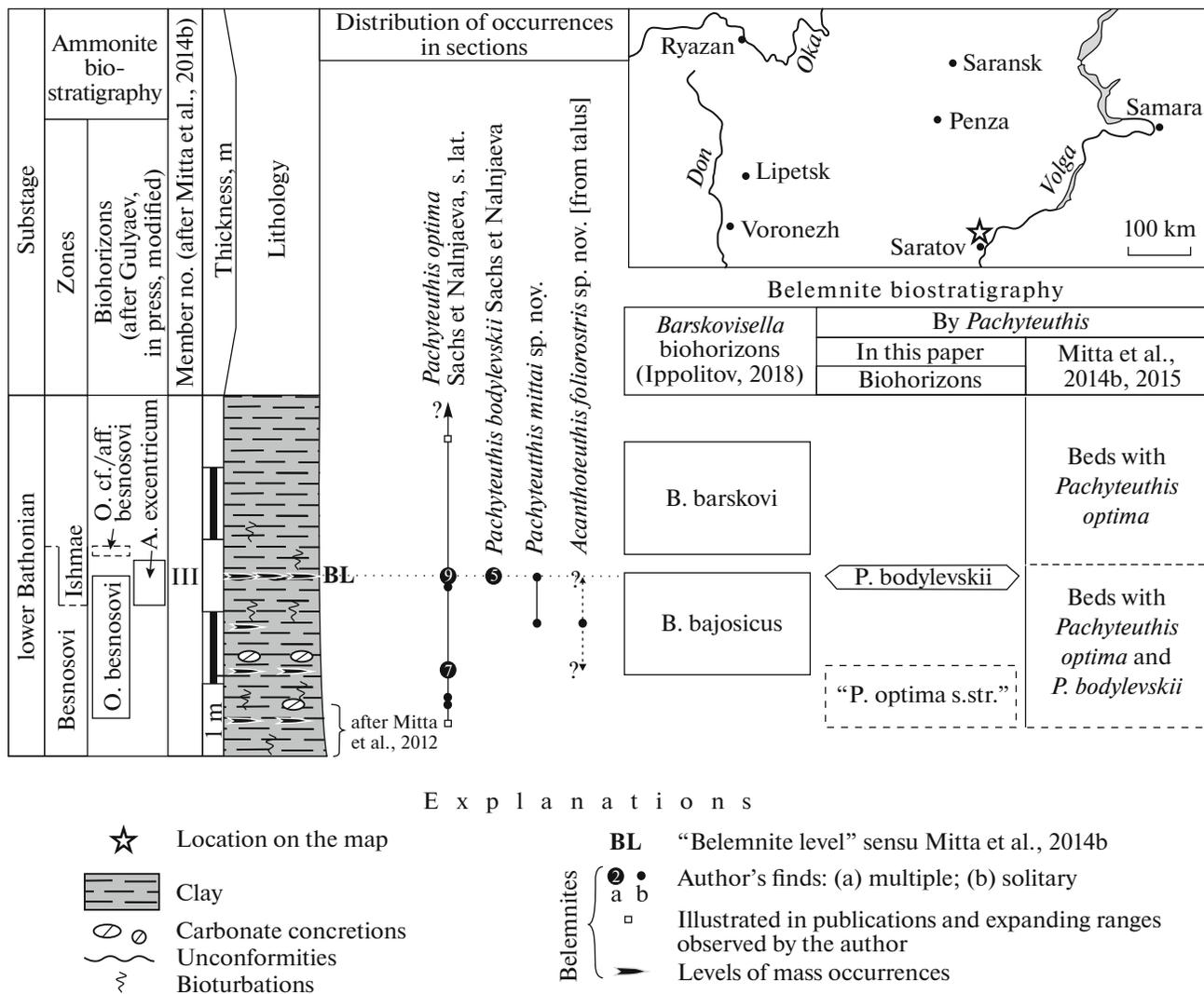


Fig. 1. Distribution of the studied belemnite species in the section of the Sokur Quarry (Saratov). *A.*—*Arcticoceras*; *O.*—*Oraniceras*.

territory of European Russia in the early Bathonian (Mitta et al., 2015; Seltzer, 2009).

This study is the second and final part of a revision of the early Bathonian belemnites of the Russian Plate; in the previously published part one (Ippolitov, 2018), I discussed in detail the members of the family Megateuthididae.

## MATERIALS AND METHODS

Detailed descriptions of the localities material from which is employed in the present paper—Pletnyovka Quarry (Issa district of Penza region) and Sokur Quarry (northwestern suburbs of Saratov)—are provided in part one of this study (Ippolitov, 2018). The distribution of occurrences of Cylindroteuthididae and Belemniteuthididae in the section of the Sokur Quarry is shown in Fig. 1.

To characterize and analyze the cylindroteuthidid sample sets, the following measurements, ratios, and abbreviations were used (Fig. 2):

**Measurements:** R—total preserved length; DV—dorsoventral diameter at the alveolus tip; LL—lateral diameter at the alveolus tip; PA—length of the postalveolar part of the rostrum ("rostrum solidum") (reconstructed in the case of a missing apical part);  $dv^{0.5}$ —dorsoventral diameter in the middle of the post-alveolar part;  $ll^{0.5}$ —lateral diameter at the same section;  $dv^{0.75}$ —dorsoventral diameter at a distance of 3/4 PA from the alveolus tip (=1/4 PA from the apex);  $ll^{0.75}$ —lateral diameter at the same section; DV'—dorsoventral diameter of a cross section near the alveolus tip (ideally, this parameter coincides with DV, and the section coincides with the section near the tip of the alveolus, but can in fact be located slightly anteriorly/posteriorly);  $R_v$ —distance from apical line to

ventral side (ventral radius) in the same section;  $\beta(\Pi)^\circ$ —alveolar angle in outline;  $\beta(dv)^\circ$ —alveolar angle in profile.

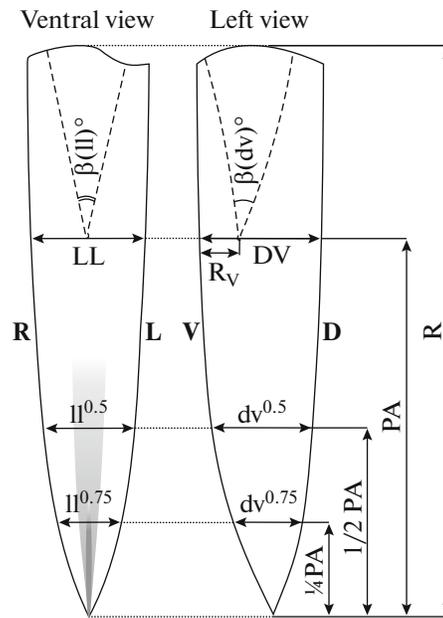
**Ratios:**  $D = \sqrt{(DV \times LL)}$ —basic diameter at the alveolus tip;  $d^{0.5} = \sqrt{(dv^{0.5} \times \Pi^{0.5})}$ —basic diameter in the middle of the postalveolar part;  $E = PA/\sqrt{(DV \times LL)} \times 100\%$ —relative elongation of the postalveolar part;  $LL/DV$ —compression ratio at the alveolus tip;  $\Pi^{0.5}/dv^{0.5}$ —compression ratio in the middle of the postalveolar part;  $\Pi^{0.75}/dv^{0.75}$ —compression ratio at 3/4 PA distance from the alveolus tip (=1/4 PA from the apex);  $d^{0.5}/D$ —tapering coefficient (= 0.5 in ideally conical rostra, = 1 in ideally cylindrical rostra, >1 in fusiform rostra; in addition to the above ratio, the ratio  $dv^{0.5}/DV$ —tapering coefficient in profile—was used);  $R_v/DV$ —apical line displacement.

There are two essential differences in measurements used in comparison to those taken by previous authors (Dzyuba, 2004; Gustomesov, 1964; Sachs and Nalnjaeva, 1964).

The first is the replacement of the dorsoventral diameter (DV) by the basic diameter (D) as a principal size character, which was explained in part one (Ippolitov, 2018).

The second essential difference is the use of two alternative cross sections, the position of which is strictly determined in relation to the protoconch, instead of a “cross section in the apical part” (Sachs and Nalnjaeva, 1964, 1966, 1975, etc.). These are the cross section at a distance of 1/2 PA from the alveolus tip (= in the middle of the postalveolar part) and that located at distance of 3/4 PA from the alveolus tip (= in the middle of the posterior half of the postalveolar part). They are equivalent to section nos. 2 and 3 used by Mutterlose (1983, text-fig. 12) for analyzing the variability of the rostra of the Lower Cretaceous family Oxyteuthididae. A classical parameter, “length of apical part” (AR) extensively used by Sachs and Nalnjaeva and later by Dzyuba is used in my descriptions as a semiquantitative character rather than a precise measurement. Although there is a formal method of obtaining this parameter using a system of parallel lines (Swinnerton, 1936, text-fig. 2), in practice, the use of this method is difficult because the anterior end of the alveolus is never completely preserved. All Russian authors, without exception, who used the AR parameter (along with the associated “dorsoventral and lateral diameters in the apical region”) have noted the subjective nature of its identification (Dzyuba, 2012, p. 58; Sachs and Nalnjaeva, 1964, p. 22).

The rationale for the introduction of new parameters instead of those discussed above, is to enable *objective* interspecific comparisons and evaluation of the intraspecific variability, which are often defined in the literature only qualitatively (e.g., “posterior end is more attenuated”), semiquantitatively (“apical part is longer”), or quasi-quantitatively (based on measurements with a significant degree of subjectivism), whereas the



**Fig. 2.** Measurements of the belemnite rostrum used in this study. Rostrum margins: R—right, L—left, V—ventral, D—dorsal. Explanations of the measurements see in the text.

advantages are demonstrated in this paper. The analysis of tapering coefficients, similar to those originally introduced by Schlegelmilch (1998), were not systematically used for cylindroteuthidids, but turned out to be a particularly important for the intra- and interspecific comparisons in a group of closely related *Pachyteuthis* spp. described below. A similar coefficient for cylindroteuthidids previously proposed by Dzyuba and Glushkov (2000) was essentially based on the parameters of a “cross section at the apical part,” the position of which is ambiguous, and therefore, Schlegelmilch’s tapering coefficient appears to be a more reliable option.

Measurements were taken from both specimens and photographs (where possible from the author’s own photographs, where not possible from published photographs), in the latter case using the CorelDraw software tools. While measuring photographs, the position of the alveolus tip was determined for the rostra showing the alveolar margin, by application of templates, according to which the alveolar angle in the outline for all *Pachyteuthis* was accepted as  $21^\circ$ . Such an approximate determination, as well as imprecise scaling of photos in publications, affects the precision of absolute values (LL, VD, PA,  $vd^{0.5}$ , etc.), but have almost no effect on the ratios (except for E), which were used for the intra- and interspecific comparisons.

The material described below is housed in the Vernadsky State Geological Museum (VSGM, Moscow). I also had the opportunity to examine originals to numerous publications, including type specimens of all the species discussed below: the collection of Krimholz (1929), housed in the Chernyshev Cen-

tral Research Geological Prospecting Museum (CCRGM), St. Petersburg; collections of Gustomesov (1964) and I.S. Barskov (Mitta et al., 2004, 2011), both housed in the VSGM, Moscow; collections of Sachs and Nalnjaeva (1964, 1966, 1975) and Dzyuba (2000), housed in the Central Siberian Geological Museum (CSGM), Novosibirsk.

## RESULTS

### SYSTEMATIC PALEONTOLOGY

#### SUBCLASS COLEOIDEA

#### ORDER BELEMNITIDA VON ZITTEL, 1895

##### Family *Cylindroteuthididae* Stolley, 1919

At present, a large mass of data on the biodiversity and stratigraphic distribution of the cylindroteuthidid species has been accumulated in publications, but the exact interpretation of these data is often problematic. There are two main problems. Firstly, the intraspecific variability for many nominal species is poorly studied, while their type series represent stratigraphically and geographically mixed sets. Secondly, numerous published identifications with no illustrations often groundlessly expand the stratigraphic and geographic ranges of known species (see reviews of the species described below in Dzyuba, 2004), but in fact can be a result of either incorrect identification or overlooked differences.

The classification of species of the genus *Pachyteuthis* from the Sokur Quarry provided below is based on the study of the trends of changes in the main ratios across the succession and their comparison with ratios of previously described early Bathonian species (Fig. 3). To substantiate species identification, only figured types and topotypical specimens were used.

#### Genus *Pachyteuthis* Bayle, 1878

##### *Pachyteuthis optima* Sachs et Nalnjaeva, 1966 s. lat.

Plate I, figs. 1–6

*Megateuthis* sp. indet.: (?) Ivanova, 1959, pp. 366–367, pl. 16, fig. 2 [can also belong to *P. tschernyschewi*].

*Pachyteuthis (Pachyteuthis) tschernyschewi*: (pars) Gustomesov, 1964, pp. 170–172, pl. 15, figs. 1–5 [partly belong to *P. tschernyschewi*].

*Pachyteuthis (Pachyteuthis) optima*: Sachs and Nalnjaeva, 1966, pp. 20–23, pl. 1, figs. 2a, 2b (= Nalnjaeva in Repin et al., 2006, pl. 54, fig. 2), pl. 2, figs. 1–4, text-fig. 2; (pars) Doyle in Doyle and Kelly, 1988, pp. 30–31, pl. 6, figs. 3–5 [non figs. 1–2, 6–8].

*Pachyteuthis optima*: (non) Barskov in Mitta et al., 2011, pl. 1, fig. 4 [= *P. tschernyschewi*]; Dzyuba in Mitta et al., 2014b, figs. 7.9, 8.1, 8.2, 8.4, (cf.) 8.3; Dzyuba in Mitta et al., 2015, fig. 8.6.

*Pachyteuthis (Pachyteuthis) bodylevskii*: Doyle in Doyle and Kelly, 1988, pp. 29–30, pl. 5, figs. 15–17.

*Pachyteuthis bodylevskii*: Dzyuba in Mitta et al., 2012, pl. 3, fig. 4; Dzyuba in Mitta et al., 2014b, figs. 7.1, 7.2, 7.3, 7.10.

*Pachyteuthis subrediviva*: (pars) Barskov in Mitta et al., 2004, pp. 24, 26, pl. 4, figs. 1–4 [except for the unfigured specimen CR-2797/VSGM BP-09679; = *P. bodylevskii*].

*Cylindroteuthis spathi*: Barskov in Mitta et al., 2011, pl. 1, figs. 1–2, ?3.

**Description.** See (Sachs and Nalnjaeva, 1966, pp. 20–21).

**Dimensions and ratios.** See Table 1.

**Comparison** (see Sachs and Nalnjaeva, 1966, pp. 21, 23). In addition to the differences provided in the cited book, the following should be considered. This species differs from the lower Callovian species *P. subrediviva* (Lemoine, 1915), to which the rostra from the Sokur Quarry were assigned by Barskov in the earliest paper (Mitta et al., 2004), in the lateral compression near the apex ( $(ll^{0.75}/dv^{0.75} = 0.88–0.98$ , rarely more, vs. 1.04 in the holotype of *P. subrediviva*). In addition, in *P. optima*, lateral compression always increases toward the posterior end ( $(ll^{0.75}/dv^{0.75} < LL/DV$ ), while in the holotype of *P. subrediviva* it, instead, decreases (Table 1), and this distinguishes the type material of *P. subrediviva* not only from the Sokur rostra but also from specimens identified as *P. subrediviva* from northern Siberia (Sachs and Nalnjaeva, 1966).

This species differs from *P. mittai* sp. nov. in the presence of elongated flattened zones on the lateral and ventral sides and expressed subconical ( $d^{0.5}/D = 0.82–0.87$  in *P. optima* s. lat.), rather than cylindrical ( $d^{0.5}/D = 0.92–0.93$  in *P. mittai* sp. nov.) rostrum shape.

**Occurrence and age.** Bajocian–lower Bathonian–lower Callovian; Central Russia, Pechora Basin, northern Siberia, Spitsbergen. In the lower Bathonian of the Russian Plate (Sokur Quarry), it is found within the *O. besnosovi* ammonite Zone (starting from the *O. besnosovi* Biohorizon)–*A. ishmae* Zone.

**Remarks.** The presence of this species in the assemblage of the Sokur Quarry was originally established by Nalnjaeva (Meledina et al., 2009), who reidentified belemnites previously described by Barskov (Mitta et al., 2004) as *P. subrediviva*. *P. optima* is currently an extremely broadly understood species (see a review in Dzyuba, 2004), which includes both lower Bathonian (holotype is from the *Arcticoceras ishmae* Zone of the Pechora Basin), and Callovian representatives. I also identified this species in the lower Callovian of Central Ukraine (Ippolitov and Gulyaev, 2013), and the differences of these specimens with those from the Sokur Quarry are so far unclear. Records from the upper Bathonian–Callovian interval are not included in the synonymy list in this paper.

In this paper, all specimens previously figured from the Sokur Quarry by Dzyuba (Mitta et al., 2012; 2014b) as *P. bodylevskii* (interval 190–200 cm below the “belemnite level”) and *P. optima* (starting from a level of 100–110 cm below the “belemnite level” and above) are assigned to *P. optima* s. lat. The diagrams (Fig. 3) clearly show that the differences in all major ratios between these varieties are insignificant, whereas the ranges of variability are potentially high. The assignment of the Sokur specimens of *P. bodylevskii* sensu Dzyuba in Mitta et al., 2014b to *P. optima* was largely

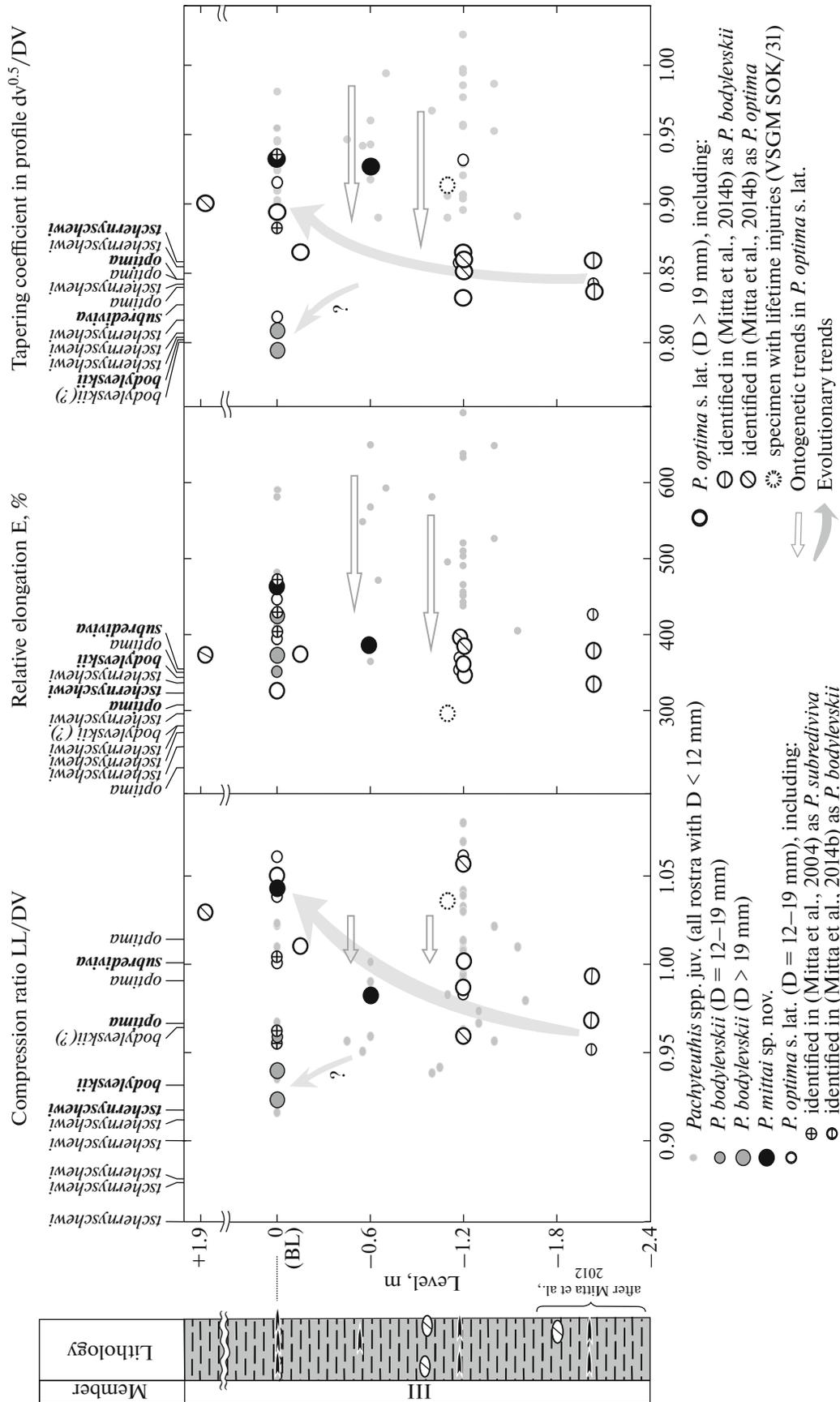
**Table 1.** Measurements and ratios of the *Pachyteuthis* spp. rostra from the lower Bathonian of the Sokur Quarry and their comparison with type and topotypical specimens of some Bathonian and early Callovian species

No./name	MM	Position relative to BL/status	R, mm	PA, mm	LL, mm	DV, mm	ll <sub>0.5</sub> , mm	dV <sub>0.5</sub> , mm	ll <sub>0.75</sub> , mm	d <sub>0.75</sub> , mm	D, mm	D <sub>0.5</sub> /D	dV <sub>0.5</sub> /DV	LL/DV	ll <sub>0.5</sub> /dV <sub>0.5</sub>	ll <sub>0.75</sub> /dV <sub>0.75</sub>	E, %	Notes/reference	
<i>Pachyteuthis optima</i> Sachs et Nalijaeva, 1966 s. lat.																			
C	C	↓190–200	165.9	84.9	25.0	25.8	19.4	22.1	13.0	14.8	25.4	0.82	0.86	0.97	0.88	0.87	335	Mitta et al., 2014b, fig. 7.1	
C	C	↓190–200	125.3	88.4	23.5	23.7	19.6	19.8	14.3	14.7	23.6	0.83	0.84	0.99	0.99	0.97	375	Mitta et al., 2014b, fig. 7.3	
C	C	↓190–200	86.5	65.5	15.0	15.7	12.4	13.2	9.3	9.5	15.3	0.83	0.84	0.95	0.94	0.98	427	Mitta et al., 2014b, fig. 7.10	
A	A	↓120	93.8	66.0	17.7	18.0	13.7	15.4	9.5	11.1	17.9	0.81	0.86	0.98	0.89	0.86	369	Plate I, fig. 2	
A	A	↓120	77.9	44.5	12.9	12.2	11.1	11.4	8.4	8.7	12.6	0.89	0.93	1.06	0.97	0.97	354	Plate I, fig. 1	
A	A	↓120	126.9	85.7	23.5	23.8	18.8	19.9	13.6	14.3	23.6	0.82	0.83	0.99	0.95	0.95	362	Plate I, fig. 1	
A	A	↓120	88.7	72.8	20.8	20.7	17.2	17.9	12.1	13.4	20.7	0.84	0.86	1.00	0.96	0.90	351	Mitta et al., 2014b, fig. 8.1	
C	C	↓100–120	95.5	80.6	19.9	20.7	16.0	17.7	10.9	12.2	20.3	0.83	0.85	0.96	0.90	0.89	397	Mitta et al., 2014b, fig. 8.1	
C	C	↓100–120	118.1	90.5	24.0	22.7	19.6	19.6	13.5	14.0	23.4	0.84	0.86	1.06	1.00	0.97	387	Mitta et al., 2014b, fig. 8.2	
A	A	↓110	80.6	56.5	19.4	18.8	16.8	17.2	12.6	12.9	19.1	0.89	0.91	1.04	0.98	0.98	296	with predatory bites; Plate I, fig. 5	
A	A	↓15	106.4	82.4	22.1	21.9	18.8	18.9	13.1	14.6	22.0	0.86	0.87	1.01	0.99	0.90	374	Plate I, fig. 3	
A	A	0	62.3	19.3	18.5	18.5	13.1	13.1	8.7	8.6	18.9	0.87	0.92	1.04	0.97	1.01	447		
A	A	0	69.2	53.8	12.4	11.7	10.4	10.7	8.7	8.6	12.0	0.87	0.92	1.06	0.97	1.01	447		
A	A	0	81.4	69.9	18.5	18.5	14.8	15.1	9.9	10.0	18.5	0.81	0.82	1.00	0.98	0.98	394		
A	A	0	91.8	63.1	16.4	15.6	12.5	12.2	9.9	10.0	18.5	0.81	0.82	1.00	0.98	0.98	394		
A	A	0	71.3	72.9	18.3	17.4	15.1	14.6	10.9	11.6	19.5	0.88	0.89	1.05	1.01	1.00	326	Plate I, fig. 4	
A	A	0	87.4	63.4	20.0	19.0	17.2	17.0	13.1	13.0	19.5	0.88	0.89	1.05	1.01	1.00	326	Plate I, fig. 4	
A	A	0	86.2	62.6	15.2	15.1	13.1	13.1	10.9	10.6	15.1	0.88	0.89	1.01	1.01	1.03	413	Mitta et al., 2004 (unfigured)	
A	A	0	86.3	61.4	14.9	15.5	13.6	13.7	11.3	11.1	15.2	0.90	0.88	0.96	0.99	1.02	404	Mitta et al., 2004, pl. 4, fig. 2	
A	A	0	73.0	57.9	11.9	12.4	10.9	11.6	8.8	9.4	12.2	0.93	0.94	0.96	0.94	0.94	476	Mitta et al., 2004, pl. 4, fig. 3	
C	C	↑190	122.5	82.8	22.5	21.9	19.2	19.6	15.1	15.5	22.2	0.88	0.90	1.03	0.98	0.97	374	Mitta et al., 2014, fig. 8.4	
A	A	0 (?) <sup>3</sup>	106.9	76.8	20.6	20.6	16.8	17.6	12	12.9	20.6	0.83	0.85	1.00	0.96	0.93	373	Mitta et al., 2004, pl. 4, fig. 1	
A	A	From talus	112.8	74.0	22.4	23.5	18.1	20.0	14.1	15.6	22.9	0.83	0.85	0.95	0.91	0.91	323	Plate I, fig. 6	
A	A	From talus	65.4	61.7	15.6	15.6	11.9	13.1	8.2	9.6	15.6	0.80	0.84	1.00	0.90	0.85	392		
A	A	From talus	75.6	52.8	15.9	16.3	13.9	13.9	11.2	11.3	16.1	0.87	0.86	0.98	1.00	1.00	328		
A	A	From talus	84.0	61.7	14.8	13.2	13.9	13.9	8.9	9.2	14.0	0.87	0.86	1.12	1.00	0.97	438		
A	A	From talus	41.1	20.3	18.8	18.8	9.7	10.7	7.5	8.1	19.6	0.82	0.83	0.94	0.90	0.93	426	Mitta et al., 2011, pl.1, fig. 2	
A	A	From talus	96.9	53.2	12.1	12.9	9.7	10.7	7.5	8.1	12.5	0.82	0.83	0.94	0.90	0.93	426	Mitta et al., 2011, pl.1, fig. 2	
<i>Pachyteuthis bodylenskii</i> Sachs et Nalijaeva, 1966																			
A	A	0	83.9	64.0	17.9	18.6	11.9	12.8	18.2	0.96	0.94	0.93	0.93	351				Plate II, fig. 3	
A	A	0	82.9	82.9	18.2	19.7	15.1	16.5	12.7	12.7	20.0	0.81	0.81	0.94	0.95	0.95	424	Plate II, fig. 2	
A	A	0	84.5	85.0	19.4	20.7	15.9	16.7	12.1	13.6	21.1	0.80	0.79	0.92	0.94	0.87	372	Plate II, fig. 1	
A	A	0	105.2	78.5	20.3	22.0	16.4	17.4	11.8	13.6	21.1	0.80	0.79	0.92	0.94	0.87	372	Plate II, fig. 1	
A	A	0	112.4	77.9	15.9	16.3	13.9	13.9	11.2	11.3	16.1	0.87	0.86	0.98	1.00	1.00	328		
A	A	0	62.8	49.8	8.2	8.7	7.4	8.3	6.0	6.3	8.5	0.93	0.96	0.95	0.89	0.95	590	Mitta et al., 2004 (unfigured);	
A	A	From talus	45.8	21.7	23.5	23.5	9.7	10.7	7.5	8.1	22.6	0.82	0.83	0.94	0.90	0.93	426	Plate II, fig. 4	

Table 1. (Contd.)

No./name	MM	Position relative to BL/status	R, mm	PA, mm	LL, mm	DV, mm	$\Pi 0.5$ , mm	$dV^{0.5}$ , mm	$\Pi 0.75$ , mm	$dV^{0.75}$ , mm	D, mm	$D^{0.5}/DV$	LL/DV	$\Pi 0.5/dV^{0.5}$	$\Pi 0.75/dV^{0.75}$	E, %	Notes/reference	
<i>Pachyteuthis ischermyschewi</i> (Krimholz, 1929)																		
VSGM BP-10405 <sup>5</sup>	A	From talus	130.0	83.0	24.6	26.6	20.7	23.3	15.8	17.9	25.6	0.86	0.92	0.89	0.88	325	Mitta et al., 2011, pl. 1, fig. 4; Plate II, fig. 8	
VSGM SOK/87	A	From talus	62.3	45.0	12.9	14.9	11.3	13.2	8.6	10.4	13.8	0.88	0.86	0.86	0.82	325	Plate II, fig. 7	
<i>Pachyteuthis mitai</i> sp. nov.																		
VSGM SOK/39	A	↓60	119.9	80.0	20.6	20.9	19.3	19.4	14.9	15.2	20.7	0.93	0.98	1.00	0.98	386	Plate II, fig. 6	
VSGM SOK/90	A	0 (?)	87.6	61.5	13.6	13.0	12.3	12.1	9.1	9.5	13.3	0.92	1.04	1.01	0.96	463	Plate II, fig. 5	
Type, topotypical and some other <i>Pachyteuthis</i> spp., as well as comparable forms of other genera																		
<i>P. optima</i> s.str.	B	Holotype	109.0	73.8	23.7	24.6	19.5	20.7	14.2	15.0	24.1	0.83	0.84	0.94	0.95	306	Sachs and Naljaeva, 1966, pl. 1, f. 2	
<i>P. optima</i> s.str.	B		113.0	58.3	26.2	25.8	20.9	21.8	14.9	15.3	26.0	0.82	0.84	0.96	0.97	225	Sachs and Naljaeva, 1966, pl. 2, f. 1	
<i>P. optima</i> s.str.	C		151.1	82.3	24.1	24.3	19.4	20.4	14.2	14.8	24.2	0.82	0.84	0.95	0.96	340	Mitta et al., 2015, fig. 8.6	
<i>P. optima</i> s.lat. <sup>1</sup>	C			83.0	22.2	23.6	17.9	20.1	12.7	15.0	22.9	0.83	0.85	0.89	0.84	362	Doyle, Kelly, 1988, pl. 5, f. 15–17	
<i>P. ischermyschewi</i>	A	Lectotype	124.0	75.0	22.4	24.5	17.7	21.0	13.0	14.7	23.4	0.82	0.86	0.84	0.88	320	Krimholz, 1929, pl. 44, fig. 1–3	
<i>P. ischermyschewi</i>	A		107.0	57.5	19.6	20.7	16.5	18.1	13.4	11.5	20.1	0.86	0.87	0.91	0.86	286	Krimholz, 1929, p. 110	
<i>P. ischermyschewi</i>	A		96.8	74.9	24.0	27.4	19.1	22.4	14.4	14.7	25.6	0.81	0.82	0.86	0.98	292	Krimholz, 1929, pl. 45, fig. 7	
<i>P. ischermyschewi</i>	B		195.0	86.4	32.4	36.0	25.8	30.8	19.1	21.3	34.1	0.83	0.86	0.84	0.90	253	Sachs and Naljaeva, 1966, pl. 3, f. 1	
<i>P. ischermyschewi</i>	B		222.5	101.6	27.3	30.9	22.5	26.4	19.2	20.1	29.1	0.84	0.86	0.85	0.96	350	Sachs and Naljaeva, 1966, pl. 4, f. 1	
<i>P. ischermyschewi</i>	B		106.8	83.5	28.0	31.9	21.1	26.8	15.2	19.6	29.9	0.80	0.84	0.79	0.77	280	Sachs and Naljaeva, 1966, Table 4	
<i>P. ischermyschewi</i>	B				22.6	24.8					23.7		0.91			269	Sachs and Naljaeva, 1966, pl. 4, f. 2	
<i>P. ischermyschewi</i>	C		156.1	71.9	25.3	28.3	20.0	22.8	14.7	15.8	26.7	0.80	0.81	0.88	0.93	269	Mitta et al., 2015, fig. 8.1	
<i>P. bodylenskii</i>	B	Holotype	108.53	72.2	20.6	22.2	17.2	17.8	13.1	14.2	21.4	0.82	0.80	0.97	0.92	337	Sachs and Naljaeva, 1966, pl. 3, f. 2	
(?) <i>P. bodylenskii</i> <sup>6</sup>	B		132.0	76.9	26.8	27.8	20.9	22.3	15.6	16.0	27.3	0.79	0.80	0.94	0.98	281	Sachs and Naljaeva, 1966, pl. 5, f. 1	
<i>P. subrediviva</i>	D	Holotype	98	55.9	16.3	16.2	13.3	13.4	9.3	8.9	16.2	0.82	0.83	1.00	1.04	344	Blake, 1905, pl. 7, fig. 1	
<i>P. pseudoexplanata</i>	C	Holotype	140.5	81.3	22.3	24.0	18.5	19.5	12.5	14.5	23.1	0.82	0.81	0.94	0.86	352	Nikitin, 1969, pl. 14, fig. 1	
<i>P. pseudoexplanata</i>	C		136	77.5	21.0	22.1	17.7	18.1	11.5	13.2	21.5	0.83	0.82	0.98	0.87	360	Nikitin, 1969, pl. 14, fig. 2	
"C". <i>eichwaldi</i>	C	Holotype	139	99.4	22.4	22.6	19.5	20.0	14.1	16.3	22.5	0.88	0.88	0.98	0.87	441	Nikitin, 1969, pl. 18, fig. 2	
"C". <i>eichwaldi</i>	C		108.5	76.9	18.2	18.9	15.7	16.5	10.8	13.1	18.5	0.87	0.87	0.95	0.83	415	Nikitin, 1969, pl. 20, fig. 1	
"C". <i>eichwaldi</i>	C		99	58.3	16.4	16.2	14.0	14.6	9.8	11.1	16.3	0.88	0.90	0.96	0.88	358	Nikitin, 1969, pl. 20, fig. 2	
"C". <i>gelida</i>	E	Holotype	131.4	77.9	17.2	17.9	15.5	16.3	12.7	13.4	17.6	0.90	0.91	0.95	0.94	444	Dzyuba and de Lagausic, 2018, fig. 5i	

(<sup>1</sup>) Identified in the original publication as *P. bodylenskii*; (<sup>2</sup>) identified in the original publication as *P. subrediviva*; (<sup>3</sup>) marked as belonging to the "belemnite horizon," but does not correspond to the latter by the state of preservation; (<sup>4</sup>) identified in the original publication as *Cylindroteuthis spathi*; (<sup>5</sup>) identified in the original publication as *P. optima*; (<sup>6</sup>) identified in the original publication as *P. ischermyschewi*. Only measurements of the rostra with  $D \geq 12$  mm are provided (except for specimen GGM BP-09679). Measurements and corresponding ratios of low precision are in italics. Measurements of holotypes and lectotypes are in bold. Explanations: BL—belemnite level; MM—measuring methods (A—from specimens; B—from author's photographs; C—from published photographs; D—from published drawings; E—major measurements are indicated by the authors, while  $\Pi^{0.5}$ ,  $dV^{0.5}$ ,  $\Pi^{0.75}$ , and  $dV^{0.75}$  are obtained from published photographs); P.—*Pachyteuthis*, C.—*Cylindroteuthis*. Indication like "↓(1)100" means "100 cm below (above) the belemnite level."



**Fig. 3.** Variability of *Pachyteuthis* spp. from the Sokur Quarry by three major ratios (LL/DV, E,  $dv^{0.5}/DV$ ) from bottom to top of the section and correlation with type and topotypical specimens. Type specimens (holotypes and lectotypes) are in bold. Specimens with low-precision measurements are not shown. All type and topotypical specimens, except for the holotype of *P. subrediviva*, are characterized by  $D > 19$  mm. Explanations of the lithological log are in Fig. 1.

on the basis of the ratio  $dv^{0.5}/DV$ : in *P. bodylevskii* sensu Dzyuba in Mitta et al., 2014b from Sokur, it is 0.83–0.86; in topotypes of *P. optima*, 0.84–0.85; and in the holotype of *P. bodylevskii*, only 0.80. In other words, the latter has a more prominent conical shape with more attenuated posterior end; such conical rostra were not found by me below the “belemnite horizon.”

The topotypical material from the Izhma River in the Pechora Basin (= *Pachyteuthis optima* s. str.; see Sachs and Nalnjaeva, 1966, pl. 3) in all cases demonstrates a weak lateral compression, and this character is specially marked as a characteristic feature in the original description. These specimens are similar to conical specimens from the lower part of the Sokur section previously described (Dzyuba in Mitta et al., 2014b) as *P. bodylevskii* (Fig. 3), whereas other Sokur specimens of *P. optima*, especially from the upper part of the section, are represented by dorso-ventrally compressed specimens ( $LL/DV = 1.01–1.06$ ; Plate I, figs. 4, 5; Mitta et al., 2014b, figs. 8.2, 8.4). Nevertheless, all these specimens are currently included by me within the variability range of *P. optima* (= *P. optima* s. lat.). The further subdivision of *P. optima* into chronosubspecies/species is not possible on the basis of material available to me at the moment: it requires the study of ontogeny, variability, and evolutionary trends of topotypical samples from the Izhma River, rather than of the Sokur material.

The synonymy of *Pachyteuthis optima* s. lat. in this paper also includes a specimen of “*P. bodylevskii*” from Kong Karls Land (Spitsbergen) figured by Doyle (Doyle and Kelly, 1988, pl. 5, figs. 15–17) with  $LL/DV = 0.94$ . It does not show the conical shape observed in the *P. bodylevskii* holotype ( $d^{0.5}/D = 0.83$  and  $dv^{0.5}/DV = 0.85$  in Doyle’s specimen vs. 0.82 and 0.80 in the holotype) and more resembles an intermediate form between *P. optima* s. str. and *P. tschernyschewi* (Krimholz, 1929). This occurrence is from the interval undoubtedly below strata with *Arcticoceras harlandi* [= *A. excentricum* sensu Gulyaev (in press)] and is associated with *Lenobelus* cf. *villigaensis* (Sachs, 1961) dominant in the assemblage along with the large-sized *Paramegateuthis nalnyaevae* Doyle in Doyle et Kelly, 1988, according to which the containing deposits were provisionally dated as late Aalenian–Bajocian (Doyle and Kelly, 1988). A rostrum of the same appearance from the Sokur Quarry, characterized by  $LL/DV = 0.95$ , is figured in Plate I, fig. 6; it is also very similar to the lectotype of *P. tschernyschewi* (Krimholz, 1929, pl. 44, figs. 1–3) in all characters except for the compression ratio.

On the contrary, among specimens of “*P. optima*” figured by P. Doyle (Doyle and Kelly, 1988) only one (Doyle and Kelly, 1988, pl. 6, figs. 3–5) can be assigned to this species. If one accepts that all specimens identified and figured as *P. optima* (Doyle and Kelly, 1988, pl. 6, figs. 1–8) come from one layer and belong to the same assemblage, this assemblage is more likely to be of early Callovian rather than Bathonian appearance.

The specimen figured by O.S. Dzyuba from the core of the Melimovskaya Well in Western Siberia as *P. cf. optima* (Dzyuba, 2000, 2004) comes from the Vasugan Formation and, hence, has a younger (upper Bathonian–Callovian) age (cf. Shurygin et al., 2000). This almost completely excludes the possibility of its placement within the early Bathonian species *P. tschernyschewi*, which it resembles in the compression ratio ( $LL/DV = 0.93$ ). This also can mean that the variability range of the compression in the Callovian “*P. optima*” is larger than in the early Bathonian members of the species. This question, as well as the validity of treatment of both early Bathonian and Callovian specimens as the same species, requires further study.

It is likely that gypsified rostra previously described from the “lower Bathonian” of the vicinity of Saratov as “*Megateuthis* sp. indet.” by Ivanova (1959) should be reidentified as *P. optima* s. lat. Their placement within the genus *Megateuthis* Bayle, 1878 disagrees with the record of a ventral groove near the apex in one of the specimens (Ivanova, 1959). In addition, the lateral compression ratio  $LL/DV$ , equaling 1.00 and decreasing posteriorly to 0.90 (Ivanova, 1959, p. 366), agrees well with that of *P. optima* s. lat. specimens from the Sokur Quarry.

The existing data suggest the possibility of evolutionary divergence of *P. optima* s. lat. from the lower part of the Sokur section (interval 120–200 cm below the “belemnite level”) into forms identified from the overlying strata (level 15 cm below the “belemnite level” and above) as *P. optima* and *P. bodylevskii* (sensu present study, non Dzyuba in Mitta et al., 2014b) (Fig. 3). This scenario appears possible, especially considering the occurrences in the lower part of the section of *P. optima* s. lat. specimens with either a pronounced subconical shape (Mitta et al., 2014b, figs. 7.3, 7.10) or strong compression in the apical zone (Plate I, fig. 3), similar in one of these characters to the typical *P. bodylevskii*.

**Material.** 17 young and adult specimens from the Sokur Quarry (interval 160–0 cm below the “belemnite level”): 12 from the section and 5 from talus;

**Plate I.** *Pachyteuthis optima* Sachs et Nalnjaeva, 1966, s. lat. from the lower Bathonian of the Sokur Quarry. Here and in Plate II all sizes (except where specifically mentioned) are natural. A dot (●) marks the approximate position of the beginning of the alveolus. In all cases: (a) ventral view; (b) left-side view; (c) alveolar view; (d) longitudinal polished section. (1) Specimen VSGM BP-11446, 120 cm below the “belemnite level”; (2) specimen VSGM SOK/09, 15 cm below the “belemnite level”; (3) specimen VSGM SOK/04, 120 cm below the “belemnite level”; (4) specimen VSGM SOK/31, with healed lifetime predatory bites; (5) specimen VSGM SOK/67, “belemnite level”; (6) specimen VSGM SOK/17, from talus.



>50 juvenile rostra, some of which may belong to other species of the genus.

*Pachyteuthis bodylevskii* Sachs et Nalnjaeva, 1966

Plate II, figs. 1–3; Fig. 4

*Pachyteuthis (Pachyteuthis) bodylevskii*: (pars) Sachs and Nalnjaeva, 1966, pp. 28–30, pl. III, figs. 2, [non fig. 3, Fig. 5; = *Pachyteuthis* sp., sp. nov.?]; (non) Doyle in Doyle and Kelly, 1988, pp. 29–30, pl. 5, figs. 15–17 [= *P. optima* s. lat.].

*Pachyteuthis bodylevskii*: (non) Dzyuba in Mitta et al., 2012, pl. 3, fig. 4 [= *P. optima* s. lat.]; (non) Dzyuba in Mitta et al., 2014b, figs. 7.1, 7.2, 7.3, 7.10 [= *P. optima* s. lat.].

*Pachyteuthis (Pachyteuthis) tschernyschewi*: (?pars) Sachs and Nalnjaeva, 1966, pl. V, fig. 1 (= Nalnjaeva, 1989, pl., fig. 5) [only this specimen].

*Pachyteuthis subrediviva*: (pars) Barskov in Mitta et al., 2004, pp. 24, 26 [only unfigured specimen CR-2797/VSGM BP-09679].

**Description.** See (Sachs and Nalnjaeva, 1966, pp. 28–30).

**Dimensions and ratios.** See Table 1.

**Comparison.** This species differs from *P. optima* s. lat. in its more pronounced conical shape of the rostrum, which is especially noticeable in the profile ( $dv^{0.5}/DV = 0.79–0.81$  vs.  $0.83–0.90$  in *P. optima* s. lat.). From *P. tschernyschewi* (Krimholz, 1929), which it resembles by the compression of the rostrum, *P. bodylevskii* can be distinguished by the subconical shape of the rostrum at the early stages and the generally more conical shape. A comparison with geochronologically younger species is provided by Sachs and Nalnjaeva (1966, pp. 29–30).

**Occurrence and age.** Lower Bathonian; Volga Region (“belemnite level,” Sokur Quarry, O. besnosovi (upper part of the O. besnosovi Biohorizon)/A. ishmae (upper part of the A. excentricum Biohorizon) ammonite Zone), basin of the Pechora River, Franz Josef Land. The assignment of several finds from stratigraphically higher horizons to *P. bodylevskii* is questionable (see below).

**Remarks.** The name *P. bodylevskii* was employed by various authors to identify rostra of a broad range of shapes. The holotype is a medium-sized specimen ( $D = 21.4$  mm), with a very prominent conical shape ( $d^{0.5}/D = 0.82$  and  $dv^{0.5}/DV = 0.80$ ); it was found on Franz Josef Land and almost certainly (Dibner and Shulgina, 1960, pp. 72–73) originates from the lower Bathonian Ishmae Zone, whereas other members of the type species (Sachs and Nalnjaeva, 1966, pl. 3, fig. 3, Fig. 5 and specimens CSGM 84-163 and 84-165) come from certainly higher stratigraphic horizons (middle–upper Callovian). Although the paratypes include very similarly shaped rostra (specimen

CSGM 84-165 from the Anabar River), they can be distinguished from the Bathonian holotype by the clearly convex lateral sides. It is likely that all Callovian occurrences should be described as a separate species.

Specimens previously figured as *P. bodylevskii* from the Sokur Quarry (Mitta et al., 2012, 2014b) and coming from the level of 110–120 cm below the “belemnite level” are included in the synonym list of *P. optima* s. lat. (see above). *P. bodylevskii* sensu Dzyuba in Mitta et al., 2014b are considerably less compressed than the holotype ( $LL/DV = 0.99–0.95$  vs.  $0.93$  in the holotype of *P. bodylevskii*) and show a clearly subconical to subcylindrical, not conical, rostrum shape with a clearly defined apical part. The most pronounced compression is observed in the specimen CSGM 256/10 (Mitta et al., 2014b, fig. 7.10), whereas specimen CSGM 256/3 (Mitta et al., 2014b, fig. 7.3) has the most prominently conical rostrum, but neither of them fit all the characters of the *P. bodylevskii* holotype.

Nevertheless, true *P. bodylevskii*, similar to the holotype, are present in the Sokur Quarry. I found several rostra directly in the “belemnite level,” and unfigured specimens of “*P. bodylevskii*” from the same level were mentioned by Dzyuba (Mitta et al., 2014b, fig. 4). The rostra at my disposal in all major characters and ratios are confidently compatible with the holotype of *P. bodylevskii*, differing only in the lateral sides slightly dorsally inclined near the alveolus, whereas in the holotype the flattened lateral sides are subparallel to each other. The polished cross section of a large specimen (Fig. 4) clearly showed that the shape of the cross section observed in the holotype is acquired by rostra at a late stage of ontogeny. *P. bodylevskii* can also be present below the “belemnite level”: some juvenile rostra identified as *Pachyteuthis* sp. juv. from levels 120 and 60 cm below the “belemnite level” are characterized by strong compression ( $LL/DV = 0.94–0.95$ ). However, as noted above, the variability and ontogeny of *P. optima* are insufficiently studied, as well as the aberrations of the earlier ontogenetic stages.

Juvenile specimens of *P. bodylevskii* (Plate II, fig. 3) from the “belemnite level” are very similar to *P. optima* from a lower interval, including the compression ratio, and are recognized only by the characteristic cross section and noticeably attenuated apical part, whereas the general shape of the rostrum differs from adult specimens in the cylindrical shape.

Despite the “intermediate” position of *P. bodylevskii* between *P. optima* and *P. tschernyschewi*, according to the compression ratio  $LL/DV$  (Fig. 3), *P. bodylevskii* can hardly be considered as a connecting link

**Plate II.** *Pachyteuthis* spp. from lower Bathonian of the Sokur Quarry. (1–3) *Pachyteuthis bodylevskii* Sachs et Nalnjaeva, 1966: (1) specimen VSGM SOK/71; (2) specimen VSGM SOK/69 (2c—cross section of the posterior end of the specimen fragment); (3) specimen VSGM BP-09679 (CR-2797 in Mitta et al., 2004), juvenile rostrum; all—“belemnite level”; (4, 5) *Pachyteuthis mitatai* sp. nov.: (4) holotype VSGM SOK/39, 60 cm below the “belemnite level” (4d—cross section behind the protoconch); (5) paratype VSGM SOK/90, (?) “belemnite level”; (6, 7) *Pachyteuthis tschernyschewi* (Krimholz, 1929): (6) specimen VSGM SOK/87; (7) specimen VSGM BP-10405 (CR-2887 in Mitta et al., 2011, pl. 1, figs. 4); both specimens from talus.



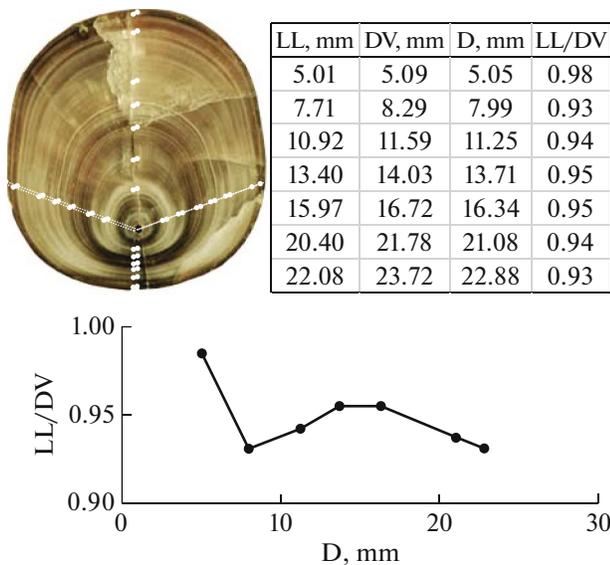


Fig. 4. Ontogeny of *P. bodylevskii* in the cross section near protoconch (specimen VSGM SOK/109; Sokur Quarry, collected loose).

between them, although at first glance the data on the stratigraphic distribution of these species in the Sokur Quarry (this study) and on the Izhma River (Mitta et al., 2015, fig. 3) suggest exactly such a scenario. The young rostra of the geochronologically later species *P. tschernyschewi* are prominently cylindrical in shape (Sachs and Nalnjaeva, 1966, text-fig. 3), poorly compatible with the rostrum shape of *P. bodylevskii* at all growth stages (Plate II, fig. 2d), but almost identical in shape to *P. optima* at similar growth stages (Plate I, fig. 6d). In addition, it has repeatedly been noted that the rostra of *P. tschernyschewi* acquire pronounced lateral compression only at later growth stages (Krimholz, 1929, p. 110, pl. 45, fig. 7), whereas a high compression ratio DV/LL in *P. bodylevskii* is acquired early in ontogeny and is maintained throughout growth (Fig. 4). This agrees with the existing concept that both species (*P. bodylevskii* and *P. tschernyschewi*) directly evolved from *P. optima* (Sachs and Nalnjaeva, 1966; Dzyuba, 2004).

Despite an opinion that *P. bodylevskii* is absent from the lower Bathonian sections of the Izhma River (Pechora Basin; Mitta et al., 2015), large specimens which could belong to this species have been figured from there (Sachs and Nalnjaeva, 1966, pl. V, fig. 1), and in some publications, this species is also mentioned in faunal lists (Kravets et al., 1976, p. 14; Repin, 2005, p. 22; Repin et al., 2006, p. 6—as *Cylindroteuthis* (*C.*) *bodylevskii*).

**M a t e r i a l.** 6 young and adult specimens from the Sokur Quarry: 5 from the section (“belemnite level”) and 1 from talus; several juvenile rostra.

### *Pachyteuthis tschernyschewi* (Krimholz, 1929)

Plate II, figs. 6, 7

*Cylindroteuthis Tschernyschewi*: Krimholz, 1929, pp. 110–111 (1028–1029), pl. 44, figs. 1–3 [= lectotype, designated by Sachs and Nalnjaeva (1966) but cited as “holotype”]; pl. 45, fig. 7; Ognev, 1933, pp. 219, pl. I, figs. 1–12.

*Pachyteuthis (Pachyteuthis) tschernyschewi*: (pars) Gustomesov, 1964, p. 170–172, pl. 15, figs. 1–5 [partly may belong to *P. optima*]; (pars?) Sachs and Nalnjaeva, 1966, pp. 23–25, text-fig. 3; pl. III, fig. 1; pl. IV, fig. 1; pl. V, fig. 2 [?non pl. V, fig. 1 (= Nalnjaeva, 1989, pl., figs. 5) = *P. bodylevskii* (?)]; Meledina et al., 1998, pl., fig. 3 (= Repin et al., 2006, pp. 131, pl. 54, fig. 1a).

*Pachyteuthis tschernyschewi*: Mitta et al., 2014a, text-fig. 1; Dzyuba in Mitta et al., 2015, fig. 8.1.

*Pachyteuthis tschernyschovi* [sic!]: (non) Gerasimov et al., 1996, pl. 28, figs. 1, 2 [= *Cylindroteuthis* aff. *pusoziana* (d’Orbigny, 1842)].

*Cylindroteuthis subrediviva*: Spath, 1932, pp. 99–100, pl. 12, fig. 3; (?) pl. 21, figs. 2, 3.

*Megateuthis* sp. indet.: (?) Ivanova, 1959, pp. 366–367, pl. 16, fig. 2 [can also belong to *P. optima* s. lat.].

*Pachyteuthis optima*: Barskov in Mitta et al., 2011, pl. I, fig. 4.

**Description.** See (Sachs and Nalnjaeva, 1966, pp. 23–25).

**Dimensions and ratios.** See Table 1.

**Comparison.** See (Sachs and Nalnjaeva, 1966, pp. 23, 25). The similarity of the major proportions of the lectotype of *P. tschernyschewi* (LL/DV = 0.92, E = 320%,  $d^{0.5}/D = 0.82$ ) and holotype of *P. optima* (LL/DV = 0.97 [0.94 after Sachs and Nalnjaeva (1966)], E = 306%,  $d^{0.5}/D = 0.83$ ) complicates differentiation of the considered pair of species; Gustomesov (1990) could not distinguish between them. Judging from the range of the LL/DV parameter in the topotypical sets of both species (Fig. 3) measured by the author and also cited by Sachs and Nalnjaeva (1966), it would be reasonable to accept the delineation on the compromise value of LL/DV = 0.94, below which is the variability range of *P. tschernyschewi*, and above which is the variability range of *P. optima*. However, because the characteristic lateral compression of *P. tschernyschewi* rostra develops only later in ontogeny (Krimholz, 1929, pl. 45, fig. 7), the problem of separation of young specimens remains.

**Occurrence and age.** Lower Bathonian, Arcticoceras ishmae Zone and Subzone; Volga Region (Sokur Quarry), basin of the Pechora River, northern Siberia, Franz Josef Land, western Canada, Greenland.

**Remarks.** Just two specimens belonging to this species were found in the Sokur Quarry, and both are not precisely localized within the section. The largest and more characteristic specimen (Plate II, fig. 7), almost identical in size and ratios to the lectotype, was found by amateur paleontologist V.A. Grigoriev in 2010 and later figured by Mitta et al. as *Pachyteuthis optima* (Mitta et al., 2011, pl. I, fig. 4). As Mitta et al. illustrated this rostrum only from its ventral and anterior sides, the similarity to the typical *P. tschernyschewi* remained unnoticed by the subsequent authors. The second specimen (Plate II, fig. 6) was found by the

present author in 2013 and is represented by a medium-sized ( $D = 13.8$  mm) rostrum with a very strong compression along the entire length ( $LL/DV = 0.88$ ,  $dV^{0.75}/ll^{0.75} = 0.82$ ). If one considers the increasing compression in the lineage *P. optima*–*P. tschernyschewi*, this second find should correspond to a geochronologically later morphotype of *P. tschernyschewi*, in which a strong compression develops at comparatively early ontogenetic stages.

Various authors figured and recorded relatively different forms from the topotypical region as *P. tschernyschewi*. For example, Sachs and Nalnjaeva (1966, pl. 5, fig. 1) figured a sharply conical rostrum with  $LL/DV = 0.96$ , possibly representing the terminal stage of *P. bodylevskii* (see above), and a similar rostrum is present in the type series of *P. tschernyschewi* (specimen CCRGM no. 8/2807). On the other hand Gustomesov (1990, p. 68) did not distinguish this species from *P. optima*, and measurements of *P. tschernyschewi* in his early work (Gustomesov, 1964, p. 171), judging from  $LL/DV = 0.94$ – $0.96$ , more likely characterize *P. optima* than typical *P. tschernyschewi*. Considering the morphological similarity, close phylogenetic relations between the species *P. tschernyschewi* and *P. optima*, and the fact that a strong compression characterizing *P. tschernyschewi* is manifested only at the latest ontogenetic stages, it appears likely that some specimens identified from the Sokur Quarry as *P. optima* s. lat. in fact may belong to *P. tschernyschewi* that did not reach the terminal growth stage. In turn, topotypical samples from sections on the Izhma River evidently contain not only specimens of both species but also intermediate forms between them. Therefore, the belemnites that are identified in the literature as *P. tschernyschewi* but which are not figured in the lateral view, or their  $LL/DV$  ratio is not provided (cf. Meledina et al., 1998, pl., fig. 3; Mitta et al., 2014a, text-fig. 1), strictly speaking, cannot be identified without examining the actual specimens.

**Material.** 1 specimen from the Sokur Quarry (collected loose).

*Pachyteuthis mittai* sp. nov.

Plate II, figs. 4, 5

**Etymology.** In honor of Dr. Vasily Mitta (Paleontological Institute of the Russian Academy of Sciences), who was in charge of the preparation of all major reviews of the fossil assemblages from the type locality (Mitta and Seltzer, 2002; Mitta et al., 2004, 2011, 2012, 2014b).

**Holotype:** VSGM SOK/39; Sokur Quarry, 60 cm below the “belemnite level”; paratype VSGM SOK/90, Sokur Quarry, collected loose (judging from the state of preservation, certainly from the “belemnite level”); both from the lower Bathonian, O. besnosovi ammonite Zone and Biohorizon/A. excentricum ammonite Biohorizon.

**Diagnosis.** Consistently cylindrical *Pachyteuthis*, moderately elongated ( $E = 386\%$  in holotype,  $463\%$  in a young specimen), with rounded cross-section ( $LL/DV = 0.96$ – $1.01$  along entire length in adult rostra) with no pronounced flattenings along the lateral sides, with convex ventral side. Tapering coefficient  $d^{0.5}/D = 0.92$ – $0.93$ . Apical groove weakly developed; ventral side flattened only in posterior third of rostrum. Apical part relatively short; its length about  $1/3$ – $2/5$  of that of postalveolar region.

**Description.** The rostrum is large, moderately elongated to elongated, cylindrical both in profile and in outline. All four margins (lateral, dorsal, and ventral) are straight. The profile is symmetrical; the apex is central. The length of the apical region is  $2/5$  of the postalveolar portion of the rostrum in the holotype and  $1/2$  in the paratype. The transition to the apical region is rapid but smooth, with no pronounced angular bends.

The rostrum cross section is rounded, just slightly compressed laterally, almost consistent along the entire length of the rostrum; a pronounced lateral compression appears only immediately near the apex. The lateral flattenings are noticeable only in the apical region of the rostrum and near it, and ventral flattening is observed only in the apical region.

The apical ventral groove is short and shallow and does not extend beyond the apicalmost zone of the rostrum.

The alveolus occupies approximately  $1/3$  of the rostrum length, is slightly laterally compressed, and has a ventrally displaced tip ( $R_v/DV = 0.26$  in the holotype).

**Dimensions.** See Table 1. The paratype surface is somewhat less well preserved compared to the holotype, so its calculated ratios can be slightly distorted.

**Comparison.** This species is distinguished from the co-occurring *P. optima* s. lat. in the absence of the elongated flattened regions on the lateral and ventral sides of clearly pronounced cylindrical ( $d^{0.5}/D = 0.92$ – $0.93$ ) rather than subconical ( $d^{0.5}/D = 0.82$ – $0.87$  in *P. optima* s. lat.) shape of the rostrum at a comparable size and in the absence of a pronounced lateral compression in the apical part of the rostrum. Two more species described from the lower Callovian of Central Ukraine—“*Cylindroteuthis*” *eichwaldi* I. Nikitin, 1969 and *P. pseudoexplanata* I. Nikitin, 1969—closely resemble the species under discussion. *P. mittai* sp. nov. is distinguished from “*Cylindroteuthis*” *eichwaldi* by the shorter apical region and from *P. pseudoexplanata* by the slightly more elongated rostrum (Table 1). The most reliable difference with the two above-mentioned species is a higher tapering coefficient of *P. mittai* sp. nov. ( $d^{0.5}/D = 0.92$ – $0.93$  vs.  $0.88$  and less in “*C.*” *eichwaldi* and *P. pseudoexplanata*) and especially a rounded cross section in the apical part, almost not compressed laterally ( $ll^{0.75}/dV^{0.75} =$

0.96–0.98 in *P. mittai* sp. nov. vs. 0.83–0.88 and less in “*C. eichwaldi* and *P. pseudoexplanata*).

**Occurrence.** Lower Bathonian of the Volga Region; Oranicerias besnosovi ammonite Zone and Biohorizon/Arcticoceras ishmae ammonite Zone, A. excentricum Biohorizon; (?) basin of the Pechora River, Arcticoceras ishmae ammonite Zone.

**Remarks.** O.P. Dzyuba (pers. comm., 2017) noted that a sample set she studied from the basin of the Pechora River (Mitta et al., 2015) contained rostra morphologically similar to *P. mittai* sp. nov. that she considered within the intraspecific variability range of *P. optima*.

A rostrum of a young specimen figured by Mitta et al. (2011, pl. I, fig. 3), at first glance, has a shape characteristic of *P. mittai* sp. nov. However, it shows strong flattening on the lateral sides and should apparently be classified as *P. optima* s. lat. or *P. bodylevskii*.

The described species has atypical morphology for the genus *Pachyteuthis*: considerable elongation and definitely cylindrical shape of the rostrum with a convex ventral side. In the shape of the cross section, it is comparable with the representatives of the genus *Cylindroteuthis*, rather than *Pachyteuthis*, although a considerable ventral shift of the axial line suggests a close affinity to *Pachyteuthis* or *Lagonibelus*. In its elongation, *P. mittai* sp. nov. is similar to representatives of the genus *Lagonibelus*, but it does not have a characteristic flattened region on the ventral side, which is characteristic of early representatives of *Lagonibelus* (see Dzyuba, 2004).

Very recently (Dzyuba and de Lagausie, 2017), a similar but slightly more elongated rostrum was described from the uppermost lower Bajocian (Cranoccephalites gracilis Zone) of northern Siberia as *Cylindroteuthis gelida* de Lagausie. This belemnite was interpreted as an archaic representative of the genus *Cylindroteuthis*, retaining characters of the ancestral genus *Pachyteuthis*. *C. gelida* has considerably more flattened lateral sides than *P. mittai* sp. nov. and a deeper groove, while the most striking difference from *P. mittai* sp. nov. is the compression near the apex ( $(l^{0.75}/d^{0.75} = 0.94$  vs.  $0.96–0.98$  in *P. mittai* sp. nov.). So far, there are not sufficient data to consider *P. gelida* and *P. mittai* sp. nov. as elements of a single phylogenetic cluster, although this seems possible. This interpretation is supported by the similarity of all major ratios, but is contradicted by the fact that, unlike *P. mittai* sp. nov., *C. gelida* has clearly flattened lateral sides, a character shared by another species of early *Cylindroteuthis* (Bajocian–Bathonian)—*C. spathi* Sachs et Nalnjaeva, 1964.

However, the newly described species could also be an independent endemic *Cylindroteuthis*-like derivative of *P. optima* s. lat., the origin of which was connected with the colonization of new ecological niches in the marine early Bathonian basin in the Russian Plate, atypical for the genus *Pachyteuthis*. If one considers this possible, the evolution of this species should have been related to fetalization of characters: in particular, to retaining the compression and tapering coefficient characteristic of juvenile rostra.

**Material.** 2 rostra from the Sokur Quarry: 1 adult and 1 young.

## ORDER BELEMNOTHEUTIDA STOLLEY, 1919

### FAMILY BELEMNOTHEUTIDIDAE VON ZITTEL, 1884

Owing to the limited own data, in the present paper, I uncritically follow the taxonomic system of the most recent revision of the family (Doyle and Shakides, 2004), although several important aspects, e.g., the synonymy of the genera *Belemniteuthis* Pearce, 1842 and *Acanthoteuthis* R. Wagner in Münster, 1839, have been the subject of much debate in the literature (see Donovan and Crane, 1992; Doyle and Shakides, 2004) and are not supported by some recent authors (e.g., Fuchs et al., 2007).

### Genus *Acanthoteuthis* R. Wagner in Münster, 1839

#### *Acanthoteuthis foliorostris* sp. nov.

Plate III, figs. 1, 2

**Etymology.** From the Latin folium (leaf) and rostrum (rostrum).

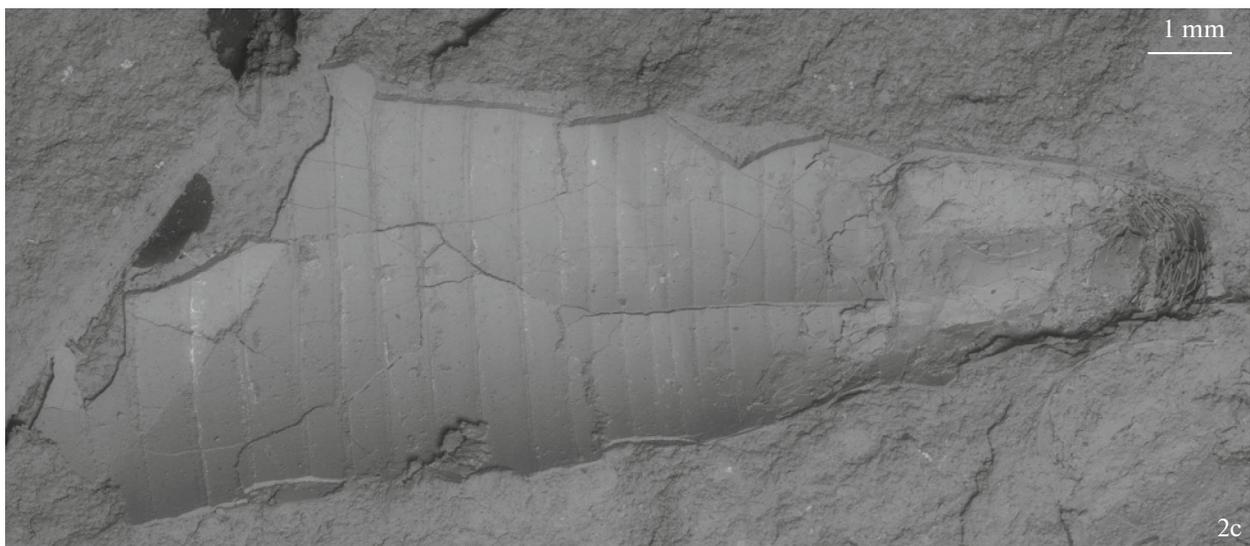
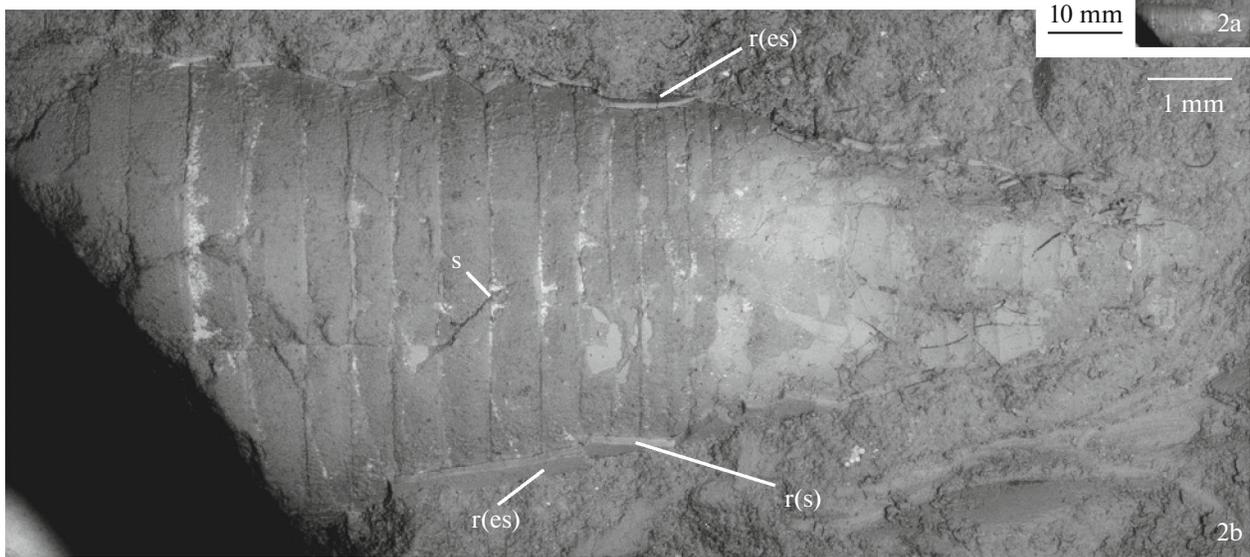
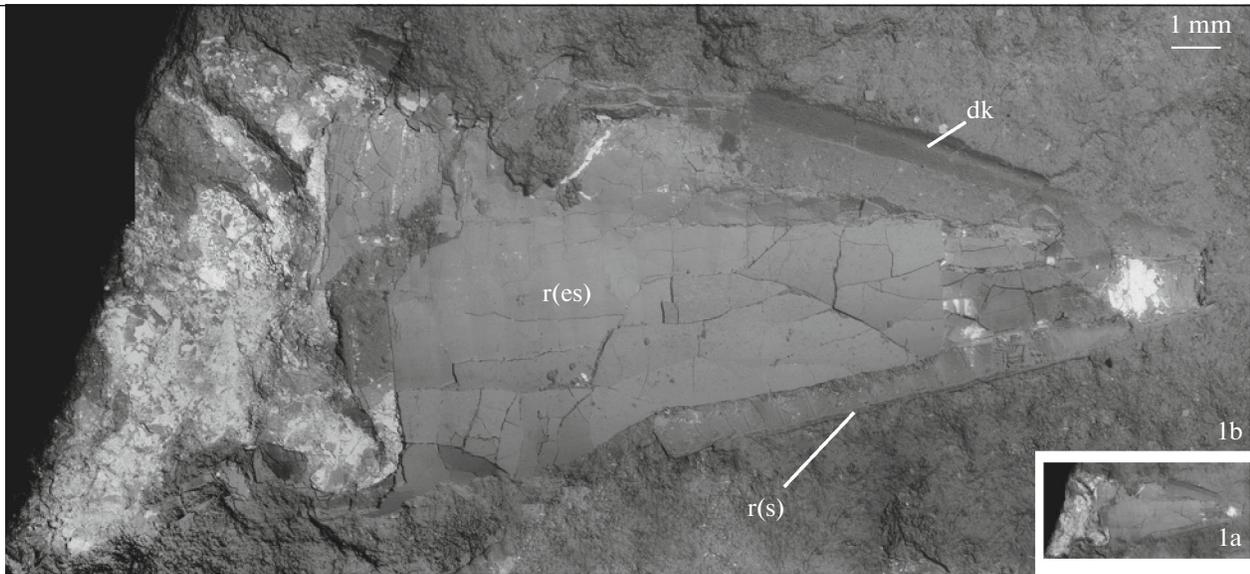
**Holotype.** VSGM ISS/22, Pletnyovka Quarry, 40 cm above the base of Bed 1, lower Bathonian, Oranicerias besnosovi ammonite Zone, O. sp. A Biohorizon (sensu Gulyaev and Ippolitov, 2017); paratype: VSGM SOK/00, Sokur Quarry, from the talus (interval below the “belemnite level”); lower Bathonian, O. besnosovi Zone and Biohorizon.

**Diagnosis.** Small representative of *Acanthoteuthis*, with very thin rostrum (thickness not exceeding 0.1 mm) and narrow and low dorsal keel.

**Description.** The rostrum has the appearance of a thin sheath surrounding the phragmocone. It has a consistent thickness which does not exceed 0.1 mm even near the posterior end. In the holotype, on the dorsal side near the posterior end of the phragmocone, there is an imprint of a thin (0.4 mm) keel with a rounded cross section. It is not clear whether this keel corresponds to one of the branches of the typical

**Plate III.** *Acanthoteuthis foliorostris* sp. nov. from the lower Bathonian of Pletnyovka and Sokur quarries. Magnification  $\times 1$  (figs. 1a, 2a),  $\times 6.1$  (fig. 1b), and  $\times 7.6$  (figs. 2b, 2c). Explanations: dk—dorsal keel, s—siphuncle; r(es)—rostrum external surface; r(s)—rostrum, section. (1) Holotype VSGM ISS/22, Pletnyovka Quarry, 40 cm above the base of Bed 1; (1a) natural size; (1b) enlarged; (2) paratype VSGM SOK/00, Sokur Quarry, interval 0–120 cm below “belemnite level”; (2a) natural size; (2b) enlarged; (2c) counterpart; all the figures are obtained with SEM.

Plate III



bipartite keel of *Acanthoteuthis* or is solitary. The rostrum surface is smooth, matt, and slightly pinkish.

The phragmocone is small; its length in the holotype taking into account the missing initial part is only 25 (?30) mm, and in the paratype, 16 mm.

The phragmocone angle in the holotype (calculated from a presumably completely flattened phragmocone) is 21°. The relative chamber length near the anterior end is 0.14 of the phragmocone diameter. The phragmocone and relative chamber length can only be measured approximately, and only on the holotype, as the paratype is partly covered by the rock matrix.

The paratype clearly shows that the septa tend to become denser over certain intervals and more widely spaced in others. The remains of a siphuncle with retrochambered septal necks are present.

**Dimensions.** See the text at the end of the description.

**Comparison.** *A. foliorostris* sp. nov. clearly differs from the undescribed lower Callovian species from the Elatmae Zone of the Russian Plate (“*Volgobelus* sp.” in Rogov and Bizikov, 2008) in its small size. It is distinguished from *A. antiqua* (Pearce, 1847) [?= *A. polonica* Makowski, 1952], a species widespread in the middle–upper Callovian with a poorly studied variability of the rostrum and which in fact may represent a wastebin taxon consisting of a number of closely related species, by the thinner rostrum and the very narrow keel on the dorsal side (even though it corresponds only to one branch of a bipartite keel). The comparison of *A. foliorostris* sp. nov., as well as of the Callovian taxa, with the geochronologically younger (Tithonian) species *A. mayri* Engeser et Reitner, 1981 and *A. leichi* Reitner, 1986 is difficult because of the lack of data on the rostra in the latter taxa.

**Occurrence.** Lower Bathonian (Oraniceras besnosovi Zone), Volga Region.

**Remarks.** Detailed interspecific comparisons are difficult because a large number of nominal species are described from samples in very different states of preservation (phragmocones, rostra, arm and ink sacs imprints, etc.; see review in Donovan and Crane, 1992). The above comparison is based on the generic composition considered by Doyle and Shakides (2004).

The described finds should certainly be classified within the genus *Acanthoteuthis* owing to the presence of a dorsal keel, which is absent in other Jurassic members of the group with a thin sheath-like rostrum (Toarcian *Chondroteuthis* Bode, 1933, Tithonian–Berriasian *Antarctiteuthis* Doyle et Shakides, 2004). A juvenile rostrum with a partly preserved phragmocone from the lower part of the Sokur section, previously identified as *Belemnoides* indet. (Mitta et al., 2004, p. 3; 2011, p. 36, 2014b, p. 102), may also belong to the described species.

Species of the genus *Acanthoteuthis* are common in the Boreal Callovian and Upper Jurassic deposits of

Europe, including European Russia (Fuchs et al., 2007; review in Rogov and Bizikov, 2008). The earliest confirmed records of the genus are represented by an undescribed species from the lower Callovian of Central Russia (see Rogov and Bizikov, 2008, pl. 1, fig. 1); in other Boreal regions, representatives of the genus are reported from slightly higher level—the lower Callovian Proplanulites koenigi Zone (Page, 1991). Phragmocones of “belemnite” have been recorded, but not described, from the middle Bathonian of Greenland (Callomon, 2004); and it is not clear whether they belong to the true Belemniteidae and more so to the genus *Acanthoteuthis*. There are also records of the presence of isolated “phragmocones” in Bathonian beds in some Siberian sections, in particular, from the Ishmae Zone (Meledina et al., 1991, p. 10), which may in fact belong to *Acanthoteuthis*.

Thus, the described species represents the earliest representative of the genus *Acanthoteuthis* known so far and is of great interest for solving the problem of the biogeographic origin of this taxon. Considering its co-occurrence with belemnites of strictly Boreal origin (*Pachyteuthis*) or the derivatives of Boreal taxa (*Barskovisella* Ippolitov, 2018), and the general association of most records with high latitudes (Rogov and Bizikov, 2008), the immigration of this taxon into the Middle Russian Sea during the early Bathonian from high latitudes appears to be the most likely hypothesis.

**Material.** 2 specimens: 1 from Pletnyovka Quarry (40 cm above the base of Bed 1), 1 from the Sokur Quarry (interval 0–120 cm below the “belemnite level”; collected by A.V. Guzhov).

#### REMARKS ON SOME PREVIOUSLY PUBLISHED IDENTIFICATIONS OF BELEMNITES FROM THE LOWER BATHONIAN OF THE RUSSIAN PLATE

Except for the studies on the Sokur Quarry repeatedly cited above (Mitta et al., 2004, 2011, 2012, 2014b) and an old paper by Ivanova (1959), occurrences of the late Bajocian and early Bathonian belemnites in the Volga Region, even when mentioned in publications, were not accompanied by illustrations, which would have enabled a more reliable analysis of the species diversity of this group.

The most extensive list of belemnites was provided in the monograph by Saltykov (2008) on the Middle Jurassic deposits in the vicinity of the town of Zhirnovsk (northern part of Volgograd region) from the Karaulnaya [≈ upper Bajocian] and Zhirnovsk [≈ lower Bathonian] formations (both of them are now considered as synonyms of the Pochinki Formation—see *Unifitsirovannaya...*, 2012). In the Karaulnaya Formation, Saltykov mentioned occurrences of the following species (the author’s orthography is preserved here and below): *Megateuthis elliptica* (Mil.)—1 specimen, *Holcobelus* aff. *tschegemensis* (Krim.)—5 speci-

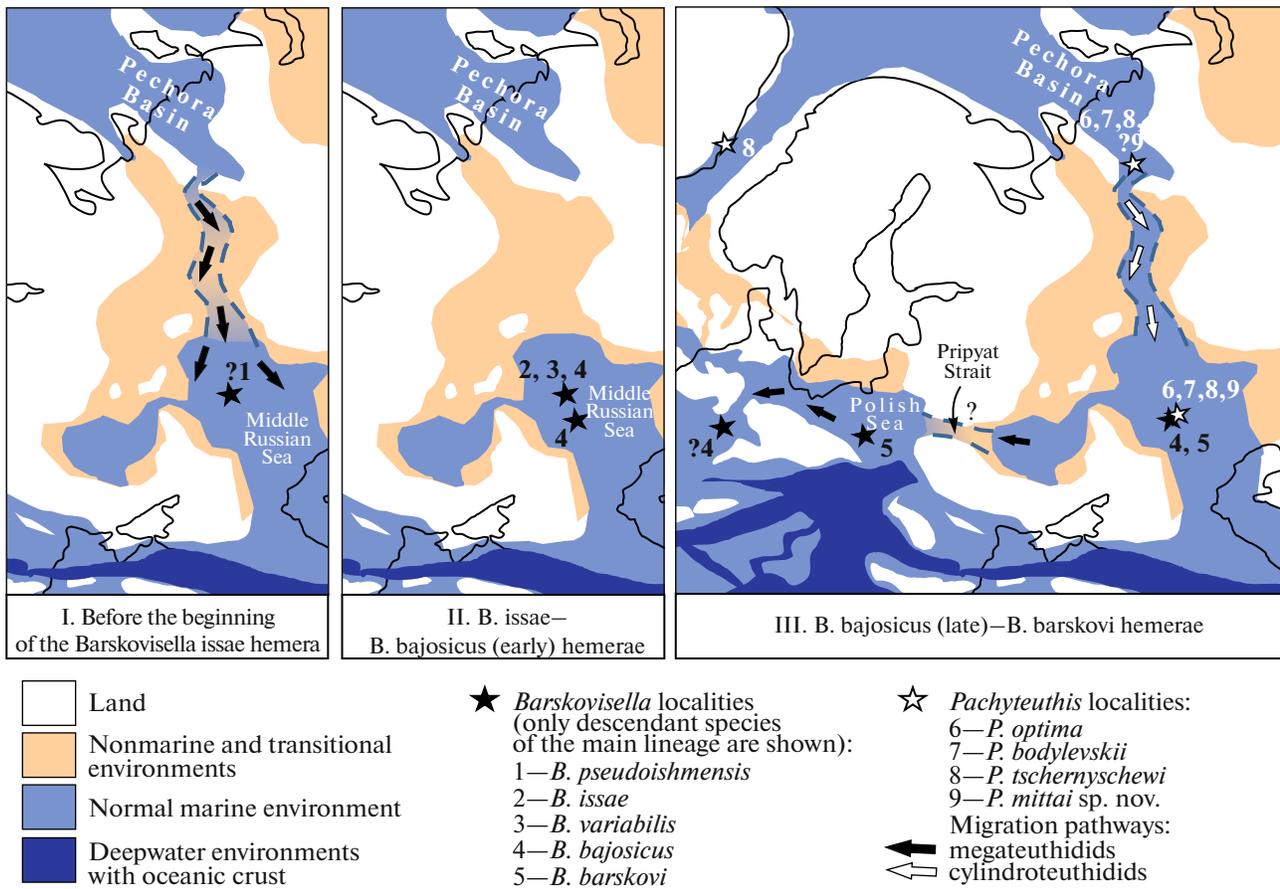


Fig. 5. Opening of the straits from the Middle Russian Sea during the early Bathonian on the basis of belemnite data and migration pathways of *Barskovisella* and *Pachyteuthis*. Paleogeographic background is combined: for the east European Platform after (Sazonova and Sazonov, 1967, simplified); for Europe and southern margins of the East European Platform after (Thierry, 2000: map for the middle Callovian).

mens, *Holcobelus* cf. *blainvillei* (Volt.)—2 specimens, *Mesoteuthis* aff. *dorsetensis* Krim.—1 specimen. From the Zhirnovsk Formation (also cited in Saltykov et al., 2008), Saltykov mentions *Megateuthis* cf. *elliptica* (Mil.)—2 specimens, *Megateuthis* cf. *linga* (Vol.)—1 specimen, *Hibolites* cf. *fusiformis* (Park.)—1 specimen, *Holcobelus tschegemensis* (Krim.)—2 specimens and *Cylindroteuthis* (*Cylindroteuthis*) cf. *spathi* Sak.—1 specimen.

All the listed belemnites originate from boreholes and are not connected to a single succession or to ammonite occurrences, and therefore their dating as “late Bajocian” or “early Bathonian” is quite conventional. The interpretation of the above identifications raises many questions, as the assemblages contain nominal species which certainly do not occur in the late Bajocian and Bathonian deposits and hence were apparently incorrectly identified (e.g., Aalenian-early Bajocian *Holcobelus* spp., “*Mesoteuthis dorsetensis*” [= late Toarcian–early Aalenian species *Salpingoteuthis dorsetensis* (Oppel, 1857) in modern classification]). Judging from the morphotypes of the

rostra from the above list and taking into account their interpretation in the Russian-language literature, it is possible to propose a number of hypotheses for their true taxonomic affinities.

The genus *Holcobelus*, common in the Aalenian–early Bajocian, is characterized by the presence of a long ventral groove. A similar groove, even though different in details, among late Bajocian taxa is observed in, e.g., representatives of the family Belemnopseidae (genera *Hibolites* de Montfort, 1808 and *Belemnopsis* Bayle, 1878), commonly occurring in the late Bajocian Garantiana Zone of the Donets Basin (Nikitin, 1975, 1981). Note that the species *H. tschegemensis* mentioned by Saltykov (Krimholz, 1931) has a readily recognizable elongated rostrum, generally similar to those described by Nikitin (1975) in *Belemnopsis nalivkini* and *B. grigorjevi*. Also note that, in the adjacent region (Donets Basin), the uppermost Bajocian (Pseudocosmoceras michalskii Zone) contains only records of Belemnopseidae—*Hibolites fusiformis* (Parkinson) and *Belemnopsis* cf. *anomala* (Phill.) (Yamnichenko, 1969). Similarly, “*Holcobelus blainvillei*” can

be reinterpreted as *Belemnopsis* ex gr. *bessinus*–*apiciconus*—a morphotype present in the Garantiana Zone of the Donets Basin (Nikitin, 1981). Another species in the list of Saltykov (2008) of the early Bathonian taxa, *Hibolites* cf. *fusiformis*, was employed in the Russian literature for a number of different Bajocian–Bathonian representatives of Belemnopseidae with a fusiform rostrum (cf. Borissjak, 1908; Krimholz, 1947; Krimholz and Repin, 1989; Nikitin, 1981). In the examined sections, representatives of the family Belemnopseidae (genera *Belemnopsis* and *Hibolites*) are absent; moreover, all the occurrences of early Bathonian belemnites are represented by the taxa of definitely (*Barskovisella*, *Pachyteuthis*) or supposedly (*Acanthoteuthis*) Boreal origin. If Belemnopseidae are indeed present in the lower Bathonian of the Volga Region, they should occur in even lower stratigraphic horizons than the studied interval (i.e., from the hypothetical ammonite *Oranicerias scythicum* and *O. mojarowskii* Biohorizons (after Gulyaev, in press), which are presently not characterized by any belemnite occurrences.

With regard to the records of *Megateuthis* spp. and *Mesoteuthis* aff. *dorsetensis* by Saltykov (2008), they are difficult to comment on. In fact, they can represent various species of the early Bathonian genus *Barskovisella* Ippolitov, 2018 or true *Megateuthis* Bayle, 1878, the presence of which is recorded in the upper Bajocian of adjacent regions—Donets Basin (Borissjak, 1908; Nikitin, 1975, 1981) and the Caucasus (Gulyaev et al., 2015)—or even *Pachyteuthis* (if the identification was based on a large size of the rostra).

Finally, a specimen identified by Saltykov (2008) as *Cylindroteuthis* (*Cylindroteuthis*) cf. *spathi* is apparently a representative of one of the species of *Pachyteuthis* described above from the Sokur Quarry.

#### THE HISTORY OF THE EARLY BATHONIAN BELEMNITE FAUNA OF THE RUSSIAN PLATE AND PALEOBIOGEOGRAPHICAL IMPLICATIONS

Previously, Mitta et al. (2014b) established the level of first invasion of the Boreal biota to the Russian Plate during the early Bathonian at the level 8 m below the Sokur Quarry bottom on the basis of the occurrence of the Boreal–Arctic foraminifer *Ammodiscus arangastachiensis* Nik. in the core of a borehole drilled directly in the Sokur Quarry. However, no co-occurring Boreal mollusks were found in this borehole core, despite cylindroteuthidids start from the quarry bottom. Considering the fact that the first appearance of Boreal ammonites was recorded only near the “belemnite level,” it was proposed that the immigration of the Boreal–Arctic mollusks (ammonites, belemnites, inoceramids) to the territory of the Russian Plate could be slower than that of the microfauna (Mitta et al., 2014b, p. 118). New finds of belemnites from the Pletnyovka Quarry allow the history of the meridional

strait opening through the East European Platform previously discussed by Seltzer (2009) and Mitta et al. (2014b), as well as the history of the immigration and spreading of early Bathonian mollusks into the Middle Russian Sea, to be reinterpreted (Fig. 5).

The present author has previously noted (Ippolitov, 2018) that the earliest records of the megateuthidid *Barskovisella* that evolved from the Arctic genus *Paramegateuthis* in the Russian Plate are two ammonite biohorizons earlier than the mass immigration of other groups of Boreal cephalopods—ammonites (*Arcticoceras*, *Greencephalites*) and belemnites of the family Cylindroteuthididae. This suggests that the connection of the Middle Russian Sea to the Boreal basins through a meridional strait (Seltzer, 2009), the precise location of which in the northern part of the platform remains unresolved, was not established simultaneously. The level of the first appearance of megateuthidids apparently corresponds to the appearance of the Boreal–Arctic foraminifers *Ammodiscus arangastachiensis* found in the Sokur borehole at a depth of 8 m (Mitta et al., 2014b) and the entry of ostracodes *Camptocythere* (*Anabarocythere*) *arangastachiensis* slightly above (Shurupova and Tesakova, 2017), thus marking the episode of the earliest confident opening of the strait.<sup>1</sup> Judging from the penetration to the Volga Region in this phase of only a few taxa from the Arctic, the strait in places was very narrow and extremely shallow, and this created a bathymetric barrier for large-sized Cylindroteuthididae and

<sup>1</sup> There is also some published evidence of earlier, pre-early Bathonian, episodes of a Jurassic meridional strait through the Russian Plate. In particular, such a conclusion was suggested on the basis of the repeated appearance of presumably Boreal ostracode genus *Camptocythere* in the lower part of the section of the Sokur borehole (Shurupova et al., 2016), corresponding to the upper Bajocian (Michalskii ammonite Zone). In a later paper by the same authors (Shurupova and Tesakova, 2017), these occurrences were reinterpreted as related to western European rather than Arctic taxa; hence, the former conclusion of a multiphase strait opening from the Pechora Basin in the late Bajocian is no longer relevant. It has also been suggested that the strait could have opened even earlier, at the early–late Bajocian boundary (Dzyuba and de Lagausie, 2018). This conclusion was initially based on the finds of the species *Paramegateuthis subishmensis* Stoyanova-Vergilova, 1983, originally described from Bulgaria (Humphreisianum Zone), in northern Siberia. This interesting hypothesis is currently not supported by direct geological data. Firstly, on the Russian Plate, marine deposits of early–late Bajocian boundary strata are only known from the territory of the Dnieper–Donets Folded Structure and adjacent southeastern part of the Dnieper–Donets Basin, and no Boreal forms have ever been recorded in these strata (see fossil lists in Yamnichenko, 1969). Secondly, the hypothesis of the co-occurrence of Boreal cylindroteuthidids and the Aalenian–early Bajocian Tethyan genus *Holcobelus* Stolley, 1927 in the northwestern part of the Dnieper–Donets Basin (Dzyuba and de Lagausie, 2018) results from an erroneous identification by Nikitin (1969, 1977) of leached rostra of early Callovian cylindroteuthidids as representatives of *Holcobelus* (Ippolitov, unpublished data). Accordingly, the idea that the lower Callovian (Nikitin, 1989) beds containing this assemblage could be redated to the early Bajocian on the basis of the presence of *Holcobelus* cannot be supported.

ammonites. Except for taxa close to the root of the *Barskovisella* lineage (*B. pseudoishmensis* Ippolito, 2018) and directly comparable with some Siberian species of *Paramegateuthis*, species comparable with the subsequent members of this lineage are recorded neither from northern Siberia nor from the Pechora Basin. And by the beginning of the Ishmae phase, the composition of megateuthidid assemblages in sections of the Pechora Basin (see Mitta et al., 2015) has a completely different appearance both at species and genus levels compared to the Russian Plate (Ippolito, 2018). This suggests a complete isolation of faunas during the *Oraniceras* sp. A–*O. sp. B hemerae* and suggests the closing of the marine corridor in that time interval.

The high rate of morphogenesis of megateuthidids of the genus *Barskovisella* in the early Bathonian basin of the Russian Plate is apparently explained by an intense adaptation of immigrants to the new habitats of the Middle Russian Sea. In particular, the recognized trend toward the shortening of the rostrum (Ippolito, 2018) in the main *Barskovisella* lineage (*B. issae* → *B. variabilis* → *B. bajosicus* → *B. barskovi*) can be related to a decrease in the migration distances within a small basin and general adaptation to shallower environments. For instance, according to existing concept, belemnites with shorter rostra inhabited coastal zones and were nektonic, more bottom-associated than forms with elongated rostra (Dzyuba, 2005; Gustomesov, 1961; etc). At the same time, the divergent appearance at several levels of taxa with morphologies deviating from the main trend (*B. gracilis* Ippolito, 2018; *B. renegata* Ippolito, 2018) suggests ecological radiation of *Barskovisella* and colonization of various niches in the early Bathonian basin of the Russian Plate. The development of the endemic belemnite fauna connected to the high-Boreal ancestors can be considered as the first isolated episode of formation of the Boreal-Atlantic Province on the basis of belemnites, which became fully defined later, starting from the Callovian time (Sachs and Naljaeva, 1966).

Remarkably, the part of the Sokur Quarry section lying immediately below the succession and exposed by the quarry in the 2000s was assigned to the upper Bajocian on the basis of a single ammonite find made in the late 1980s and identified as “*Medvediceras masarowici*” (Mitta and Seltzer, 2002; Mitta et al., 2004; in the later papers as “*Pseudocosmoceras masarowici*”: Mitta, 2009; Mitta et al., 2011, 2014b). In turn, the earliest occurrences of Boreal-Arctic foraminifers and ostracodes (in the Sokur Borehole) come from below that level, and this resulted in an idea, widely cited in recent papers, that the meridional strait opened in the late Bajocian time (Dzyuba and de Lagausie, 2018; Mitta et al., 2014b). However, this ammonite occurrence was recently reidentified by D.B. Gulyaev as belonging to genus *Oraniceras* (Gulyaev, in press); hence, the upper part of the section of the Sokur Borehole should be dated to the early Bathonian, rather than late Bajocian. Even leaving aside the disagree-

ments about this ammonite determination, a sole occurrence of the species *M./P. masarowici* from a depth of 5 m below the “belemnite level” (≈ wellhead of the Sokur Borehole) hardly agrees with multiple occurrences of the same species from the interval 27–29 m deep in the Sokur Borehole, which would imply an abnormally large thickness for the terminal Bajocian *masarowici* Biohorizon (cf. Mitta, 2009). In addition, if one places the Bajocian/Bathonian boundary at the base of the open pit of the Sokur Quarry (cf. Mitta et al., 2014b), no space remains for the portion of the succession which corresponds to the *O. sp. A*–*O. sp. B* ammonite biohorizons (Gulyaev and Ippolito, 2017) and the correlated *Barskovisella issae*–*B. variabilis* belemnite biohorizons (Ippolito, 2018). Thus, the statement about the late Bajocian opening of a meridional strait (Dzyuba and de Lagausie, 2018; Mitta et al., 2014b) does not look entirely correct, and currently it is possible to state only the “early Bathonian” Boreal event, as was done in earlier papers (Mitta et al., 2014c; Seltzer, 2009).

A strait that opened up during the second phase marked by a mass immigration of Arctic cephalopods (*Pachyteuthis*, *Arcticoceras*, *Greenecephalites*) and bivalves (*Retroceramus*) (Mitta et al., 2014b) was wider and consistently existed over a long time. At the species level, the ammonite and cylindroteuthidid assemblages from the Volga Region are almost identical to those from the Pechora Basin, and it is quite likely that the vertical change in the species-group taxa of Cylindroteuthididae is equivalent to that of the Izhma River, suggesting a constant faunal exchange with the Boreal Ocean. Compared to the taxa found in the synchronous beds of the Pechora Basin, the Volga Region assemblage lacks only representatives of the genus *Paramegateuthis*, the penetration of which into the Middle Russian Sea was apparently prevented by a biotic factor—the presence of *Barskovisella* spp. with a similar lifestyle, which by the beginning of the Ishmae Phase had produced a number of living forms, preoccupying ecological niches otherwise suitable for *Paramegateuthis*.

A portion of the early Bathonian marine succession exposed in the Sokur Quarry pit (Member III of Mitta et al., 2014b) was interpreted, using a complex of lithological and microfaunistic characters, as corresponding to the maximum highstand of the early Bathonian sea (Mitta et al., 2014b). In this connection, it is interesting to mark the sudden appearance of two late species of the principal *Barskovisella* lineage (later morph of *B. bajosicus* (Ivanova, 1959) and *B. barskovi* Ippolito, 2018) in Switzerland and Poland. These finds may indicate the short-term opening of Pripyat Strait during the Ishmae Phase, corresponding to the maximum sea highstand on the Russian Plate. This strait directly connected the Middle Russian and Polish seas (Fig. 5) and was stabilized starting from the middle Callovian (Sazonova and Sazonov, 1967). An alternative migration route around the Ukrainian Shield via

the Caucasus and Crimea during the early Bathonian appears unlikely. As noted above, the latest taxa of the *Barskovisella* lineage were poorly adapted to long migrations, especially across deep marine environments; neither early nor later representatives of the genus have so far been recorded from the northern Tethyan margins (Crimea, Caucasus, Carpathians).

#### LOWER BATHONIAN BIOSTRATIGRAPHY OF THE VOLGA REGION USING CYLINDROTEUTHIDAE

Dzyuba (Mitta et al., 2014b) proposed two belemnite units for the series of Lower Bathonian clay available for direct observation in the Sokur Quarry in the 2000s—Beds with *Pachyteuthis optima* and *Pachyteuthis bodylevskii* (interval 0–200 cm below the “belemnite level”) and Beds with *Pachyteuthis optima* (part of the lower Bathonian succession beginning slightly above the “belemnite level”).

Below, I describe the belemnite units recognized or established on the Russian Plate for the first time and also offer emendations for the previously described units.

##### *I. Beds with Pachyteuthis optima s. lat. Dzyuba in Mitta et al., 2014b, emend.*

= Beds with *Pachyteuthis optima* and *P. bodylevskii* Dzyuba in Mitta et al., 2014b + (pars) Beds with *P. optima* Dzyuba in Mitta et al., 2014b.

**Index.** *P. optima* s. lat.

**Stratotype.** Sokur Quarry (Member III, interval 200 cm below–190 cm above the “belemnite level,” also possibly higher up in the section).

**Belemnite assemblage.** *Barskovisella bajosicus*, *B. parabella*, *B. barskovi*, *B. renegata*, *Pachyteuthis optima*, *P. bodylevskii*, *P. mittai* sp. nov., *Acanthoteuthis foliorostris* sp. nov.

**Lower boundary.** FAD of *Pachyteuthis optima* s. lat.

**Upper boundary.** FAD of *Pachyteuthis tschernyschewi* (the precise position in the Sokur Quarry has not yet been established).

**Age and correlation.** Lower Bathonian. In the Volga Region, it corresponds to the *Arcticoceras excentricum* (sensu Gulyaev, in press) ammonite Subzone (/Biohorizon) or the upper part of the *Oraniceras besnosovi* Zone (*O. besnosovi* and *O. cf./aff. besnosovi* biohorizons), and in the upper part, it corresponds to an interval lacking ammonites, but on the basis of the occurrences of the bivalve *Retroceramus cf. vagt/vagt* (Mitta et al., 2012, 2014b) correlated with the *Arcticoceras ishmaei* ammonite Subzone/Biohorizon. This upper interval contains the boundary with the overlying unit (Beds with *P. tschernyschewi*), but the precise position of this boundary remains uncertain.

**Geographic range.** Volga Region (Saratov and ?Volgograd regions), basin of the Pechora River.

**Localities.** Sokur Quarry.

**Biohorizons.** Two biohorizons can be recognized within the studied interval.

**Ia. [*P. optima* s. str.], nov. Biohorizon** is tentatively recognized in the Sokur Quarry in the interval 120–200 cm below the “belemnite level.” *Pachyteuthis bodylevskii* sensu Dzyuba in Mitta et al., 2014b is the index species; these are weakly conical rostra, distinct from the specimens from the upper part of the section by the greater compression and lower tapering coefficient (Fig. 3). In their main ratios, these specimens are compatible with the type material of *P. optima*, but are slightly smaller. This biohorizon corresponds to the lower part of the *O. besnosovi/A. excentricum* ammonite biohorizons and the middle part of the *Barskovisella bajosicus* belemnite Biohorizon.

**Ib. *Pachyteuthis bodylevskii*, nov. Biohorizon** Stratotype—Sokur Quarry, “belemnite level.” This corresponds to the uppermost part of the *O. besnosovi/A. excentricum* ammonite biohorizons and the upper part of the *Barskovisella bajosicus* belemnite Biohorizon.

A higher portion of the succession is not subdivided into biohorizons owing to the lack of identifiable material.

**Remarks.** Beds with *P. optima* s. lat. correspond to both belemnite units previously proposed by Dzyuba (in Mitta et al., 2014b) for the lower Bathonian deposits of the Sokur Quarry—Beds with *Pachyteuthis optima* and *Pachyteuthis bodylevskii* and (partly) Beds with *P. optima*. As shown above, the demarcation of the index species *P. optima* and *P. bodylevskii* sensu Mitta et al., 2014b in all intervals of the Sokur section, apart from the “belemnite level,” is not evident. Dzyuba’s upper unit, “Beds with *Pachyteuthis optima*,” corresponding to most of the interval above the “belemnite level,” was in fact defined by the absence of conical and subconical rostra of *P. bodylevskii* sensu Dzyuba in Mitta et al., 2014b. However, belemnites in this interval are generally scarce and are poorly preserved (e.g., Mitta et al., 2014b, text-fig. 8.3). Therefore, the proposed scheme of subdivision appears premature.

Beds with *P. optima* can be recognized, apart from on the Russian Plate, in sections of the Pechora Basin: existing data suggest a gradual vertical replacement of *P. optima* by *P. tschernyschewi* (Mitta et al., 2015, text-fig. 3), which is the index species of the eponymous zone (beds) (Meledina et al., 1998; Nalnjaeva, 1989). The FAD of the latter species marks the base of the Beds with *P. tschernyschewi*, and it would be logical to accept the same level as the top of the Beds with *P. optima*.



## II. Beds with *Pachyteuthis tschernyschewi* Meledina et al., 1987

This unit, originally established as a zone in northern Siberia (Meledina et al., 1987, 1991) and included in the Boreal standard (Meledina et al., 2011; etc.; Zakharov et al., 1997), is widely used in zonal scales for the sections of the Pechora Basin ranked either as beds (de Lagausie and Dzyuba, 2017; Nalnjaeva, 1989) or as a fully defined zone (Meledina et al., 1998; Mitta et al., 2015; Repin et al., 2006). Judging from the loose occurrences of *P. tschernyschewi*, it also should be present in the Sokur Quarry. The precise position of the finds in the section (and, accordingly, the boundary with the underlying Beds with *P. optima* s. lat.) remains unknown, but if one considers the occurrence of the bivalves *Retroceramus vagt* (Mitta et al., 2012, 2014b, text-fig. 2), which, like *P. tschernyschewi*, is characteristic of the Ishmae ammonite Subzone/Biohorizon (see Zakharov et al., 1997), the unit under consideration should cover a considerable portion of clay series above the “belemnite level.”

### A COMPLEX BELEMNITE ZONAL AND INFRAZONAL SCHEME FOR THE LOWER BATHONIAN OF THE VOLGA REGION AND ITS CORRELATION WITH THE EXISTING AMMONITE AND BELEMNITE SCALES

The results obtained in this study and its first part (Ippolitov, 2018) are summarized in Fig. 6. It is possible to recognize for the lower Bathonian of the Volga Region a series of parallel biostratigraphic subdivisions based on the evolution of *Barskovisella* and *Pachyteuthis* and embracing the range of the *Oraniceras* sp. A–O. cf./aff. *besnosovi* ammonite biohorizons of the O. *besnosovi* Zone, as well as a higher interval in the section (lacking ammonites and parallelized with the A. *ishmae* Subzone/Biohorizon of the A. *ishmae* Zone). The recognition of the belemnite units in the lowermost part of the lower Bathonian (provisional *Oraniceras scythicum* and O. *mojarowskii* biohorizons of D.B. Gulyaev) is so far not possible because of the absence of finds.

The simultaneous collecting of belemnites and ammonites in the field has allowed the newly recognized belemnite units to be precisely correlated with the ammonite scale (both zonal and infrazonal). Note that the boundaries of the most detailed belemnite units (biohorizons based on the evolution of *Barskovisella*) coincide with those of the ammonoid scale only because they are conventionally correlated owing to the discrete occurrences of one or both groups, which were completely uncoordinated in their evolution.

The correlation with the succession in the high-Boreal and Arctic basins using data from many groups of fossils (ammonites, belemnites, foraminifers, bivalves) is discussed in detail by Mitta et al. (2014b),

and Dzyuba’s scheme of belemnite correlations published in the same paper needs only few additional remarks. The Pechora Basin (sections on the Izhma River) is a key region for interregional correlation using belemnites, because the Boreal fauna immigrated to the Volga Region from there (Mitta et al., 2015). It is interesting that, although all species of Boreal ammonites from the Sokur Quarry are present in the sections of the Izhma River (Mitta et al., 2015), the list of belemnites formerly included only one species in common—*P. optima*. This phenomenon was explained by the idea that Sokur section represents a lower stratigraphic level “eroded” on the Izhma River (Mitta et al., 2015, p. 321). The present study suggests an opposite conclusion—all the representatives of the family Cylindroteuthididae described from the Sokur Quarry are also present in the Izhma River sections (*P. optima*, *P. bodylevskii* [as *P. tschernyschewi*—Sachs and Nalnjaeva, 1966, pl. 5, text-fig. 1], *P. tschernyschewi*, *P. mittai* sp. nov.). Only the *Barskovisella* lineage, neoendemic for the Russian Platform (Ippolitov, 2018), is absent on the Izhma River, as well as *Acanthoteuthis foliorostris* sp. nov. The tracing of two biohorizons established in the Sokur Quarry—[*P. optima* s. str.] and *P. bodylevskii*—in the sections on the Izhma River is a future concern.

Synchronous lower Bathonian belemnite units of Europe can only be indirectly correlated with the Russian Platform—via the correlation of the ammonite scales. Species of the genus *Barskovisella* and representatives of *Pachyteuthis* and *Acanthoteuthis* are unknown from the early Bathonian either in the Caucasus or outside European Russia. The only exceptions are occurrences of *B. bajosicus* and *B. barskovi* in the Bathonian of Switzerland (Gilliéron, 1873) and Poland (Pugaczewska, 1961), which allow the eponymous biohorizons to be traced. Anyway, judging from the paucity of these occurrences in Europe, it is possible to assume that representatives of *Barskovisella* are extremely rare outside the Volga Region. Existing Tethyan scales are of almost no use for correlations: such scales are constructed for the Middle Jurassic very formally, whereas the ranges of their belemnite units (*Duvalia disputabilis* Zone and *D. disputabilis*–*Belemnopsis fusiformis* Subzone according to Combémorin in (*Biostratigraphie...*, 1997) or the *Belemnopsis fusiformis* Zone according to Combémorin in Hardenbol et al., 1998) in fact embrace the entire lower Bathonian and part of the middle Bathonian.

## CONCLUSIONS

The conclusions are briefly summarized below.

(1) The belemnite family Cylindroteuthididae from the lower Bathonian of the Volga Region is revised. This family includes four species (one new) belonging to a single genus *Pachyteuthis*.

(2) The analysis of variability of the *Pachyteuthis* rostra from the Sokur Quarry allowed reinterpretation of the diversity of the genus in the lower Bathonian of the Russian Plate, recognition of the major evolutionary trends in the studied interval, and establishing of demarcation criteria for several closely related species employed in the literature. The occurrences of the Siberian zonal index *P. tschernyschewi* support the presence of the equivalents of the ammonite Arcticoceras ishmae Subzone/Biohorizon by belemnites in the marine series of the Volga Region.

(3) Belemnites with a thin sheath-like rostrum belonging to the genus *Acanthoteuthis* are reported from the pre-Callovian deposits of the Russian platform for the first time. The newly described species *A. foliorostris* sp. nov. is the earliest reliable record of the genus.

(4) The short but eventful evolutionary history of belemnites in the early Bathonian of the Middle Russian Sea allowed some paleogeographical conclusions to be proposed. The immigration of the Boreal-Arctic biota to the Volga Region from the Pechora Basin in the early Bathonian was two-phased. During the first phase, the meridional seaway was shallow and short-lived. Among cephalopods, only representatives of the belemnite family Megateuthididae penetrated into the Middle Russian Sea and formed here a neoendemic short-lived lineage of *Barskovisella*, and this can be considered as the first isolated episode of separation of the Boreal-Atlantic Province, which became fully established later, starting from the Callovian time. The second phase, characterized by the stable existence of a wide seaway, is marked by mass immigration of various groups of macrofauna, including the belemnite family Cylandroteuthididae. The maximum highstand coincides with the appearance of evolutionary young members of *Barskovisella* lineage—*B. bajosicus* (later morphotype) and *B. barskovi*—in Switzerland and Poland, which suggests a short-term episode of opening of the Pripyat Strait, directly connecting the Middle Russian and Polish seas.

(5) The study of belemnites from the lower Bathonian of the Volga Region (Ippolitov, 2018 and present paper) allows a new system of belemnite-based parallel zonal and infrazonal scales of the lower Bathonian or the Russian Platform to be proposed. This system is based on migration events and evolutionary trends in the two independent belemnite groups—*Pachyteuthis* (family Cylandroteuthididae) and *Barskovisella* (family Megateuthididae). The resolution of the most detailed units of the proposed scales corresponds and sometimes exceeds that of the ammonite biohorizons, which are sometimes referred to as “atoms of biostratigraphy.”

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