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New Data on the Upper Bathonian (Middle Jurassic) Cephalopods of the Russian Platform

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Abstract—The Upper Bathonian locality of Alatyr III bis in Central Russia is described for the first time. The predominantly sandy deposits of this age, unconformably overlain by Lower Callovian clays, belong to the *Calyx* Zone (with the ammonites *Cadoceras calyx* Spath and *Eckhardites atmensis* Mitta) and the *Apertum* Zone (with *Cadoceras apertum* Callomon et Birkelund). The new locality is the only one in Russia where the sequence of the *Calyx* and *Apertum* zones is established in the same outcrop. An emended description of *C. calyx*, a species originally described from East Greenland, is presented. Some belemnite rostra are identified as *Communicobelus subextensoides* (Gustomesov), described for the first time from the Upper Bathonian of the Boreal regions.

Keywords: Ammonoidea, Cardioceratidae, Belemnoidea, Cylindroteuthididae, biostratigraphy, taxonomy, Central Russia

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INTRODUCTION

In the last few decades, outcrops of late Bathonian coastal-marine (mainly sandy) beds with abundant fossils, primarily ammonites, were discovered in Central Russia (Middle Volga region). These sections are located in the Republic of Mordovia and Nizhny Novgorod Region; their study facilitated zonal subdivision of the Upper Bathonian of the Russian Platform into the following zones (from bottom to top): *Alatyroceras keuppi* (with the *efimovi, nageli,* and *keuppi* faunal horizons), *Cadoceras calyx*, and *Cadoceras apertum* (Mitta, 2005a, 2024; Kiselev, 2022; etc.). The *Calyx* and *Apertum* zones, originally established in East Greenland (Callomon, 1976, 1985, 1993; etc.) in the Central Russian sections have been shown to be poor in fossils, and their validity required additional confirmation, especially of the *Calyx* Zone, the index species of which was initially described from the Russian Platform (Mitta, 2005a) based on material without precise locality details. Furthermore, the sequence of *Calyx* and *Apertum* zones in the Central Russian sections had not been observed in a single outcrop until recently (Mitta et al., 2025).

The Upper Bathonian in Mordovia has been studied for two decades at three localities representing sand mining for local needs and named Alatyr I (near the village of Repyevka, Ichalki District), Alatyr II (the right bank of the Ladka River near the village of Bolshaya Pestrovka in the same district), and Alatyr III (near the village of Trofimovshchina, Romodanovo District) (Mitta, 2005a; etc.). In the last decade, sand dredging began on the other outskirts of the village of Trofimovshchina, 2 km southwest of the Alatyr III locality (Fig. 1); this locality was named Alatyr III bis (Mitta et al., 2025). As in other Upper Bathonian sections in Mordovia (and the neighboring Nizhny Novgorod region), the sandy layer of the Upper Bathonian is transgressively overlain here by clays of the Lower Callovian (Fig. 2).

The article is primarily based on field observations and findings by I.A. Meleshin (fall 2016, spring 2025), as well as V.V. Kostyleva and V.V. Mitta (summer 2025). To establish the level of fossil finds from previous years, field photographs by I.A. Meleshin (2016 and 2025) and R.A. Gunchin (2024) were studied. The section description was compiled by V.V. Kostyleva with the participation of V.V. Mitta and I.A. Meleshin; ammonites were studied by V.V. Mitta, belemnites by O.S. Dzyuba.

The material studied is housed in the A.A. Borissiak Paleontological Institute (PIN RAS), collection no. 5029 (ammonites) and the A.A. Trofimuk Insti-

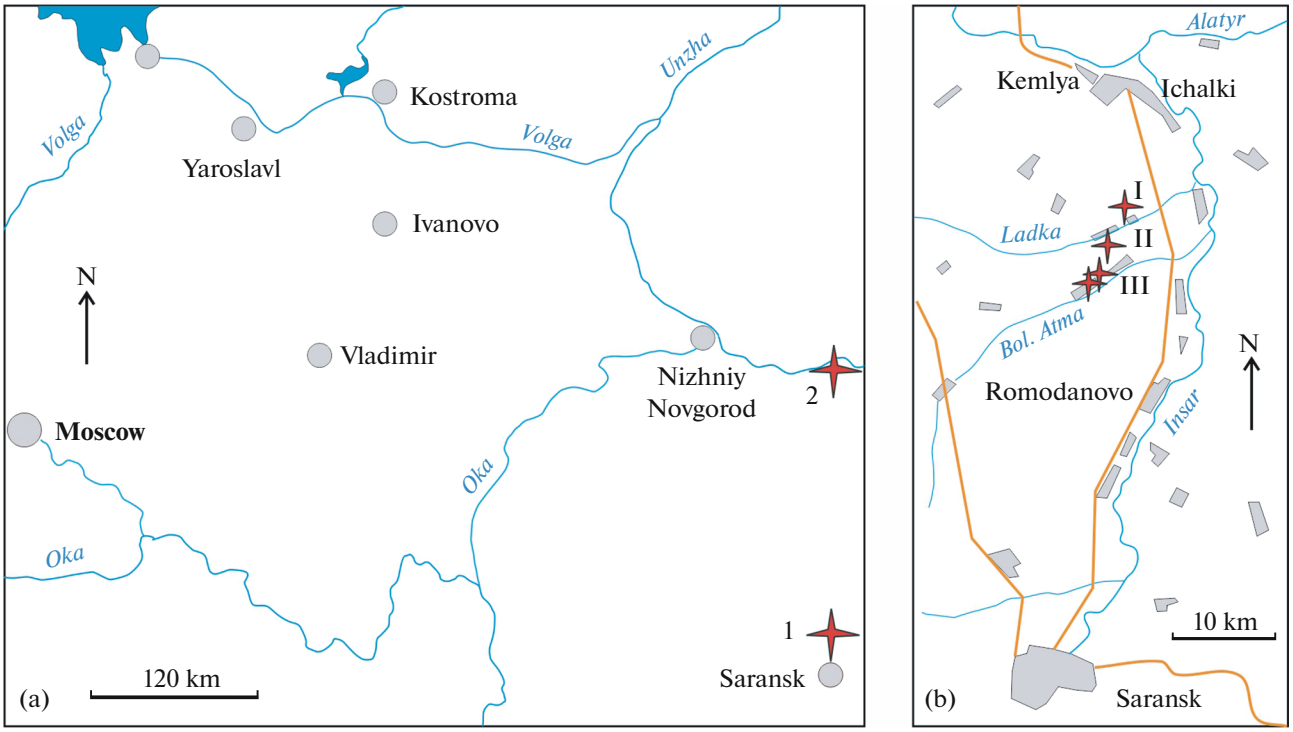


Fig. 1. The layout of the mentioned Upper Bathonian sections: (a) general map (numbers indicate: (1) localities Alatyr I, II, III, III bis in Mordovia; (2) locality near the village of Prosek in the Nizhny Novgorod Region, (b) detailed map (I—Alatyr I locality, II—Alatyr II locality, III—Alatyr III and III bis localities).

Fig. 2. Part of the Alatyr III bis locality (Republic of Mordovia, Romodanovo District, sand pit near the village of Trofimovshchina); exposed sandy deposits of the Upper Bathonian, transgressively overlain by Lower Callovian and Upper Oxfordian clays; photo by V.V. Mitta, 2025.

tute of Petroleum Geology and Geophysics, Siberian Branch of the Russian Academy of Sciences, Collective Use Center "GEOCHRON Collection", collection no. 898 (belemnites).

LOCALITY AND AGE

The Alatyr III bis location is a series of sand excavations in the slope of a hill (coordinates: beginning of the section N 54°31′21.8″, E 45°14′4.6″; end of the section N 54°31′22.0″, E 45°13′50.3″), partially covered by scree and landslides.

From bottom to top, the following beds are exposed (Fig. 3):

Member I. Light gray sand, predominantly medium-grained, well-washed, with medium-scale parallel, alternately multidirectional cross-bedding, suggesting coastal-marine environment. The boundaries of the series of cross-beds (up to 0.4 m thick) are marked by horizontal interbeds (1–2 cm) of grey calcareous clay or horizontal alternation of sand and clay. A single lens (0.2 m thick) of dark-gray calcareous clay, not consistent along the strike, was observed, containing fragments (up to 7 cm) of light-yellow marl with ferruginous oolites, intraclasts of gray calcareous clay, rare redeposited phosphorite nodules, gravel-sized quartz grains, and fragments of belemnite rostra.[1] In the upper third of the section, a consistent layer of reddish-brown medium-grained ferruginous calcareous sandstone nodules, 0.2–0.4 m thick, can be traced along the strike. Some concretions of this interlayer contain accumulation of ammonites (Fig. 4); *Cadoceras calyx* Spath and *Eckhardites atmensis* Mitta were identified. Shells of the same taxa were also found lower down the section, in sandstone nodules scattered throughout the strata (Fig. 5). Single finds of belemnites *Cylindroteuthis* sp. are confined to the middle part of the member. In the upper part of the member, charred wood remains are occasionally encountered, up to trunks ~2 m long (Fig. 6). A single shell of *Cadoceras apertum* Callomon et Birkelund, found by R.A. Gunchin, comes from the upper part of the member (Mitta et al., 2025, pl. 2, fig. 1). Belemnite rostra, usually heavily weathered, were found in a sandy matrix at the top of the member—*Communicobelus subextensoides* (Gustomesov), Belemnitida indet.; in talus—*Cylindroteuthis* sp. indet. The exact level of finds of several ammonite shells and belemnite rostra (collected in 2016) has not been established. The lower part of the member is usually obscured by talus, and no fossils have been found there. The visible thickness is 7.5–8 m.

Member II. Dark-gray, dense clay, at the base (along a weakly erosive boundary) with a horizon of rewashed underlying sandy and clayey deposits, with rare gray clayey pellets. A dark-gray marl concretion with a shell of *Cadoceras suevicum* Callomon et Dietl (specimen 5029/214, not shown) and a well-preserved young rostrum of *Cylindroteuthis puzosiana* (d'Orbigny) were found in the scree. In addition, a gray phosphorite nodule was found in a landslide in the upper part of the member, light-gray on the surface, with *Amoeboceras* sp. (specimen 5029/221, also not shown). The visible thickness of the member (where its upper part is not cut off by overlying works) is up to 4 m.

Based on its ammonite finds, Member I clearly belongs to the *Calyx* and *Apertum* zones of the Upper Bathonian (Lukoyanov Formation, according to: *Unifitsirovannaya*..., 2012). The lower third of the member, not characterized by index fossils, based on its position in the section, could theoretically belong to the underlying *Keuppi* Zone. However, this zone in the Alatyr I and Alatyr II localities is characterized by fairly numerous and diverse ammonites of the genera *Kepplerites* (subfamily Keppleritinae family Kosmoceratidae) (Mitta, 2008; etc.) and *Alatyroceras* (subfamily Arctocephalitinae family Cardioceratidae) (Mitta, 2016; etc.); the presence of these taxa in the studied locality has not been established.

We have not studied the clays of Member II in detail due to their occurrence features. The lower part of this member, based on the find of *Cadoceras suevicum* in a scree concretion of marl, which definitely originates from the clays of the Elatma Formation (*Unifitsirovannaya*..., 2012), belongs to the *Elatmae* Zone of the Lower Callovian; *C. suevicum* shells were previously found at the Alatyr III locality in the same concretion with *C. elatmae* (Nikitin) (Mitta, 2004, p. 128; Mitta et al., 2015, text-fig. 7.4). The find of *Amoeboceras* indicates that the Callovian clays are overlain here, as in most other sections of Mordovia, by clays of the Vechkusy Formation of the Oxfordian-Kimmeridgian (Mitta, 2004; Rogov et al., 2025).

DISCUSSION

This section requires a brief excursion into the history of the formation of the zonal scale of the Middle Jurassic of East Greenland and its correlation with the standard (Western European) scale.

L.F. Spath considered the interval of interest to us as a horizon with *Kepplerites tychonis* Ravn and *Cadoceras victor* Spath, overlain by a horizon with *Kepplerites pauper*; these two horizons were combined into the *Kepplerites* and *Cadoceras* Beds (Spath, 1932, p. 138). These beds were correlated by Spath with the upper part of the *Kepplerites gowerianus* Zone and the *Sigaloceras calloviense* Zone of the Lower Callovian of the standard scale (ibid., p. 145).

In the following decades, researchers of the Mesozoic in East Greenland gradually refined the Bajocian, Bathonian, and Callovian zonation scales of the region. In particular, Donovan (1953) accepted the

[1] Further study is required to establish the origin of this lens.

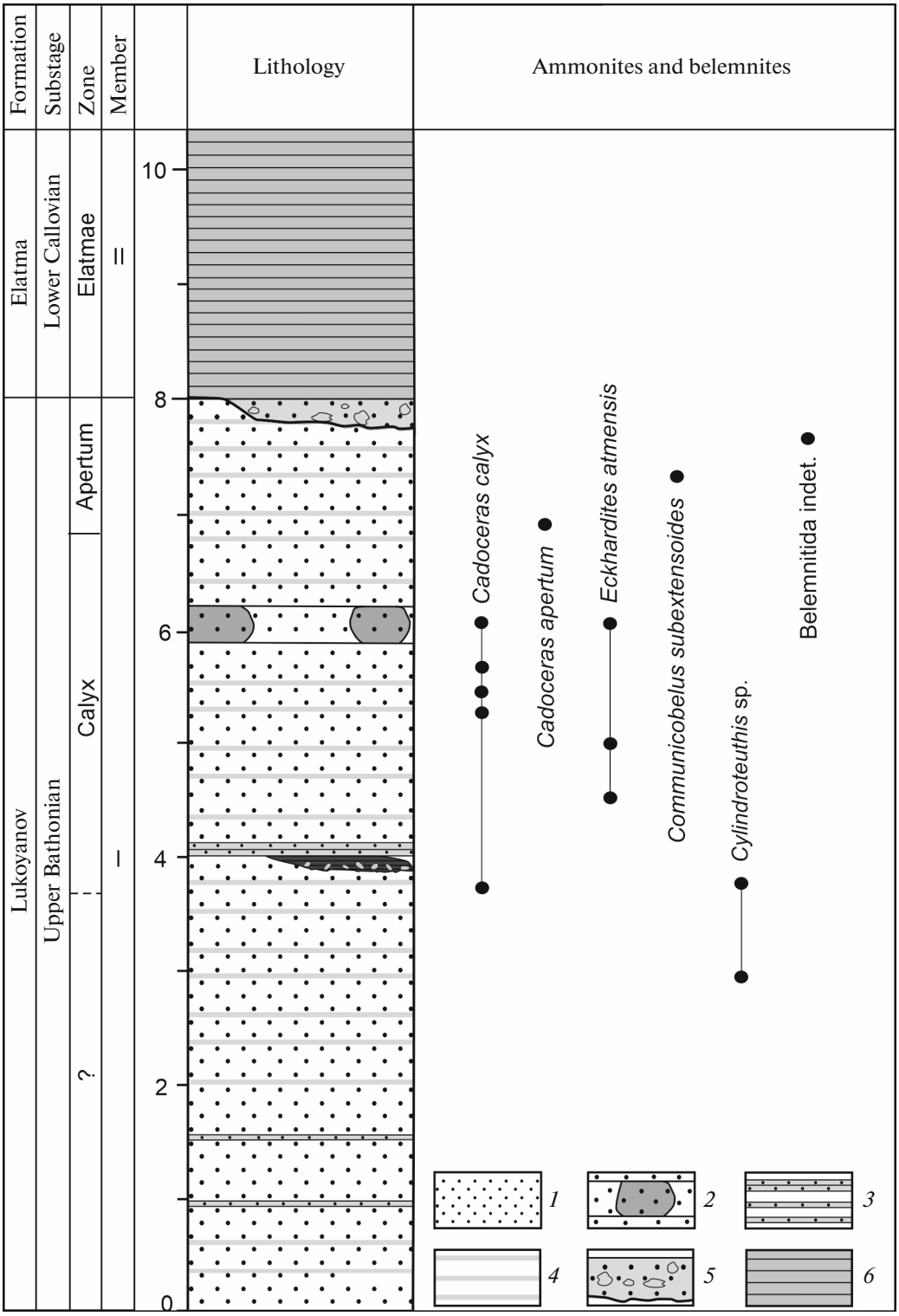


Fig. 3. Lithological log of the geological section at the Alatyr III bis locality and intervals of cephalopod finds: (I) sandy member, (II) clay member. (*1*) Sand, (*2*) sandstone concretions, (*3*) interbedded sand and clay, (*4*) banded clay interlayers, (*5*) reworked horizon, (*6*) clay.

Fig. 4. Ammonites *Cadoceras calyx* Spath from a bed with sandstone concretions in Member I of the Alatyr III bis locality: (a) in a concretion in situ, (b) cores and imprints in a concretion extracted from the bed and split; Upper Bathonian, *Calyx* Zone; photo by V.V. Kostyleva and V.V. Mitta, 2025.

Kepplerites and *Cadoceras* Beds, as defined by Spath, as the *Tychonis* Zone, suggesting that the new zone corresponded more closely to the lower and middle parts of the Lower Callovian of the standard scale. This proposal was accepted by J.H. Callomon, who correlated the *Tychonis* Zone directly with the Lower Callovian lowermost zone of Western Europe (Callomon, 1959, pl. I).

In the mid-1970s, Callomon, refined the "Boreal Bathonian"[2] scale by establishing new zones, in particular, by distinguishing two zones within the *Tychonis* Zone interval: *Calyx* (at the top of the Bathonian) and *Apertum* (at the base of the Callovian) (Callomon, 1976, 1979; Callomon and Birkelund, 1980; and others). However, the description of the species *Cadoceras apertum* was published much later (Callomon and Birkelund, 1985), as was the paleontological characterization of the new zonal and infrazonal subdivisions (Callomon, 1993). It should be noted that, beginning with the 1993 publication and in later ones, Callomon admitted that the lower faunal horizons of the *Apertum* Zone could in fact be Upper Bathonian.

At the very beginning of the 21st century, a Boreal–Tethyan ecotone was established in Central Russia (the outskirts of Saratov), where both high-latitude *Arcticoceras* (subfamily Arctocephalitinae, family Cardioceratidae) and undoubtedly early Bathonian ammonites of Tethyan origin, the genus *Oraniceras* (family Parkinsoniidae), were found in the same section. This discovery made it possible to clarify the position of the East Greenland *Arcticoceras ishmae* Zone, which for many decades was considered Lower Callovian (Spath, 1932; Sasonov, 1957; Meledina, 1987; etc.), and later supposedly Middle Bathonian (Callomon, 1993; Meledina, 1994; etc.). As a result, the *Ishmae* Zone began to be considered as quite definitely Lower Bathonian (Mitta and Seltzer, 2002; Mitta et al., 2004, 2011, 2012, 2014; etc.) and brought doubts about the correctness of the dating of the overlying units of the "Boreal Bathonian".

A study of ammonites from the Lukoyanov Formation of the Alatyr River basin in the Republic of Mordovia has established that these predominantly sandy deposits belong to the *Keuppi*, *Calyx*, and *Apertum* zones (from bottom to top) (Mitta, 2004, 2005a, 2005b; Kiselev and Rogov, 2007b; etc.), unambiguously dating to the Upper Bathonian. The index species of the *Calyx* Zone was found (initially not in situ) only at the Alatyr-II locality, and the index species of the *Apertum* Zone was found only in thin sandstone at the top of the sandy member at the Alatyr-III locality (no ammonites were found lower down the section at this locality). Accordingly, the Alatyr-III bis locality is currently the only one on the Russian Platform that contains the sequence of the *Calyx* and *Apertum* zones. In addition, only in this locality Bathonian representatives of the genus *Eckhardites* were found (Mitta et al., 2025); species of this genus until recently were known only from the Lower Callovian (Smorodina, 1929; Mitta, 2000, 2009; etc.).

It should also be noted that, unlike other Upper Bathonian sections of the Russian Platform, the Alatyr-III bis locality contains exclusively cardioceratid macroconchs—neither their microconchs nor species of the genus *Kepplerites*, which primarily accompany cardioceratids in the Upper Bathonian–Lower Callovian interval, including on the Russian Platform, have been found. Meanwhile, at the nearby Alatyr III locality, ammonites (*Cadoceras apertum* and its microconchs, formally classified as *Pseudocadoceras*) were found only in a sandstone interbed at the top of the sandy member (Mitta, 2005a).

[2] Under this term, Callomon united the Bajocian, Bathonian, and partly Callovian of East Greenland, which at that time did not have a direct correlation with the standard zonal scales of these stages.

Thus, the Alatyr-III bis locality is unique in its own way: here, for the first time in the region, the sequence of the *Calyx* and *Apertum* zones has been established, and for the first time, rostra of late Bathonian belemnites, identifiable to the species level, have been found (in another Upper Bathonian section, only juvenile rostra had previously been found, heavily weathered and usually not identifiable even to genus).

Literature data indicate the discovery of late Bathonian belemnite rostra (dated by foraminifers) on the western margin of the Russian Platform, in the region of the Kanev dislocations, at the junction of the Ukrainian Shield and the Dnieper–Donets Basin (Nikitin, 1969; 1977). However, I.I. Nikitin (1989) later attributed the enclosing deposits to the Lower Callovian, which was confirmed by subsequent studies (Gulyaev et al., 2013).

In the north of the European part of Russia, in a section on the Tsilma River near the village of Trusovo (Komi Republic), in a layer assigned to the upper part of the Upper Bathonian based on the finds of ammonites identified in the open nomenclature, only rare, indeterminate rostra of juvenile cylindroteuthidids were found (Gulyaev and Ippolitov, 2016).

The *Calyx* Zone (defined by several finds of the index species) was also discovered in the north of Eastern Siberia in the Anabar region (Knyazev et al., 2006, 2007, 2009), whereas in the adjacent Leno-Olenek region, the *Calyx* and *Apertum* zones clearly fall out of the section due to a temporary cessation of sedimentation (Shamonin et al., 2023, 2025). There are currently no data on belemnite finds in northern Siberia in the same age as the Upper Bathonian units established in Mordovia.

The only belemnite rostrum discovered in the *Calyx* Zone of East Greenland, judging by its discovery in the "*tychonis* Horizon" of the Vardekløft Formation (Spath, 1932) and in the subsequent interpretation of this horizon's age (Callomon, 1993, 2003; and others), was not illustrated. The rostrum was assigned to *Cylindroteuthis subextensa* (Nikitin), later included in a new genus-group taxon, *Communicobelus* (Gustomesov, 1964). Other rostra illustrated by Spath under the same species name come from older strata (Bathonian and Bajocian) and were later reidentified (Sachs and Nalnjaeva, 1964; Dzyuba and de Lagausie, 2018): *Microbelus parens* (Sachs et Nalnjaeva) (Spath, 1932, pl. I, fig. 5), *Cylindroteuthis spathi* Sachs et Nalnjaeva (Spath, 1932, pl. 2, fig. 2; pl. 16, fig. 2), Belemnitina (Spath, 1932, pl. 17, fig. 2). Consequently, it is unclear to which species the remaining unfigured specimen from the *Calyx* Zone belongs.

The paucity of information on Arctic belemnites from the late Bathonian is partly due to the extreme rarity of their finds, and partly because at that time they were represented exclusively by cylindroteuthidids, which were still in the initial stage of their development (Dzyuba, 2004). Pre-Callovian cylindroteuthidids are characterized by a relatively low taxonomic diversity—three genera (*Cylindroteuthis, Pachyteuthis, Microbelus*) and no more than one or two coexisting species in each (Dzyuba and de Lagausie, 2018).

Fig. 5. Ammonite shells in Member I of the Alatyr III bis locality in situ; arrows indicate: lower right, shell of *Eckhardites atmensis* Mitta, above—fragments of *Cadoceras calyx* Spath cores; Upper Bathonian, *Calyx* Zone; photo by I.A. Meleshin, 2016.

Of the belemnites in the Alatyr III bis section, only representatives of the family Cylindroteuthididae have been identified (Table 1): from the *Calyx* zone—*Cylindroteuthis* sp., from the *Apertum* Zone—*Communicobelus subextensoides* (Gustomesov, 1964), from the talus of the I member—*Cylindroteuthis* sp. indet., from the talus of the *Elatmae* Zone of the Lower Callovian comes *C. puzosiana* (d'Orbigny, 1842).

Fig. 6. Wood in Member I of the Alatyr III bis locality in situ; Upper Bathonian, *Apertum* Zone; photo by I.A. Meleshin, 2016.

The rostra of *Cylindroteuthis* sp. (Pl. 10, figs. 1–4) correspond to the juvenile (fusiform, as in all cylindroteuthidids) and early ontogenetic stages of a species, morphologically close to *C. spathi* Sachs et Nalnjaeva, 1964. Judging by the available material, the cross-section shape in the alveolar part is subject to some variability—from rounded subquadrate (Pl. 10, figs. 2a, 4) to slightly trapezoid (Pl. 10, fig. 1a). Something similar is observed in *C. spathi* (Sachs and Nalnjaeva, 1964; de Lagausie and Dzyuba, 2017). Unlike the latter species, *Cylindroteuthis* sp. from the Alatyr III bis locality is characterized by a longer ventral groove. Compared to the subcylindrical *Cylindroteuthis* sp. from the Upper Bathonian of New Zealand (Challinor and Hudson, 2017), the studied specimens at a comparable ontogenetic stage have a subconical shape (Pl. 10, figs. 1, 2). Due to the lack of information on the late Bathonian *Cylindroteuthis*, the species identification of the rostra in question is currently difficult.

Cylindroteuthis sp. indet. specimens, mostly in poor condition, have been found in the debris of Member I. In their elongation, conical shape, and

Table 1. Dimensions of the studied belemnite rostra in mm and their ratios**

Specimen no.	R	PA	DV	LL	AR	dv	ll	PA/DV ×100%	LL/DV ×100%	ll/dv ×100%
Cylindroteuthis sp.										
898/11	84.0	66.5	10.6	10.1	31	8.5	8.5	627	95	100
898/12	51	–	9.7	9.4	–	8.4	8.4	–	97	100
898/13	30.3	28.5	3.2	3.2	10.5	3.3	3.3	891	100	100
Cylindroteuthis sp. indet.										
898/14	115	>99	>12.6	13.4	–	–	–	>786	<106	–
898/15	42	–	5.9*	5.8*	15	4.7	4.7	–	98*	100
Cylindroteuthis puzosiana (d'Orbigny, 1842)										
898/16	77	65.0	7.3	6.7	22	6.3	6.1	890	92	97
Communicobelus subextensoides (Gustomesov, 1964)										
898/17	135	90.0	19.2	19.0	34	15.3	15.2	469	99	99
898/18	120	73.8	15.3	15.9	31	12.8	12.7	482	104	99
898/19	81	>61	13.0	13.2	>28	11.5	11.5	>469	102	100

* At the preserved anterior edge of the rostrum.

** Measurements were made of the established (preserved) length of the rostrum (R), the length of the postalveolar part (PA) and apical (AR) region, the dorsal-ventral diameter at the apex of the alveolus (DV) and in the apical region (dv), the lateral diameter at the apex of the alveolus (LL) and in the apical region (ll).

slightly laterally compressed to dorsoventrally depressed cross-section, they are similar to *C. tsytovitchae* I. Nikitin, 1969 but are too poorly preserved for a confident identification with any specific representative of the genus *Cylindroteuthis*. In particular, the ventral side of the only nearly complete rostrum (Pl. 10, Fig. 5) and several fragments is heavily eroded, in the postalveolar part—almost to the apical line. This may create the illusion of a deep and long ventral apical groove.

A fragment of the rostrum from an early stage of ontogeny, originating from the Upper Bathonian of the Alatyr III locality (Pl. 10, fig. 6), was also identified as *Cylindroteuthis* sp. indet.; the ventral groove of this specimen is not so prominent.

Finds of *Communicobelus subextensoides*, first established in the Upper Bathonian of the European part of Russia, are characterized below in the description of this species. Previously, *C. subextensoides* was known here from the Lower Callovian (Gustomesov, 1964, 1990; Nalnjaeva, 1989), although initially Gustomesov (1964) did not exclude its rare presence in the Middle Callovian as well. Outside the European part of Russia, this species has been described only from the Shaimsky District of Western Siberia based on a single specimen from the Abalak Formation, presumably its Lower Callovian part, exposed by the Malo-Shushminskaya 10527 borehole (Dzyuba, 2001). The species is the type species for the genus *Communicobelus* Gustomesov, 1964. It is possible that the find of an unidentifiable belemnite from the top of Member I of the Alatyr III bis locality, which is represented by a fragment of the anterior part of a fairly large rostrum (Pl. 10, fig. 12), also belongs to *C. subextensoides*.

The surface of all rostra collected from the Upper Bathonian sand unit is corroded, to the greatest extent in specimens from the *Apertum* Zone. The *Cylindroteuthis puzosiana* specimen found in the scree (Pl. 10, fig. 7) shows no traces of sandy matrix either on the rostrum surface or in its alveolus. Unlike the Bathonian rostra, it is remarkably well preserved, with a smooth rostrum surface. It can be concluded that *C. puzosiana* definitely comes from the clay member II of the studied section, dated in the lower part to the early Callovian. This species, synonymized with *Belemnites oweni* Pratt, 1844, *Cylindroteuthis karitzkii* I. Nikitin, 1969, and also presumably *Belemnites borealis* d'Orbigny, 1845, *B. attenuatus* Mantell, 1848, *B. extensus* Trautschold, 1862, and *B. skidegatensis* Whiteaves, 1884 (Dzyuba, 2004), is the type species for the genus *Cylindroteuthis* Bayle, 1878. It possesses a number of conservative characteristics of the genus (an elongated, cylindroconical rostrum with a narrow, shallow ventral groove developed near the apex, and a rounded-subrectangular, laterally compressed cross-section), which allowed it to spread widely across the boreal seas during the Callovian and persist into the Kimmeridgian. In the Alatyr III bis section, the species is represented by a rostrum from an early stage of ontogeny.

SYSTEMATIC PALEONTOLOGY

Superfamily Stephanoceratoidea Neumayr, 1875

Family Cardioceratidae Siemiradzki, 1891

Subfamily Cadoceratinae Hyatt, 1900

Genus Cadoceras Fischer, 1882

***Cadoceras calyx* Spath, 1932 [M]**

Pl. 9, figs. 2–4

Cadoceras calyx: Spath, 1932, p. 69, pl. 20, fig. 1; Callomon, 1985, fig. 8K; Mitta, 2005a, p. S641, pl. 8, fig. 1; Knyazev et al., 2006, pl. fig. 2; Knyazev et al., 2007, pl. 3, figs. 1, 2; Knyazev et al., 2009, pl. 4, figs. 1, 2; Kiselev, 2022, p. 165, pl. 20, figs. 2, 3; pl. 21, fig. 1; pl. 31, figs. 1–3; pl. 32, figs. 1–3; pl. 33, figs. 1–3; Mitta, 2024, Figs. 4a, 4b; Mitta et al., 2025, fig. 2.

Cadoceras franciscus: Spath, 1932, p. 74, pl. 20, fig. 2.

Cadoceras victor: Spath, 1932, p. 67, pl. 16, fig. 6.

Cadoceras aff. *victor*: Spath, 1932, p. 67, pl. 21, fig. 1.

Cadoceras sp. ind. aff. *victor*: Spath, 1932, p. 67, pl. 17, fig. 5.

Cadoceras aff. *calyx*: Mitta, 2004, pl. 1, fig. 2.

? *Paracadoceras ammon*: Spath, 1932, p. 78, pl. 21, fig. 5.

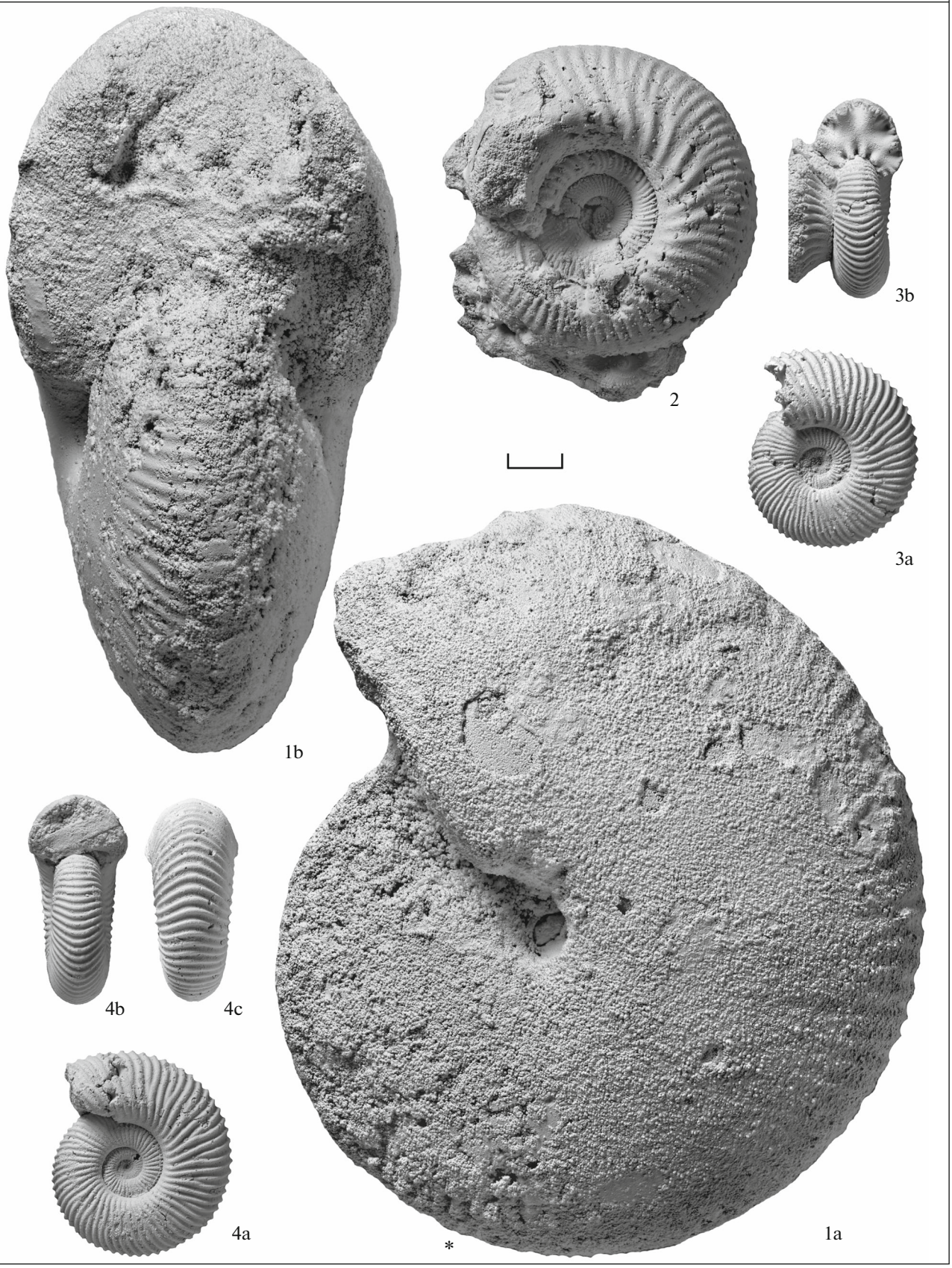
? *Cadoceras (Bryocadoceras) calyx*: Kiselev and Rogov, 2007a, pl. 3, fig. 1, 2.

Holotype. Natural History Museum, University of Copenhagen, specimen no. 9263; Spath, 1932, pl. 20, fig. 1; Kiselev, 2022, pl. 31, fig. 1; East Greenland, Vardekløft Formation; Upper Bathonian, *Kepplerites tychonis* Beds [=*Calyx* Zone].

Description (Figs. 4, 7, 8). The mature shell reaches a diameter of 100 mm. Early whorls (up to 20–30 mm in diameter) are swollen, with a whorl height comparable to its width; with age, the whorls become strongly to very strongly swollen, with a transverse oval cross-section. The umbilicus, moderately wide and shallow in the early stages, widens with age to a wide, rather gently sloping umbilical wall, which gradually becomes almost vertical with age, with a sharp bend. The body chamber occupies 0.7–0.9 of the outer whorl, and the aperture has a well-defined apertural constriction.

The ornamentation on the early whorls consists of thin, densely arranged, alternating single and bifid ribs, with a bifurcation point near the mid-flank; this is a characteristic feature of the genus as a whole. On the phragmocone, ribs are also prominent on the umbilical wall; with age, they gradually become smoother; the primary ribs are raised, forming forward-sloping, comb-like swellings continuing into 2–3 secondary ribs, sometimes with intercalated ribs. On the body chamber of adult specimens, the umbilical wall is smooth, the preumbilical comb-like swellings are clearly visible, and the secondary ribs are modified into distinct wrinkles.

Plate 9



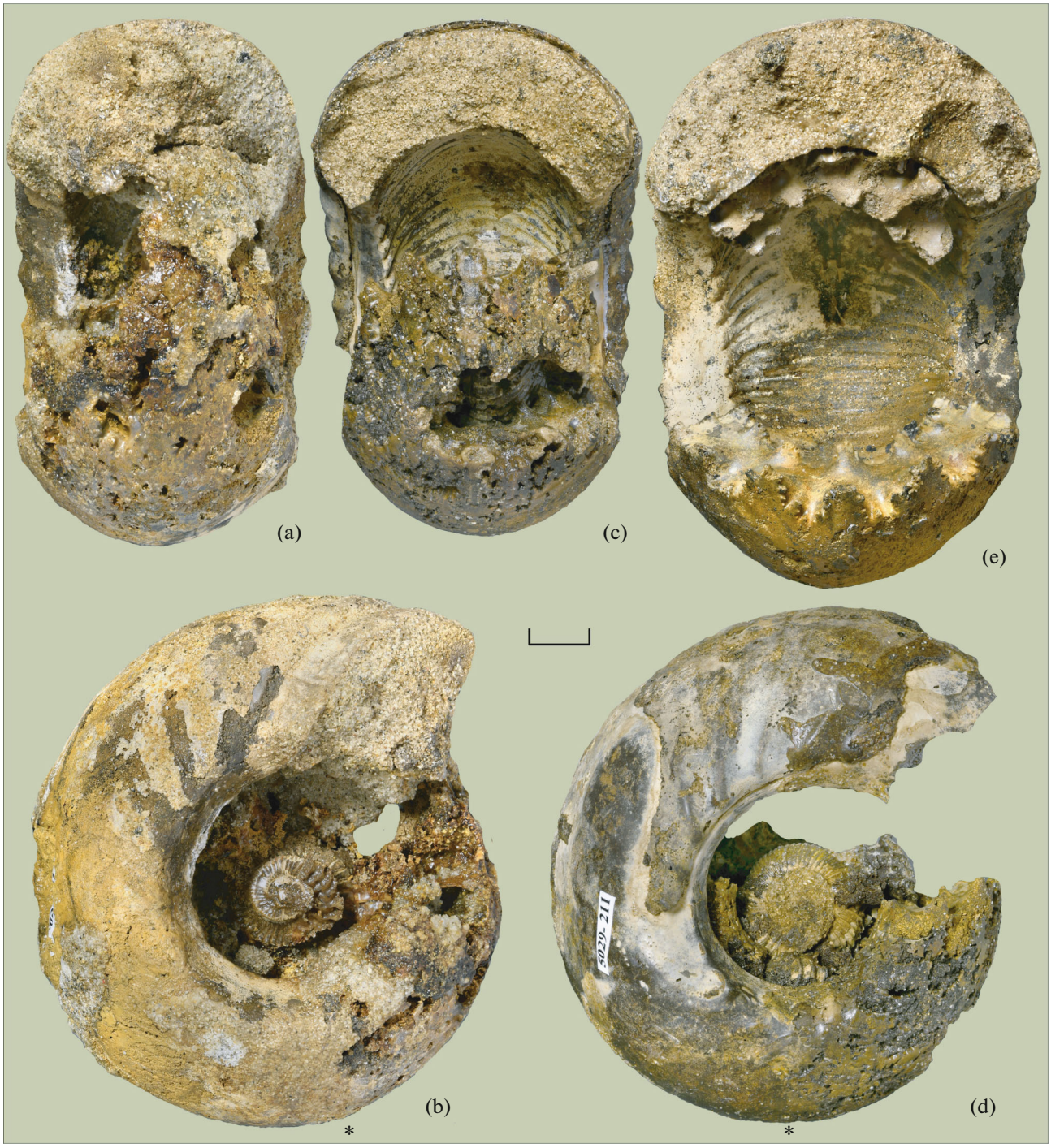


Fig. 7. *Cadoceras calyx* Spath, adult shells: (a, b) specimen PIN, no. 5029/212, (a) from the mouth; (b) from the side; (c, d) specimen PIN, no. 5029/211, (c) from the mouth; (d) from the side; (e) specimen PIN, no. 5029/210, from the mouth; Alatyr III bis locality; Upper Bathonian, *Calyx* Zone; collected by I.A. Meleshin, 2016. Scale bar 10 mm; asterisk (*) marks the beginning of the body chamber.

Explanation of Plate 9

Fig. 1. *Eckhardites atmensis* Mitta, holotype PIN, no. 5029/205: (1a) apertural view, (1b) lateral view.

Figs. 2–4. *Cadoceras calyx* Spath, phragmocones: (2) specimen PIN, no. 5029/217, lateral view; (3) specimen PIN, no. 5029/219, (3a) lateral view, (3b) apertural view; (4) specimen PIN, no. 5029/218, (4a) lateral view, (4b) apertural view, (4c) ventral view.

All: Alatyr III bis locality; Upper Bathonian, *Calyx* Zone; (1) collected by I.A. Meleshin, 2016; (2–4) collected by V.V. Mitta, 2025. Scale bar 10 mm long; the beginning of the body chamber is marked with an asterisk (*).

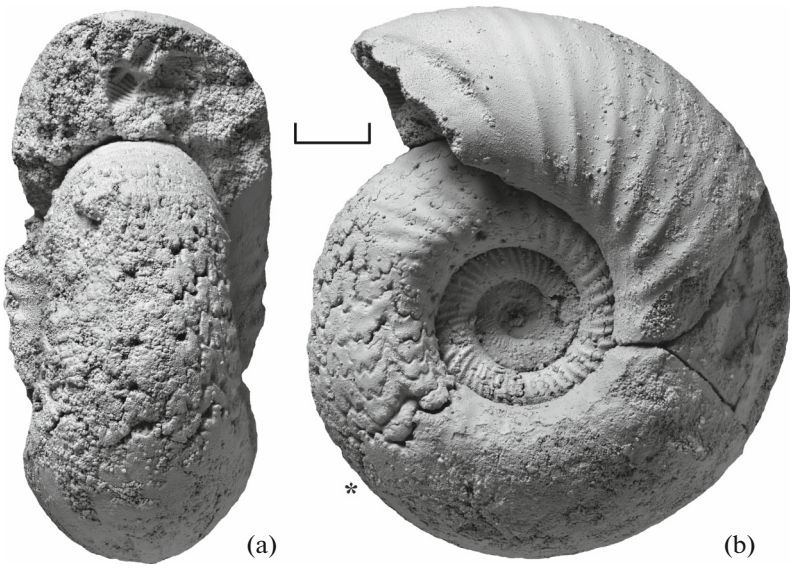


Fig. 8. *Cadoceras calyx* Spath, a tachygerontic shell with a complete body chamber, specimen PIN, no. 5029/216, (a) apertural view; (b) lateral view; Alatyr III bis locality; Upper Bathonian, *Calyx* Zone, from a concretion layer (see imprint in Fig. 4b); collected by V.V. Mitta, 2025. Scale bar 10 mm; the asterisk (*) marks the beginning of the body chamber.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	WH/Dm	WW/Dm	UW/Dm
5029/209	99	34	63	38	0.34	0.64	0.38
	82	25	59	29	0.31	0.72	0.35
5029/210	94	33	63.5	36.5	0.35	0.68	0.39
5029/213	89	31	49	33.5	0.35	0.55	0.38
5029/207	84	26.5	61	34.5	0.32	0.73	0.41
	75	22	50	30.5	0.29	0.67	0.41
5029/211	84.5	28.5	53	31.5	0.34	0.63	0.37
5029/212	83	29	44.5	31.5	0.35	0.54	0.38
5029/216	74.5	25	37.5	28	0.34	0.5	0.38
	58	20	31.5	21	0.34	0.54	0.36
5029/217	56.5	18	33	20	0.32	0.58	0.35
5029/218	36.5	13	16	13	0.36	0.44	0.36
	29	11	11	10	0.38	0.38	0.34
5029/219	32.5	13	14.5	10.5	0.4	0.45	0.32
	25	9.5	10	8	0.38	0.4	0.32
5029/220	26	11	12	8.3	0.42	0.46	0.32

Variability. It is expressed primarily in variations in the cross-sectional shape of adult shells, namely in the ratio of the height to the width of the whorl (Fig. 7); however, the cross-section remains low and kidney-shaped.

Among the new finds of the species being described, one specimen (Fig. 8) differs from the others in having a less inflated shell and smaller dimensions, although by all characteristics (the final convergence of the septa, the minimum length of the living chamber for the species, turning toward the aperture, and the presence of a pronounced apertural constriction on the mold), it represents an adult shell. Apparently, this is a tachygerontic shell, according to Teisseyre's (1889) terminology; see also Mitta, 1990, 2025; Kiselev, 2023; etc.), that is, reaching adulthood at a smaller than usual size.

Comparison. The described species is clearly distinguished from the most similar (and probable descendant) of *C. apertum* Callomon et Birkelund, by its transverse-oval kidney-shaped section and long primary ribs at the adult stage.

Remarks. The concepts about the specific characters of the discussed species of Callomon (a researcher of the Jurassic ammonites of East Greenland and elsewhere, the first reviser of *C. calyx*) are well set out in the published excerpt from his private letter (Kiselev, 2022, p. 165); Callomon's opinion about the range of variability of this taxon completely coincides with our data.

The ammonite illustrateed by Spath as *Paracadoceras ammon* is included in the synonymy conditionally due to its poor preservation.

Two ammonite shell molds from the *Calyx* Zone of the section near the village of Prosek, identified as *Cadoceras (Bryocadoceras) calyx* (see synonymy), were illustrated by Kiselev and Rogov (2007a). One of these specimens is represented by small internal whorls and, without taking into account the find level, could hardly have been identified closer than Cadoceratinae indet.

The second find was later re-identified as *Cadoceras (Catacadoceras) infimum* morpha '*perrarum*' Voronetz (Kiselev, 2022, p. 552, pl. 20, fig. 5). Judging by the very prominent and sparse ornamentation for such

a diameter, it is highly doubtful that this specimen belongs to *C. calyx*. However, this raises questions about nomenclature: the species *C. perrarum* Voronetz, 1962 was described earlier than *C. infimum* Gulyaev et Kiselev, 1999; the presence of this specimen in the synonymy of *C. calyx* (ibid., p. 165) is likely a misprint.

Occurrence. Upper Bathonian *Calyx* Zone of East Greenland, Northern Siberia, and the Middle Volga region.

Material. 3 specimens from the Alatyr II locality (collection by V.M. Efimov, without exact reference) and over 20 specimens from the Alatyr III bis locality, in varying states of preservation (collections by Meleshin (2016 and 2025), Zenina (2024), and Mitta (2025)).

Order Belemnitida Zittel, 1895

Suborder Belemnitina Zittel, 1895

Family Cylindroteuthididae Stolley, 1919

Subfamily Lagonibelinae Gustomesov, 1977

Genus *Communicobelus* Gustomesov, 1964

***Communicobelus subextensoides* (Gustomesov, 1964)**

Plate 10, figs. 8–11

Cylindroteuthis tornatilis: Ognev, 1933, p. 219, pl. 2, figs. 1, 2.

Cylindroteuthis subextensa: Ivanova, 1959, p. 372, pl. 19, fig. 2 (? fig. 1).

Cylindroteuthis (Communicobelus) subextensoides: Gustomesov, 1964, p. 155, pl. 10, figs. 2–8; Nalnjaeva, 1989, p. 105, pl., figs. 7–8.

Communicobelus subextensoides: Dzyuba, 2001, p. 68, fig. 2.

Lagonibelus (Communicobelus) subextensoides: Dzyuba, 2004, p. 137, pl. 23, fig. 13.

Holotype. Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, specimen no. VI-145/48; Gustomesov, 1964, pl. 10, fig. 6; the Oka River bank near the town of Elatma (Ryazan Region), Russia; Lower Callovian.

Diagnosis. Rostrum large, elongated, subconical and conical. Apex centrally located. Cross-section rounded. Ventral groove occupying half the rostrum's length. Alveolus deep, and apical line significantly eccentric.

Description. The rostrum is large, elongated (Table 1), from subconical to conical in shape with a slightly elongated apical part, the profile of which is slightly asymmetrical. The apex of the rostrum occupies a position close to the central one. The venter can be flattened in the middle part of the rostrum, the dorsal and lateral aspects are convex along their entire length. The ventral groove is well defined (in the studied specimens it is somewhat deepened due to corrosion), long, but developed no more than to the middle of the rostrum. The cross-section is rounded. The alveolus is deep, in adult specimens occupying up to 1/3 of the rostrum or more, and the tip of the alveolus is ventrally displaced. The apical line is eccentric, in the apical region, judging by the transverse split of specimen no. 898/19, it is very close to the venter.

Comparison. It differs from its morphologically closest relative, *C. subextensus* (Nikitin, 1884), in that it is less laterally compressed, has a rounded cross-section, a slightly longer ventral groove, and a more eccentric apical line. Compared to *C. tornatilis* (Phillips, 1870), it is less elongated and overall, more massive.

Remarks. Specimens identified as *Belemnites panderi* d'Orbigny, 1845 from Franz Josef Land (Newton, Teall, 1897, p. 498, pl. 39, figs. 11 (12–13)?) and *Cylindroteuthis subextensa* (Nikitin, 1884) from East Greenland (Spath, 1932, p. 99, pl. 1, fig. 5), placed by Gustomesov (1964) in the synonymy of the described species, belong to other taxa (Dzyuba, 2004; Dzyuba and de Lagausie, 2018). However, the rostrum of *Cylindroteuthis tornatilis* Phillips, 1870 from Hooker of Franz Josef Land, indicated from the Callovian (Ognev, 1933, p. 219, pl. 2, figs. 1, 2), was previously overlooked. The specimen described and illustrated under this name is indistinguishable from *C. subextensoides* and is included here in its synonymy.

The described species shares some external similarities with Middle Jurassic representatives of the genus *Cylindroteuthis*, a subfamily of Cylindroteuthidinae—the Bajocian-Bathonian *C. spathi* Sachs et Nalnjaeva, 1964 and the early Callovian *C. reznitchenkovi* I. Nikitin, 1969—but differs in a less elongated rostrum at all stages of ontogeny, as well as a better-developed ventral groove. Compared to *C. spathi*, it has a more pronounced conical shape.

Distribution. Upper Bathonian, *Apertum* Zone of European Russia (Mordovia); Lower Callovian of European Russia (Ryazan, Kostroma, Saratov regions, Franz Josef Land) and Western Siberia (Shaimsky District). The assumption of a distribution in the Middle Callovian of European Russia (Gustomesov, 1964) has not been confirmed.

Material. Four specimens from the Alatyr III bis locality, 0.65 m below the top of Member I and close levels; Upper Bathonian, *Apertum* Zone; collection of I.A. Meleshin, 2016 and 2025.

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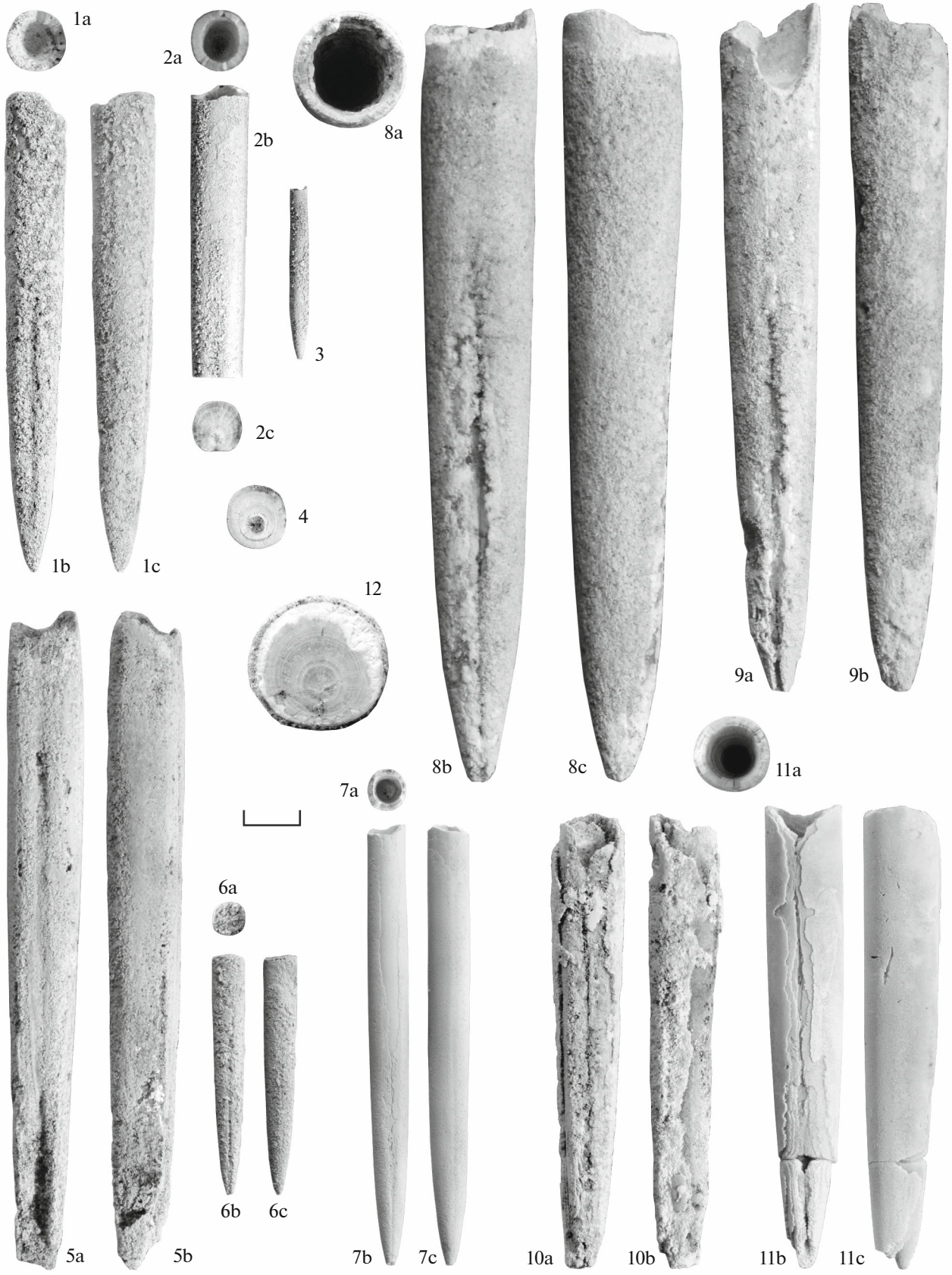
Plate 10


1a
2a
8a
2b
3
2c
4
1b
1c
12
9a
9b
8b
8c
11a
7a
6a
5a
5b
6b
6c
7b
7c
10a
10b
11b
11c

Explanation of Plate 10

Figs. 1–4. *Cylindroteuthis* sp.: (1a) cross-section at the anterior end, (1b) ventral view, (1c) lateral view; (2) specimen GEOCHRON, no. 898/12: (2a) cross-section at the anterior end, (2b) ventral view, (2c) cross-section at the posterior end; (3) specimen GEOCHRON, no. 898/13: ventral view; (4) specimen GEOCHRON, no. 898/21, cross-section in the alveolar region of the rostrum.

Figs. 5, 6. *Cylindroteuthis* sp. indet.: (5) specimen GEOCHRON, no. 898/14: (5a) ventral view, (5b) lateral view; (6) specimen GEOCHRON, no. 898/15, fragment of the postalveolar part of the rostrum: (6a) cross-section at the anterior end, (6b) ventral view, (6c) lateral view.

Fig. 7. *Cylindroteuthis puzosiana* (d'Orbigny, 1842), specimen GEOCHRON, no. 898/16: (7a) cross-section at the anterior end, (7b) ventral view, (7c) lateral view.

Figs. 8–11. *Communicobelus subextensoides* (Gustomesov, 1964): (8) specimen GEOCHRON, no. 898/17: (8a) cross-section at the anterior end, (8b) ventral view, (8c) lateral view; (9) specimen GEOCHRON, no. 898/18: (9a) ventral view, (9b) lateral view; (10) specimen GEOCHRON, no. 898/20: (10a) ventral view, (10b) lateral view; (11) specimen GEOCHRON, no. 898/19: (11a) cross-section at the anterior end, (11b) ventral view, (11c) lateral view.

Fig. 12. Belemnitida indet., specimen GEOCHRON, no. 898/22, cross-section of the postalveolar part of the rostrum near the tip of the alveolus.

Figs. 1–5, 8–12. Alatyr III bis locality; Upper Bathonian, (1–4) *Calyx* Zone, (5, 8, 9, 11, 12) Apertum Zone; (7) Lower Callovian, talus; (10) Upper Bathonian, talus (collected by I.A. Meleshin, 2016 and 2025); (6) Alatyr III locality; Upper Bathonian, 0.5 m below the top of Member I (collected by V.V. Mitta, 2011). Scale bar 10 mm.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not include any studies involving human or animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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