

Detailed biostratigraphy of the Middle Callovian – lowest Oxfordian in the Mikhaylov reference section (Ryazan region, European part of Russia) by ammonites

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Key words: Callovian, Oxfordian, the center of European Russia, infrazonal scale, reference section, ammonites, palaeobiogeography.

Abstract. Study of the sections near the Mikhaylov (Ryazan region) has made it possible to improve the infrazonal subdivision of the Middle Callovian – Lower Oxfordian of the European Russia by ammonites. The Athleta Zone is the most complete in the studied sections. A sequence of kosmoceratid biohorizons (*phaeinum*, *proniae*, *rowlstonense* and *kuklikum*) is established here, as well as infrazonal units based on a phylogenetic sequence of species of the genus *Funiferites*. A study of the paleobiodiversity and frequency of occurrence of ammonites at different intervals of the section showed that the ammonite assemblages of the Athleta Zone are Sub-Boreal or Sub-Tethyan, while in the Lamberti Zone they are Boreal, and in the Lower Oxfordian they are Arctic. It is also shown that the change in ammonite composition in the sections coincides with the cycles of transgressions and regressions of Boreal basins. New species and subspecies of the ammonites *Funiferites allae compressum*, *Cadoceras (Eichwaldiceras) intermedium*, *Brightia (B.) lominadzei*, *B. (B.) progzhellensis*, *B. (B.) eccentrica*, *B. (Glyptia) canaliculata stankevitchae*, *Zieteniceras rarecostatum* are described.

INTRODUCTION

The study of the Callovian and Lower Oxfordian beds of European Russia in recent years is characterized by the transition to a more detailed level of subdivision and the development of new stratigraphic scales based on recognition of biohorizons. As a result of the study of classical and new sections, mainly in Central Russia and the Komi Republic, new variants of the stratigraphic subdivision for the Lower Callovian (Mitta, Starodubtseva, 1998; Gulyaev, 1999, 2001; Mitta, 2000; Gulyaev *et al.*, 2002; Kiselev, Rogov, 2007), Middle Callovian (Kiselev, 1999, 2001, 2006; Kiselev, Meledina, 2004) and Upper Callovian (Mitta, 2003; Kiselev *et al.*, 2003; Kiselev *et al.*, 2013), as well as the Lower Oxfordian (Kiselev *et al.*, 2013), have been pro-

posed. However, the Upper Callovian stratigraphic succession remains relatively poorly proven until now. This is mainly due to the fact that the Upper Callovian deposits are not so widespread in European Russia in comparison with the Lower and Middle Callovian. Also, most of the known Upper Callovian sections are characterized by the development of distinct condensation levels, which reduce the completeness of the sections. For this reason, sections in which the Upper Callovian is represented in the full extent of both the *Peltoceras athleta* and *Quenstedtoceras lamberti* zones are quite rare in this region. The completeness of the Upper Callovian in the axial part of the area of Callovian deposits of the Russian Platform (the meridional sector of the Middle-Russian Sea), which includes the Izhma, Sysola and Unzha river basins, Nizhny Novgorod region and the Republic

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of Mordovia, is especially reduced. Here, the Upper Callovian is either completely eroded (the Izhma and Sysola river basins, the Makaryev and Manturovo district of the Unzha river basin, the Ivanovo region, the Nizhny Novgorod region and Mordovia) or is represented by the lower part of the Athleta Zone (Kologriv district of the Kostroma region). In this regard, the territory of the south of the Moscow syneclide, mainly the Ryazan and Moscow regions, is of key importance for the development of the standard infrazonal scale of the Upper Callovian and the Lower Oxfordian of the whole European Russia.

In the lateral and southern parts of the area of Callovian deposits (the Ryazan, Tula, Moscow, Yaroslavl, Orenburg, Saratov regions and Tatarstan) the Upper Callovian is represented by both zones, less often by one zone (Lamberti Zone – Tarkhanovskaya Pristan, Dubki). In most sections, where the Upper Callovian has a twofold subdivision, both zones are also reduced in completeness as a result of the lacking of peculiar intervals.

Recently several papers providing some new data on the zonal and infrazonal subdivision of the Upper Callovian have been published. So, D.N. Kiselev (1999, 2001) confirmed the presence of the Phaeinum and Proniae subzones of the Athleta Zone in Central Russia. Later, V.V. Mitta (2003), on the base of observations made in the Tarkhanovskaya Pristan and Dubki sections, has recognized the *paucicostatum* biohorizon of the Lamberti Zone and suggested further the possibility of the Lamberti Zone subdivision in the Russian Platform, with the potential recognition of the standard succession of infrazonal units. A preliminary version of the detailed subdivision of the Upper Callovian including 5 subzones and 8 biohorizons was proposed by D.N. Kiselev and M.A. Rogov (in Gulyaev *et al.*, 2002; Kiselev *et al.*, 2003; Kiselev, Rogov, 2005). All subzones (Phaeinum, Proniae, Spinosum, Henrici, Lamberti) coincide with the subzones of the Sub-Boreal scale previously established in the Western Europe, but the proposed sequence of biohorizons was somewhat different from the West European one. Six new biohorizons have been recognized: *allae allae*, *allae compressum*, *patruus*, *funiferus*, *kuklikum* and *mojarowskii*. This subdivision was mostly declarative, and only recently some biohorizons (belonging to the Lamberti Zone and the Lower Oxfordian) were described in detail (Kiselev *et al.*, 2013).

In this paper we present data on the study of the most important sections of the Middle-Upper Callovian and Lower Oxfordian in the vicinity of the Mikhaylov city (Fig. 1), on the basis of which the stratigraphic subdivision of the Upper Callovian, especially of the Athleta Zone, was developed.

DESCRIPTION OF SECTIONS

Jurassic deposits in the Pronya River basin (south-western part of the Ryazan region) became known after a small article by Melchior Neumayr (1876), in which ammonites from the vicinity of the village of Chulkovo of Skopinsky district were described (Fig. 1a). He showed that the layers from which the ammonites originate are faunistically very close to the *Ornatenton*-Formation of Germany. He described 7 species of ammonites, including a new one – *Perisphinctes scopinensis*. Neumayr never actually visited this region and received a collection of ammonites put together by others. Subsequently, the fauna from the Skopin sections was studied in detail by Lorenz Teisseyre (a disciple of Neumayr), who collected ammonites directly from the sections. In his article (Teisseyre, 1883) he described an assemblage from the clay of Chulkovo Mine, which included 26 previously known species and 7 new ones: *Harpoceras rossense*, *Cosmoceras subnodatum*, *C. proniae*, *C. jenzeni*, *C. pollucinum*, *Perisphinctes subaurigerus*, *P. rjasanensis*, *P. vischniakoffi*. Most of these ammonites are represented by pyrite nuclei and are now very poorly preserved due to pyrite decay (Pl. 20: 1–6). The first descriptions of the Callovian sections on the Pronya River were made by I. Lahusen (1883). Near to Svistovo village he recognized three units with Callovian ammonites: “a” (the modern Koenigi Zone of the Lower Callovian), “b” (= Coronatum Zone of Middle Callovian) and “c” (= upper part of the Coronatum Zone and Athleta Zone). A similar description of the sections near to Svistovo and Simeon villages was subsequently made by P.A. Gerasimov in 1938 (Gerasimov, 1971; Gerasimov *et al.*, 1996). The first detailed description of the section near Mikhaylov town in the quarries of the factory “Mikhaylovtsment” was made by M.A. Rogov and D.N. Kiselev (Kiselev, 1999). In this article only the 8-meter member of relatively uniform clays of the Middle-Upper Callovian was considered. The study of the ammonite succession made it possible to establish the presence of the Grossouvrei Subzone of the Coronatum Zone and the Phaeinum Subzone of the Athleta Zone for the first time in European Russia. Here a new species of *Funiferites allae* (Kiselev) was described and stratigraphic position of the species *F. patruus* (Eichw.) was established.

The paper by V.V. Mitta (2000) provides a brief description of three sections of the Mikhaylov area (Mikhaylovtsment, Spartak and Gorenka). Of these, the Mikhaylovtsment section was described in more detail, but the whole clayey part of the succession (uppermost Middle Callovian – Oxfordian) was considered as a single bed, and details concerning the ammonite distribution here were not given.

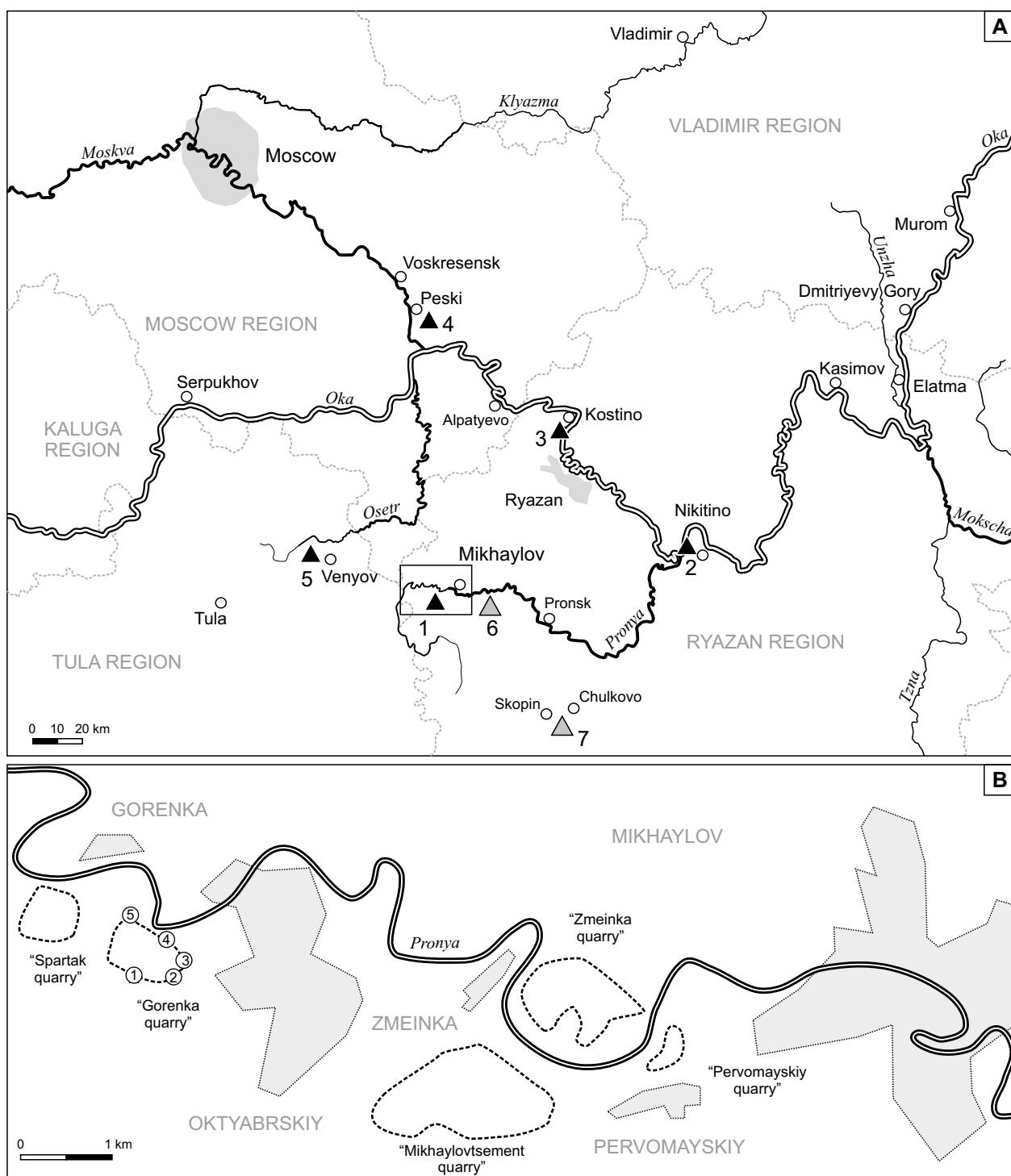


Fig. 1. Location of the described sections

A. In the southwestern part of the Moscow syncline; **B.** In the vicinity of Mikhaylov (corresponds to the territory marked with a rectangle in figure A)

Black symbols labelled the locations of modern sections of Callovian and Oxfordian, gray symbols – historical sections. 1 – Mikhaylov; 2 – Nikitino; 3 – Kostino; 4 – Peski; 5 – Venyov quarry; 6 – Svistovo; 7 – Chulkovo

In the same year M.A. Rogov (2000) described Callovian oppeliids of the genus *Brightia*, including 8 species from the sections at Mikhaylov. Among these species, 3 new ones with holotypes from the Mikhaylov area were erected.

In the paper by Kiselev *et al.* (2003) the infrazonal scheme of the Mikhaylov section and the ranges of ammonites of the genus *Funiferites* were first shown. This variant of the subdivision was adopted in this publication.

The Callovian and Oxfordian deposits in the quarries of the "Mikhaylov" factory were studied by the authors of this work near Pervomaisky and Zmeinka villages and "Serebryansky" factory (former "Spartak" factory) near Gorenka village. All of them are located 2–7 km to the west of Mikhaylov and are in close proximity to each other, at a distance of 1–2 km (Fig. 1b). Despite the close proximity, significant lateral facies variability is observed in the sections, even within a single quarry, as well as the wedging of certain layers. The sharpest facies shift is observed in the lower part of the section (Lower–Middle Callovian), where the lithological composition of isochronous deposits varies from finely dispersed clay to medium-grained sand at a distance ~500 m; in some cases thickness changes at the same distance could be nearly 15 times (from 0.5 to more than 8 m). This makes it necessary to describe several sections in one quarry.

Mikhaylov section I

The section is located in the Mikhaylov quarry. Its study was conducted in the years 1999–2005, therefore, due to the development of a quarry, at the present time this section does not exist anymore.

Directly above the Carboniferous limestones, the following sequence of Jurassic beds was exposed (Fig. 2):

Bed 1 (about 2 m): black or dark brown, soft, non-layered silt, with pronounced horizontally oriented bioturbations. The fauna is rare and is represented mainly by belemnites of *Pachyteuthis* ex gr. *subrediviva* and bivalves, predominantly *Astarte* sp.

Bed 2 (0.65–0.70 m): brown, red at the top, soft, non-layered clayey sand. The lower boundary of the bed is sharp. According to observations in 2017, analogues of bed 1–2, without fossils, are exposed in a limited area and have

a thickness of 0.5 to 2.0 m. At the base of the section, a layer of well-rounded pebbles (0.2–0.3 m), consisting of debris of Carboniferous rocks (mainly cherts) is observed.

Bed 3 (0.3–0.4 m): red-brown, carbonate-ferruginous, fine and medium-grained sandstone, with frequent oval concretions of light grey carbonate sandstone (up to $0.5 \times 0.2 \times 0.2$ m). The bottom of the bed smoothly passes into the underlying bed. Ammonites are occasionally found in nodules and are represented by *Cadoceras* (*Rondiceras*) *milaschevici milaschevici* (Nik.), *Pseudocadoceras cuneatum* Sas., *Kosmoceras* (*Gulielmites*) *medea medea* Call. In the section "Pervomaisky" from the same level, along with *K. (G.) medea medea* Call. the following taxa were found: *Cadoceras articoides* Kiselev et Meledina, *Anaplanulites submutatus* (Nik.) ("Zmeinka"), *Choffatia* cf. *graciosa* (Siem.). In the year 2017 a fragment of *Rossiensiceras uhligi* (Neum.) (Pl. 19: 7) in the analogs of this layer (section 1, bed 2 as described in 2017) was also found.

Bed 4 (0.7 m): brownish-grey, turning into intensely brown, clayey sand. Near top occasionally are found rounded concretions of carbonate sandstone with columnals of the crinoids *Acrochordocrinus* sp.

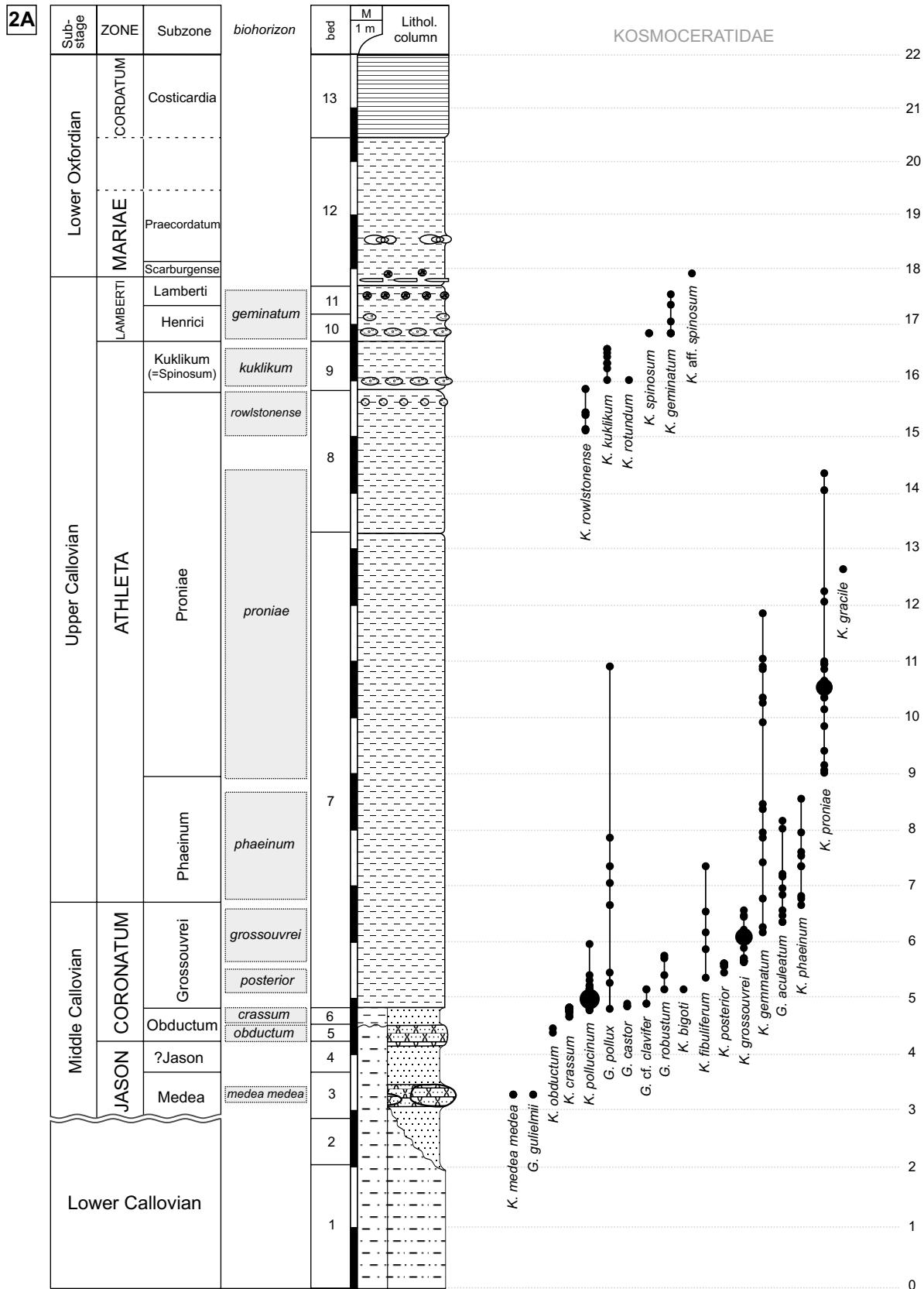
Bed 5 (0.15–0.20 m): light brownish-grey sandy siltstone, smoothly passing into the underlying bed. Fossils are rare, are poorly preserved, and are represented by nuclei. *Kosmoceras* (*Gulielmites*) *obductum* (Buckm.), *Longaeviceeras praestenolobum* Kiselev et Meledina, *Pseudocadoceras* cf. *macellum* Kiselev.

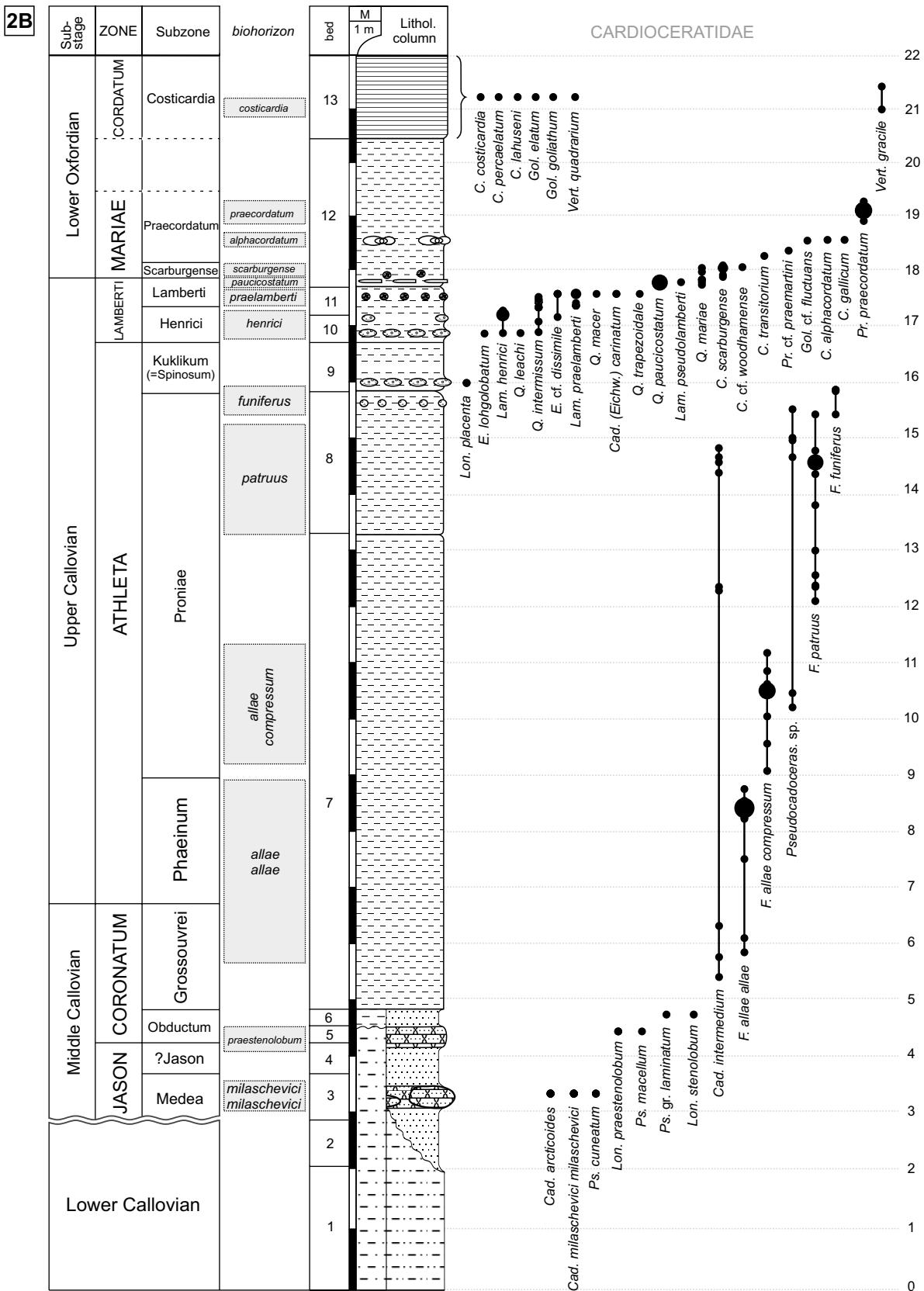
Bed 6 (0.2–0.3 m): dark-brown silty-sandy clay with *Erymnoceras* ex gr. *coronatum* (Brug.), *Rollierites* sp., *Kosmoceras* (*Zugokosmoceras*) *crassum* Tint. Laterally this bed is facially replaced by unevenly colored, rusty-brown or ocherous, laminated clayey silt, with ammonites *K. (Z.) crassum* Tint. (Pl. 22: 1), *K. (Kosmoceras) pollucinum* Teiss. (Pl. 1: 5), *Gulielmiceras* (*Spinikosmoceras*) *castor* (Rein.), *Erymnoceras coronatum* (Brug.) (Pl. 19: 3), *E. baylei* Jeanne (Pl. 19: 5), *Rollierites* sp., *Zieteniceras* cf. *rarecostatum* sp. nov., *Brightia* (*B.*) *eccentrica* sp. nov., *Orbignyiceras orbignyi* (Tsyts.), *O. lonsdalii* (Pratt) (Pl. 18: 5), *Lunuloceras fallax* (Zeiss), *Rossiensiceras rossense* (Teiss.), *Alcidia* cf. *nurrhaensis* (Spath) (Pl. 16: 22).

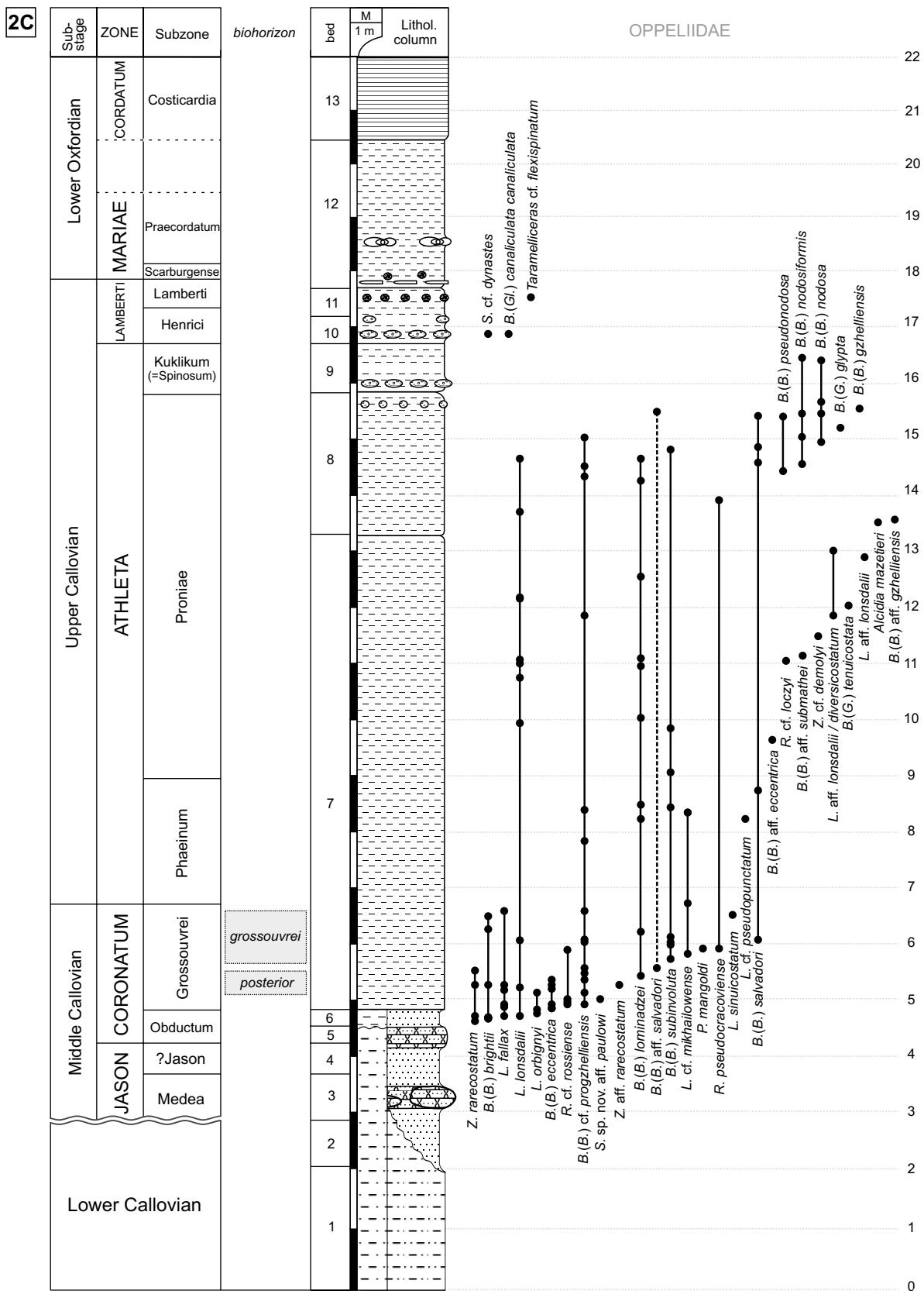
Bed 7 (8.3 m): brownish-grey, homogeneous, massive clay. Here the following sequence of ammonite assemblages (from below upwards) is observed:

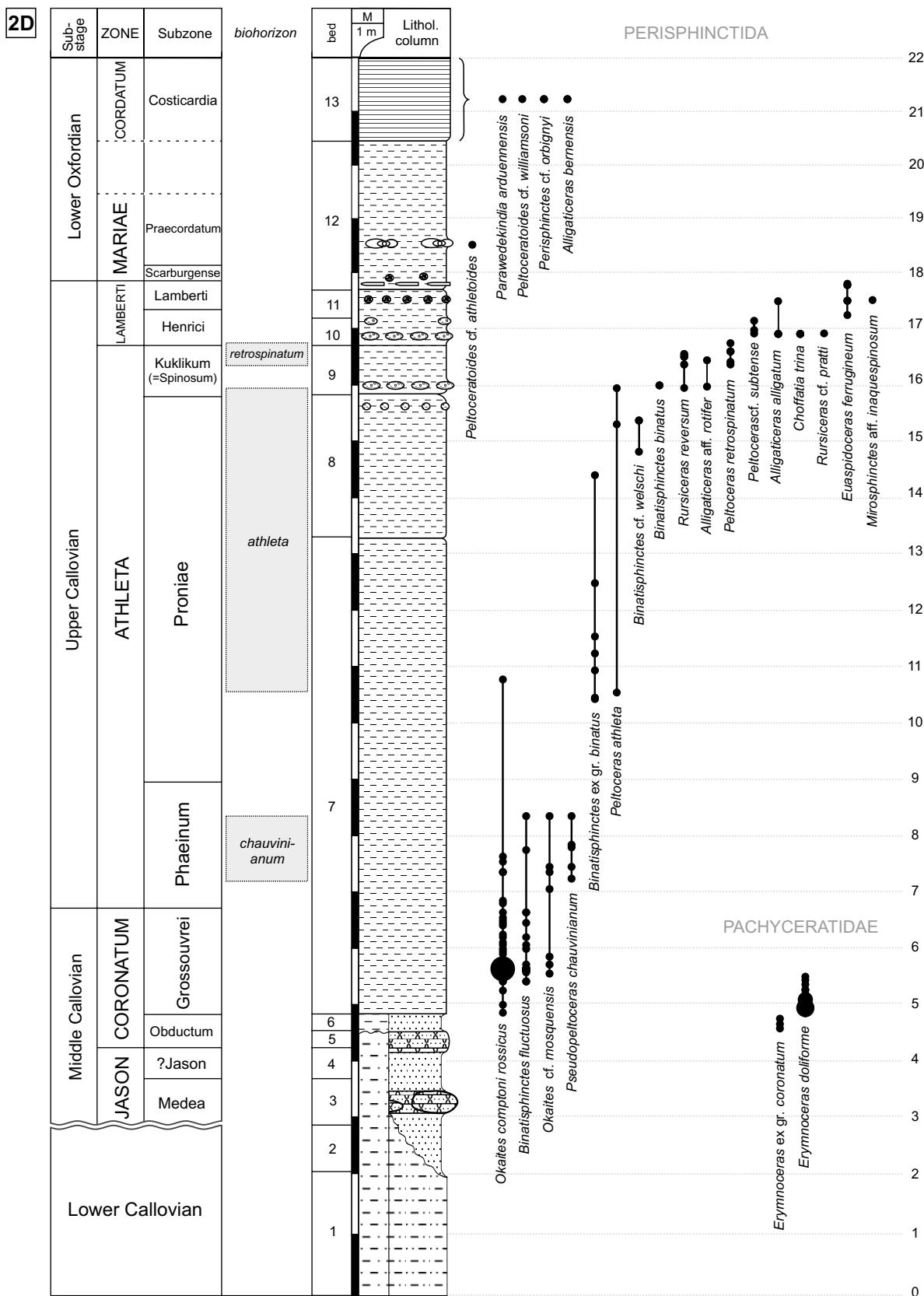
Fig. 2. Distribution of ammonites in the "Mikhaylov" section: A – Kosmoceratidae; B – Cardioceratidae; C – Oppeliidae; D – Perisphinctida and Pachyceratidae

For captions of lithology (for Figs 2–5) see Fig. 5. Abbreviations of genera names (for Figs 2–5): B. – *Brightia*; Bin. – *Binatisphinctes*; C. – *Cardioceras*; Cad. – *Cadoceras*; Ch. – *Choffatia*; Cham. – *Chamossetia*; E. – *Eboraciceras*; Euasp. – *Euaspidoceras*; F. – *Funiferites*; G. – *Gulielmiceras*; Gl. – *Glyptia*; Gol. – *Goliathiceras*; I. – *Indosphinctes*; K – *Kosmoceras*; Kepp. – *Kepplerites*; L. – *Lunuloceras*; Lam. – *Lamberticeras*; Lon. – *Longaeviceeras*; Ok. – *Okaites*; Or. – *Orionoides*; Pelt. – *Peltoceras*; Pr. – *Protocardioceras*; Ps. – *Pseudocadoceras*; Q. – *Quenstedtoceras*; R. – *Rossiensiceras*; S. – *Sublunuloceras*; Vert. – *Vertebriceras*; Z. – *Zieteniceras*









7a (0.00–0.75 m from bottom): *Kosmoceras (Zugokosmoceras) posterior* Brink. (Pl. 1: 4), *Gulielmiceras (Spinikosmoceras) pollux* (Rein.) (Pl. 2: 5), *G. (S.) cf. clavifer* (Tint.), *G. (S.) robustum* (Tint.), *Erymnoceras doliforme* Rom. (Pl. 21: 4), *Binatisphinctes fluctuosus* Buckm., *Okaites comptoni rossicus* (Siem.) (Pl. 12: 3), *Zieteniceras rarecostatum* sp. nov. (Pl. 17: 10–14), *Brightia (Brightia) eccentrica* sp. nov., *B. (B.) brightii* (Pratt), *B. (B.) rursicostata* (Buckm.), *B. (B.) progzhellensis* sp. nov. (Pl. 15: 6), *B. (B.) mangoldi* (Lominadze) (Pl. 15: 18), *Orbignyiceras lonsdalii* (Pratt), *O. orbignyi* (Tsyt.), *Lunuloceras fallax* (Zeiss) (Pl. 16: 24), *Rossiensiceras rossiense* (Teis.) (Pl. 15: 27), *Putealiceras balkarensis* (Lominadze).

7b (0.75–1.80 m): *Kosmoceras (Zugokosmoceras) grossouvrei* Douv. (Pl. 1: 1–3), *K. (Kosmoceras) fibuliferum* Buckm., *K. (K.) gemmatum* (Phillips) (Pl. 1: 6, 7), *Gulielmiceras (Spinikosmoceras) pollux* (Rein.) (Pl. 2: 6), *G. (S.) aculeatus* (Eichw.), *Binatisphinctes fluctuosus* Buckm. (Pl. 12: 5, 6; Pl. 22: 2), *Okaites comptoni comptoni* (Pratt), *Funiferites allae allae* (Kiselev) (Pl. 5: 3; Pl. 6: 1), *Cadoceras (Eichwaldiceras) intermedium* sp. nov. (Pl. 9: 1, 3), *Brightia (B.) brightii* (Pratt) (Pl. 15: 3), *B. (B.) pseudocracoviense* (Tsytvitch), *B. (B.) cf./aff. progzhellensis* sp. nov. (Pl. 15: 5), *B. (B.) subinvoluta* (Bonar.) (Pl. 16: 8), *B. (B.) mangoldi* (Lominadze) (Pl. 15: 19), *Rossiensiceras cf. rossiense* (Teiss.), *Putealiceras virile* (Zeiss), *Zieteniceras rarecostatum* sp. nov., *Orbignyiceras lonsdalii* (Pratt), *O. cf. michailowense* (Zeiss), *Lunuloceras fallax* (Zeiss), *L. sinuicostatum* (Zeiss).

7c (1.8–4.0 m): *Kosmoceras (Zugokosmoceras) phaeinum* (Buckm.) (Pl. 2: 2), *K. (Kosmoceras) fibuliferum* (Buckm.), *K. (K.) gemmatum* (Phillips) (Pl. 4: 1), *Gulielmiceras (Spinikosmoceras) ornatus* (Schlotheim) (Pl. 2: 7), *G. (Spinikosmoceras) aculeatus* (Eichw.), *Binatisphinctes fluctuosus* Buckm., *Okaites mosquensis* (Fischer) (Pl. 11: 2), *Pseudopeltoceras chauvinianum* (d'Orb.) (Pl. 11: 4), *Funiferites allae allae* (Kiselev) (Pl. 5: 1, 2; Pl. 6: 2), *Brightia (B.) progzhellensis* sp. nov., *B. (B.) luminadzei* sp. nov., *B. (B.) cf. subinvoluta* (Bonar.), *B. (B.) salvadori* (Parona et Bonar.), *Orbignyiceras cf. michailowense* (Zeiss), *Orbignyiceras pseudopunctatum* (Lahusen).

7d (4.0–8.3 m): *Kosmoceras (Lobokosmoceras) proniae* Teiss. (Pl. 2: 1), *K. (Kosmoceras) gemmatum* Phill., *K. (K.) gracile* Kopik, *Gulielmiceras (Spinikosmoceras) cf. ornatus* (Schlotheim), *G. (Spinikosmoceras) aculeatus* (Eichw.), *Binatisphinctes ex gr. binatus* Buckm., *Pseudopeltoceras aff. chauvinianum* (d'Orb.), *Peltoceras athleta* (Phillips), *Funiferites patruus* (Eichw.) (Pl. 5: 8, 10), *F. allae compressum* subsp. nov. (Pl. 5: 4, 6), *Cadoceras (Eichwaldiceras) intermedium* sp. nov. (Pl. 9: 2, 4, 5), *Orbignyiceras kasiense* Repin et Rashvan, *O. lonsdalii* (Pratt), *O. aff. lonsdalii* (Pratt), *O. diversicostatum* (Gerard et Contaut), *Brightia (Brightia) nodosiformis* Rogov, *B. (B.) luminadzei* sp. nov.,

B. (B.) cf. luminadzei sp. nov (Pl. 17: 8), *B. (B.) cf. subinvoluta* (Bonar.), *B. (B.) progzhellensis* sp. nov. (Pl. 15: 10), *B. (Glyptia) tenuicostata* sp. nov., *Rossiensiceras cf. loczyi* (Zeiss), *Zieteniceras cf. demolyi* (Lem.) (Pl. 17: 12).

Bed 8 (2.7 m): Silty clay, brownish-grey, dense, homogeneous, non-layered. In the top of the bed there is a horizon of small nutlike concretions of phosphatized marlstone. Ammonites are found in clay and nodules: *Kosmoceras (Lobokosmoceras) proniae* Teiss. (from the lowermost 2 m of the bed), *K. (L.) rowlstonense* (Young et Bird) (from the upper 2 m of the bed) (Pl. 2: 3), *K. (Kosmoceras) cf. rotundum* (Quenst.), *Funiferites funiferus* (Phill.) (Pl. 6: 3, 4), *F. patruus* (Eichw.), *Brightia (Brightia) nodosa* (Quenstedt) (Pl. 15: 20), *B. (B.) pseudonodosa* (Tsytvitch) (Pl. 17: 5), *B. (B.) nodosiformis* Rogov (Pl. 15: 22), *B. (B.) glypta* (Buckman), *B. (B.) gzhellensis* Rogov, *B. (B.) salvadori* (Parona et Bonar.), *B. (B.) aff. salvadori* (Parona et Bonar.) (Pl. 16: 5, 7), *Orbignyiceras cf. diversicostatum* (Gerard et Contaut) (Pl. 17: 17), *Sublunuloceras cf. dynastes* (Waagen) (Pl. 20: 11), *Alcidia mazetieri* (Petitclerc) (Pl. 19: 6).

Bed 9 (1.3 m): silty clay, brownish-grey, dense, homogeneous, non-layered, overgrown with ferruginous oolites. The concretions of a yellowish-grey oolitic marlstone are often located in the base of the bed. The following ammonites are found in the concretions: *Kosmoceras (Kosmoceras) rotundum* (Quenst.), *K. (Lobokosmoceras) kuklikum* (Buckm.) (Pl. 2: 4), *Longaeciceras placenta* (Leck.) (Pl. 7: 1, 2; Pl. 9: 6), *Brightia (Brightia) nodosa* (Quenstedt), *B. (B.) nodosiformis* Rogov, *Orionoides cf. termieri* Gerard et Contaut (Pl. 14: 3), *Binatisphinctes binatus* (Leckenby) (Pl. 14: 2), *Alligaticeras aff. rotifer* (Brown) sensu Cox (Pl. 14: 1). Ammonites *K. (K.) rotundum* (Quenst.), *Alligaticeras alligatum* Buckm., *Peltoceras retrospinatum* Gerard et Contaut sensu Courville et Bonnot (Pl. 13: 1) are found in the middle part of the bed, above the concretion horizon. In clay the last *Funiferites funiferus* (Phill.) occur at 2 cm below the first concretion horizon.

Bed 10 (0.5 m): silty clay, brownish-grey, dense, ferruginous-oolitic, with concretions of yellowish-grey marlstone, forming a horizon in the bottom or middle part of the bed. The following ammonites are found in the concretions: *Lamberticeras henrici* Douv. (Pl. 9: 7), *Eboraciceras longilobatum* (Buckman) (Pl. 8: 1), *Quenstedtoceras intermissum* (Buckm.), *Q. leachi* (Sow.) emend. Arkell (Pl. 9: 12), *Q. damoni* (Nikitin) (Pl. 9: 11), *Peltoceras cf. subtense* (Leckenby), *Choffatia cf. poculum* (Leckenby), *Brightia (Glyptia) canaliculata canaliculata* (Quenstedt).

Bed 11 (0.5 m): clay brownish-grey, dense, not laminated, with ferruginous oolites. In the top there is a horizon of strongly phosphatized marlstone concretions, dark at the fracture. The following ammonites were found in clay and concretions: *Kosmoceras (Lobokosmoceras) geminatum*

(Buckm.), *Lamberticeras praelamberti* (Douv.) (Pl. 9: 8, 9), *Cadoceras* (*Eichwaldiceras*) *carinatum* (Eichw.), *Quenstedtoceras trapezoidalis* Troitz., *Q. macer* (Quenst.) (Pl. 9: 10), *Rursiceras reversum* (Leckenby), *R. pratti* Spath, *Euaspidoceras ferrugineum* Jeannet, *Taramelliceras* cf. *flexispinatum* (Oppel) (Pl. 19: 8).

Bed 12 (2.5–2.7 m): silty clay dark grey, dense, homogeneous, layered. The following sequence of ammonite assemblages is observed in the bed:

12a (0.15 m from bottom): the bed enriched with the *Cylindroteuthis spicularis* (Phill.) guards and deformed, phosphatized nuclei of ammonite shells of *Kosmoceras* sp., *Lamberticeras* cf. *pseudolamberti* (Sow.), *Quenstedtoceras paucicostatum* (Lange).

12b (0.15–0.50 m): horizon with scattered shells of *Cardioceras* (*Scarburgiceras*) *scarburgense*/cf. *scarburgense* (Young et Bird) (Pl. 8: 6–8), *C. (S.) transitorium* Spath (Pl. 9: 16), *Protocardioceras* cf. *praemartini* (Spath) (Pl. 9: 14), *Quenstedtoceras* cf. *mariae* (d'Orb.), *Q. aff. paucicostatum* (Lange).

12c (0.5–0.7 m): horizon with large marlstone-phosphatized shells *Cardioceras* (*Scarburgiceras*) *alphacordatum* Spath (Pl. 11: 1), *C. (Scotiocardioceras) gallicum* Maire (Pl. 9: 13), *Goliathiceras* (*Pachycardioceras*) sp., *Peltoceras athleoides* (Lahusen).

12d (1.0–1.6 m): horizon with imprints and deformed nuclei of *Protocardioceras praecordatum* (Douville) (Pl. 11: 2, 3).

Bed 13 (1.5 m): thin-horizontally layered, dense, viscous, coal-black or brownish-grey clay with *Cardioceras* (*Cardioceras*) *corticardia* Buckman (Pl. 10: 11), *C. (C.) percaelatum* Pavlow (Pl. 9: 17), *C. (Scotiocardioceras) lahuseni* Maire (Pl. 10: 6), *Goliathiceras goliathum* (d'Orb.) (Pl. 10: 1), *G. (Pachycardioceras) elatum* (Maire) (Pl. 10: 2), *Vertebriceras quadrarium* var. *quadrarium* (Buckman) (Pl. 10: 8, 10), *V. quadrarium* var. *biplicatum* Arkell (Pl. 10: 4), *Vertebriceras gracile* Arkell (Pl. 10: 5, 7, 9), *Peltoceratoides williamsoni* (Phillips) var. *constantii* (d'Orbigny) (Pl. 21: 1, 2), *Parawedekindia arduennensis* (d'Orb.) (Pl. 21: 3), *Alligaticeras* (*Properisphinctes*) *bernensis* (Loriol), *Perisphinctes orbignyi* Tarkowski (Pl. 13: 4, 5).

Mikhaylovtsement II

Like the first section, this is located in the “Mikhaylovtsement” quarry, but its description was made in the year

2017. It differs from the Mikhaylovtsement I section in facies and thickness (Fig. 3).

Bed 1 (up to 6.5 m): dark grey or black sandy or clayey silt, sometimes turning into a weakly cemented silty sandstone. Small (0.50–0.15 cm) concretions of pyrite are scattered in the layer. Closer to the top, the bed is bioturbated in the *Nereites* type. In the bed, the deformed shells of ammonites *Cadoceras* (*Paracadoceras*) spp., which retain a pearly lustre and are filled with sediment throughout the shell, are scattered. In the upper part of the bed (0.5–0.6 m below the top) ammonites form accumulations. The following lithological horizons are distinguished in the bed (according to observations of MA Rogov):

1a (0.60 m): beige-red clayey silt, with intercalations of grey silty clay.

1b (0.35 m): grey silt with ocher spots.

1c (3.65 m): sandy silt, strongly bioturbated, dark greenish-grey, sometimes brownish. Across the bed there are pyrite nodules of irregular shape (pseudomorphs along the bioturbations and petrified wood (often associated with pyrite). In the upper 2 m of the bed comparatively often there occur small clusters of shell rock, consisting of debris and shells of bivalves, ammonites and belemnite guards.

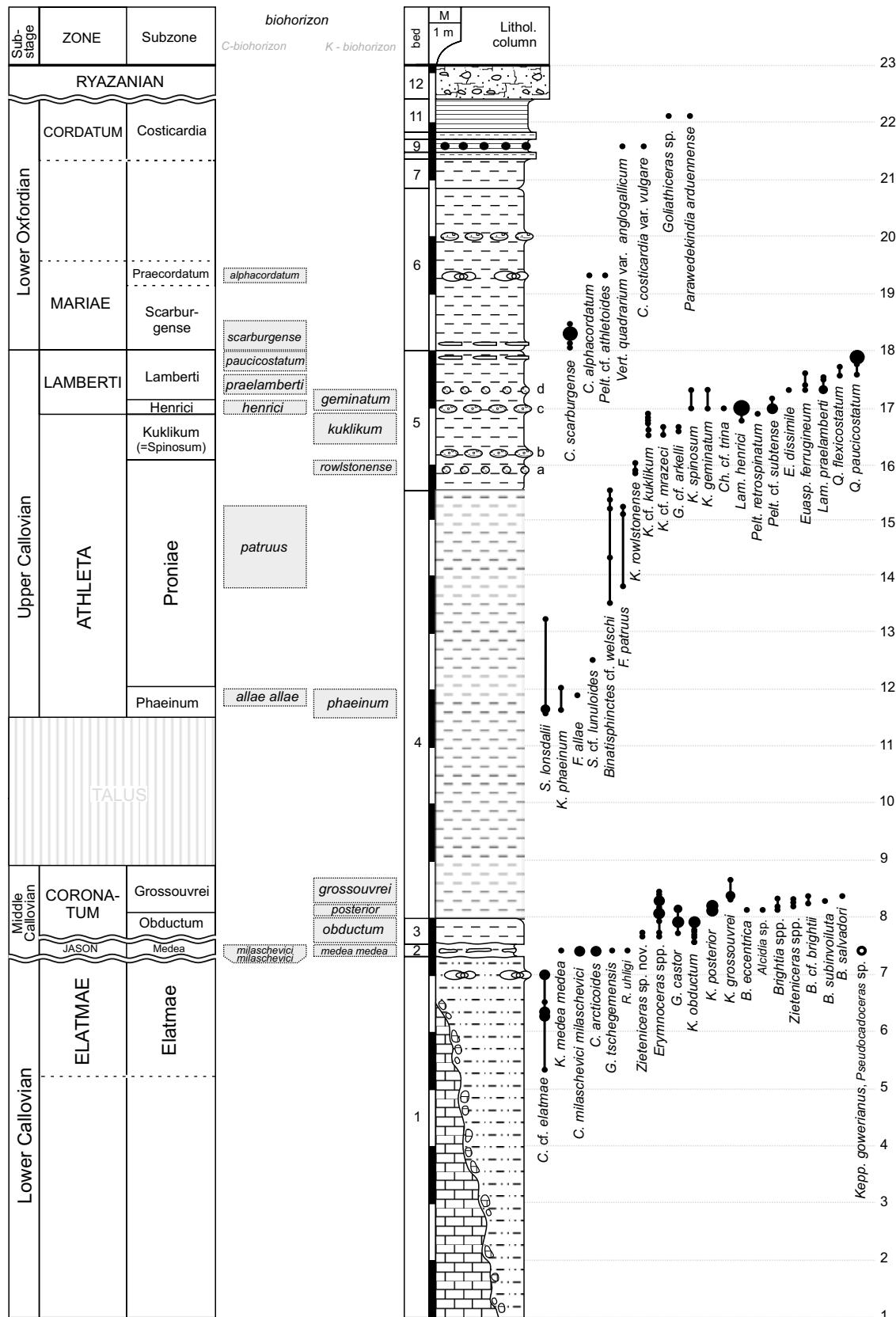
Bed 2 (0.05–0.10 m): brownish-grey or brown silt, with a mosaic inclusion of black sand and sandstone. In the bed there is a pronounced horizon of flattened redeposited concretions (20–30 × 2–5 cm) of sandy siltstone, brownish-grey inside and ocher-grey outside. A light crust on the surface of the concretions is separated by a sharp boundary, both from the dark core and from the matrix of the bed. The bed is full of broken shells of ammonites, bivalves and gastropods. Ammonites include *Cadoceras arcticoides* Kiselev (attribution of this species to any subgenus is unclear. Here and throughout the text such species are given without indication of subgenera), *C. milashevici* (Nik.), *Kosmoceras medea medea* Call., *Gulielmiceras* (*Spinikosmoceras*) *tschegemensis* (Tschichatshev), *Indosphinctes* cf. *mutatus* (Traut.). Bivalve mollusks are dominated by large *Astarte*, *Fibropecten* and *Modiolus*.

In the concretions *Kepplerites goverianus* (Sow.) (predominant) and sporadic *Pseudocadoceras* were found. Sometimes concretions are eroded and *Kepplerites* nuclei are found directly in the matrix of the bed.

Analogues of beds 1–2, without fossils have a thickness of 0.5 to 2.0 m at the opposite side of the quarry. At the base of the section there is a layer of well-rounded pebbles (0.2–0.3 m thick) consisting of fragments of Carboniferous rocks

Fig. 3. Distribution of ammonites in the “Mikhaylovtsement II” section

White circles correspond to specimens found in redeposited nodules



(Pl. 23: 1). Bed 2 in the strike is replaced by red and light grey oolitic marl. In this marl bed, in addition to cosmoceratids and cardioceratids, a *Rossiensiceras uhligi* (Neum.) fragment was also found (Pl. 19: 7).

Bed 3 (0.5 m): non laminated, bioturbated, light brownish-grey silty clay. The lower 0.05–0.10 m of the bed has a darker color. In the top there is a thin ferruginous layer, traced laterally along the entire section. Ammonites are found throughout the bed, among them *Erymnoceras coronatum* (Brug.) (Pl. 19: 1, 2), *Kosmoceras (Gulielmites) obductum* (Buckm.), *Gulielmiceras (Spinikosmoceras) castor* (Rein.), *Longaeviceras stenolobum* (Keys.). The bottom of this bed is irregular, wavy, sometimes directly overlapping the redeposited concretions of bed 2, and sometimes it is flush with them, which can lead to confusion in the definition of the boundary.

Bed 4 (7.5 m): non laminar, dense, homogeneous, light brownish-grey clay. Ammonites are found throughout the bed, in the lower part (about 1 m) they are common, in the upper part (4 m below the top) became rare. In the interval 1.0–3.5 m above the bottom the bed is covered with a talus, so it was not possible to study it. Nevertheless, a sequence of ammonite assemblages, analogous to bed 7 in the Mikhaylovtsen I, was revealed in the bed.

Bed 5 (2.2–2.5 m): dense, slightly shaly, intensely bioturbated, light grey clay. In the bed there are 4 horizons of oolitic, sometimes phosphatized, marlstone nodules, which are characterized by diverse size and habitus and smoothly pass into the matrix of the bed.

Horizon A – oolitic, slightly phosphatized marlstone, brownish grey when fractured, represented by nodules of potato size and habitus. The horizon is located 26–30 cm above the bottom and does not form a marked horizon. Ammonites are represented by *Kosmoceras (Lobokosmoceras) rowlstonense* (Young et Bird).

Horizon B – concretions of light, yellowish-whitish at the break, oolitic marlstone of elongated habit and large size (up to 0.5 m in length). This is distinctly marked horizon, well traced through all sections near to Mikhaylov, is located some 75–80 cm above the bottom of the bed. Fauna is rare. Trigoniids are most often found amongst the bivalves. Ammonites are represented by nuclei, sometimes with a deformed body chamber, without a shell layer. Among them *Kosmoceras (Kosmoceras) cf. rotundum* (Quenst.) are defined.

Between the horizon B and C there is an interval (70–75 cm) without concretions. Ammonites occurred throughout this interval as crushed clayey moulds, they are represented mainly by *Kosmoceras (Lobokosmoceras) cf. kuklikum* (Buckman), *K. cf. mrazecii* Simionescu, *Gulielmiceras cf. arkelli* (Mak.), while aspidoceratids *Peltoceras ret-*

rospinatum Gerard et Contaut sensu Courville et Bonnot and *Rursiceras* spp. are less common here.

Horizon C – marlstone concretions as in horizon B. The color of the rock on fracturing it is different – light grey, not yellowish. This horizon (1,3–1,4 m above the bottom of the bed) is also well-traced throughout all the studied sections. Ammonites are often found, they are mainly represented by *Lamberticeras henrici* (R. Douville), *Kosmoceras (Kosmoceras) spinosum* (Sow.), *K. (Lobokosmoceras) geminatum* (Buckman), *Peltoceras subtense* (Leck.), *P. retrospinatum* Gerard et Contaut sensu Bonnot (Pl. 12: 1), *Choffatia cf. trina* (Buckm.).

Horizon D – small, potato-like concretions of oolitic marlstone, with rare larger concretions (up to 20 cm). Inner parts of large nodules are strongly phosphatized, dark brown or black in color. The horizon is located at 1,7–1,9 m above the bottom of the bed, sometimes it could be missing. Ammonites are preserved as phosphatized nuclei with shell remnants. They are represented by *Lamberticeras praelamberti* (R. Douville), *Eboraciceras dissimile* (Brown), *Kosmoceras (Kosmoceras) spinosum* (Sow.), *K. (Lobokosmoceras) geminatum* (Buckman) and *Euaspidoceras ferrugineum* Jeannet.

In the upper part of the bed (5–7 cm below the top) a well-traced horizon of condensation marked by numerous belemnite rostra is occurred. Ammonites preserved as clayey moulds are regarded as belonging to *Quenstedtoceras paucicostatum* (Lange), while in the concretions of phosphatized marlstone *Lamberticeras pseudolamberti* (Sintzow) (Pl. 8: 2, 3) are found.

The top is well distinguished in the section, while the base of the bed differs indistinctly from the top of the previous bed, mainly in a light grey color.

Bed 6 (2.6–2.7 m): non laminated, grey clay, with a uniform texture. At 0–20 cm above the bottom, the horizon of redeposited belemnite guards is located. Ammonites here are represented by *Cardioceras (Scarburgiceras) scarburgense* (Young et Bird); above ammonites are very rare. In the middle part of the bed, about 130–150 cm above the bottom, there is a well-recognized horizon with horizontally oriented shells of large ammonites, up to 40 cm in diameter. They retain the final body chamber, which is always filled with sediment and deformed. The internal whorl is not deformed, and is replaced by light brown phosphatized marl. Ammonites are represented by *Cardioceras (Scarburgiceras) alphacordatum* Spath and *Peltoceras cf. athletoides* (Lahusen).

In the upper part of the bed, approximately 2 m above the base and 0.85 m below the bottom, there is a horizon of nodules of light grey marlstone of potato-like size and shape without ammonites.

Bed 7 (0.15–0.45 m): greenish-grey or grey-green clay, with a spotty texture due to frequent patches of dark grey clay on a greenish background.

Bed 8 (0.12–0.15 m): unevenly colored clay, with a patchy texture, with a mosaic alternation of red and charcoal-black spots. The lower boundary is sharp.

Bed 9 (0,3 m): viscous, black, horizontally layered clay. In the middle part there is a horizon of concretions of marly phosphorites of nutlike shape, light brown at the break. In the clay ammonite nuclei are occasionally found, entirely preserved in pyrite with the remains of nacreous layer. Of these *Cardioceras (Cardioceras) costicardia* var. *vulgare* Arkell (Pl. 10: 12) and *Vertebriceras quadrarium* var. *angogalicum* Arkell are defined.

Bed 10 (0.05–0.10 m): bioturbated clay, intensively reddish with a black clay filling of the burrows.

Bed 11 (0.77–0.80 m): dark grey, sometimes black, layered clay. Near to the bottom, the bed gradually turns yellow and acquires the color of the overlying bed. Horizontal lamination in some places is disturbed by undulating deformations, which become more intense closer to the top. Ammonites are represented by *Goliathiceras* sp. and *Parawedekindia arduennensis* (d'Orb.). The bed is disturbed by small protrusions of yellowish clay.

Bed 12 (0.5 m): medium-grained sand, often with an admixture of fine gravel, passing into the greenish-brown, weakly cemented sandstone. The fauna is represented by rare *Surites*, *Ryazanites* and *Buchia*. The bed often forms a cornice in the section profile.

Above the bed is covered with Pleistocene (?) grey loam, up to 4 m thick.

The present section, in general, repeats the lithological structure and biostratigraphic pattern of the Mikhaylovtsenement I section (Fig. 2), but differs from it in the following details:

1. The Lower Callovian is characterized by ammonites typical for the Elatmae Zone in bed 1.

2. The difference of the thickness of the lower part of the clayey beds, from the bottom to the concretionary level of the *rowlstonense* biohorizon is nearly 3 metres. On the other hand, the upper part of the clayey beds belonging to the Lower Oxfordian is three times thicker in the second section. This indicates that the section may contain small local gaps. Therefore, the most complete stratigraphic scheme of the Jurassic should be based on data from more than one section.

3. The biostratigraphic differences between the Mikhaylovtsenement I and II sections in the Middle-Upper Callovian are insignificant and appear only at the biohorizons level. In particular, in the Middle-Upper Callovian and Lower Oxfordian, the same zones, subzones and biohorizons are established, with the exception of the *crassum* biohorizon.

This makes it possible to record a small gap in the base of the Coronatum Zone of the Mikhaylovtsenement II section.

Gorenka quarry sections

The quarry is located near to the right bank of the Pronya River, between the Oktyabrsky settlement and Gorenka village. It appeared in the year 2012 near to the closed quarry of the former "Spartak" factory. The study of the Jurassic sections of the Gorenka quarry has been carried out in 2014 by D.N. Kiselev and A.P. Ippolitov. The general structure of the Jurassic deposits exposed here is the same as in the Mikhaylovtsenement quarry sections: from below it consists of sandy-argillaceous beds, which belong to the Lower Callovian – the lower part of the Middle Callovian; and the clayey Middle – Upper Callovian – Lower Oxfordian (Pl. 23: 3) sequence above. The lowermost sandy unit is characterized by significant lateral facies changes, while the thickness of the grey clays almost does not change laterally. Below description of three sections which are characterized by different structures of the lower unit (Fig. 4) is provided. A general description is given for the upper clayey beds (Fig. 4).

Section 1 is located in the southern wall of the quarry. Here Jurassic beds overlie Carboniferous limestones:

Bed 1 (1.0–1.5 m): light brownish-grey, fine-grained clayey sand, strongly bioturbated, with spotted texture. Spots are formed after bioturbation – light yellow sand fills the bodies of the ichnofossils, located in a darker and brown rock. The base of the bed is sharp and wavy.

Bed 2 (0.20–0.22 m): clayey-silty, fine-grained, slightly cemented sand, bright red with grey clay spots. The base is sharp and wavy.

Bed 3 (0.28–0.30 m): sand, as in bed 1, but with fewer bright spots in the spotted texture.

Bed 4 (0.15 m): fine-grained silty sand, strongly ferruginous, bright red with grey patchy inclusions.

Bed 5 (0.25 m): fine-grained sand, light greyish-brown or brownish-grey with bright red inclusions.

Bed 6 (0.05 m): fine-grained sand, intensely bioturbated, greyish-brown, dark with a fine speckled texture.

Bed 7 (0.20 m): fine-grained, non-laminated sand, bioturbated, greyish-buffy, with frequent greyish-brown speckled spots, the number of which increases in the upper half of the bed. In the top it passes into a thinly marked interlayer of fine-grained sandstone with a thickness of about 5 mm, covered with a fine carbonate coating on top and bottom. Sometimes the interlayer expands into rounded concretions with a phosphatized inner part. Ammonites *Cadoceras (Rondiceras) milaschevici milaschevici* (Nik.), *Indosphinctes cf. mutatus* (Traut.) were found in the concretions.

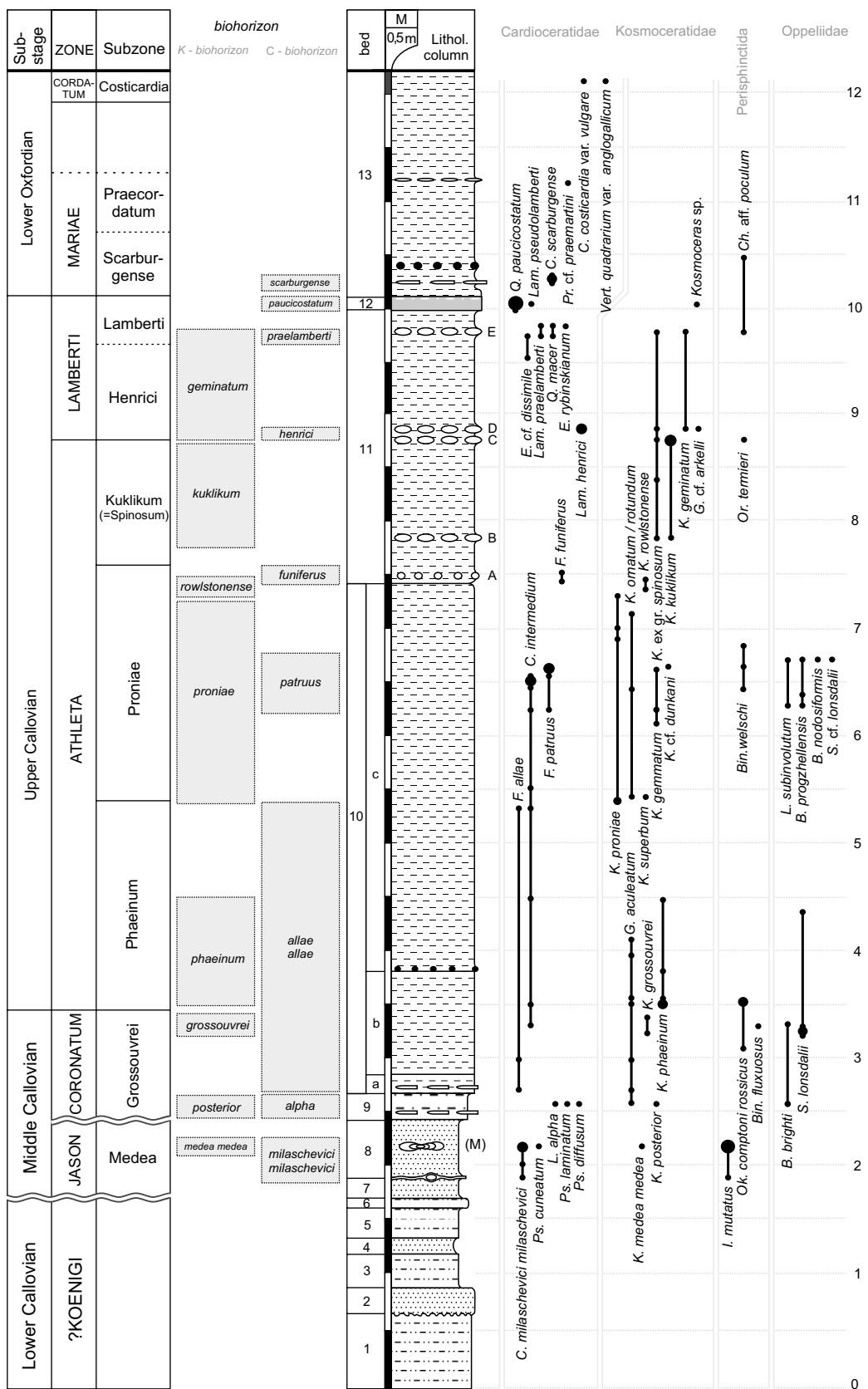


Fig. 4. Distribution of ammonites in the Middle Callovian – Lower Oxfordian in the sections of Gorenka quarry (Mikhaylov)

Bed 8 (0.50 m): fine-grained sand, turning into silt, partially cemented, sometimes passing into sandstone or siltstone. The rock is strongly ferruginous, saturated with ferruginous oolites, brownish-red or brightly red. In the middle part of the bed, approximately 0.15 m above the bottom, the horizon with large ammonite megaconchs *Indosphinctes mutatus* (Traut.) with a horizontally oriented shell is located. At the same level, uncommon *Cadoceras (Rondiceras) milashevici milashevici* (Nik.) (Pl. 7: 3) and *Kosmoceras (Gulielmites) medea medea* Call. were recorded.

Bed 9 (0.05–0.23 m): horizontally bedded greyish-red clayey silt, with a uniform texture, with slightly rounded belemnites at the base. Ammonites occur frequently, they are represented by *Kosmoceras (Zugokosmoceras) posterior* Brink., *Gulielmiceras (Spinikosmoceras) aculeatus* (Eichw.), *Longaeviceras alpha* Kiselev, *Pseudocadoceras (Novocadoceras) diffusum* Kiselev, *Ps. laminatum* Buckm., *Erymnoceras doliforme* Roman.

Bed 10 (4.5–5.0 m): massive dark grey clay with abundant finely dispersed shell detritus. Ammonites are often found throughout the bed. According to their distribution, four kosmoceratid and two cardioceratid biohorizons could be established in the bed (Fig. 5). According to the lithological features three lithological horizons can be distinguished:

10a (0.15 m): clay saturated with reddish limonitized inclusions, with a speckled texture. At the base occurs an accumulation of rounded belemnite rostra.

10b (1.4 m): horizon with an increased content of medium- and finely-dispersed shell detritus. Limonitized inclusions are absent, and the texture is homogeneous.

10c (3.5 m): the rock is saturated with microscopic shell detritus. Medium sized dispersed fragments are rare or not observed. The horizon of marly phosphorites of walnut shape is located in the bottom.

Bed 11 (2.5 m): non laminated, light grey clay with a uniform texture. In the bed there are 5 horizons of syngenetic concretions of oolitic, sometimes phosphatized marlstone.

Horizon A – slightly phosphatized, oolitic marlstone, brownish-grey on fracturing, represented by round concretions up to 5 cm in diameter. It is located in the base of the bed and does not form a remarkable horizon. Ammonites: *Funiferites funiferus* (Phillips).

Horizon B (0.4 m above horizon A) – oolitic, light yellowish-grey, oval-rounded concretions of marlstone, up to 20–30 cm along the long axis. Ammonites (*Kosmoceras (Kosmoceras) cf. rotundum* (Quenst.) and *K. (Lobokosmoceras) kuklikum* (Buckman)) are preserved as marly moulds.

Horizon C (0.9 m above horizon B) is formed by concretions similar to horizon B. They do not form a marked

horizon in the section and can be confused with the overlying concretion horizon D. Ammonites: *K. (K.) rotundum* (Quenst.) (Pl. 3: 4), *K. (K.) kuklikum* (Buckman), *Orioides cf. termieri* Gerard et Contaut (Pl. 14: 3).

Horizon D (~0.05 m above horizon C) – concretions, as in horizon B. The color of the rock is light grey. This horizon in the section also forms a noticeable marked level. Ammonites are common: *Lamberticeras henrici* Douville, *Kosmoceras (Kosmoceras) spinosum* (Sow.), *K. (Lobokosmoceras) geminatum* (Buckman), *Gulielmiceras cf. arkelli* (Mak.).

Horizon E (0.9 m above horizon D) – small (up to 15–20 cm), round or oval concretions of oolitic marlstone. The inner part of the nodules is usually strongly phosphatized, dark brown or black in color. Ammonites are preserved as phosphatized nuclei with shell remnants. They are represented by *Lamberticeras praelamberti* (R. Douville), *Eboraciceras cf. dissimile* (Brown), *Kosmoceras (Kosmoceras) spinosum* (Sow.), *K. (Lobokosmoceras) geminatum* (Buckman), *Choffatia cf. poculum* (Leckenby) (Pl. 14: 4).

Bed 12 (0.15 m): dark grey clay with frequent reddish spots, forming a mottled or spotted texture. This bed is well distinguished due to its rusty coloration. Ammonites *Quenstedtoceras paucicostatum* (Lange), *Lamberticeras pseudolamberti* Sintzow and *Kosmoceras* sp. are represented by flattened nuclei.

Bed 13 (2.5 m): non laminated, grey clay with a uniform texture. At the base of the bed, in the interval 0–20 cm above the bottom, the horizon of redeposited belemnites is located. Ammonites *Cardioceras (Scarburgiceras) scarburgense* (Young et Bird) are very common in this interval. Above, ammonites become very rare. Two horizons of nodules occur in the bed: the lower one, at 0.3 m above the base (concretions of marly phosphorite of the nutlike habit), and the upper one, situated above the previous horizon at 0.8 m (concretions of flattened habit, consisting of ash-grey marlstone). In the upper horizon *Protocardioceras cf. praemartini* (Spath) (Pl. 9: 15) is occasionally found. At the top of the bed *Cardioceras (Cardioceras) costicardia* Buckm. and *Vertebriceras quadrarium* var. *anglogallicum* Arkell (Pl. 10: 13) were collected.

In the northern and northwestern walls of the quarry (sections 4, 5), the Lower Callovian gradually becomes more sandy, up to the replacement of silts and siltstones with fine-grained sands and sandstones. At the same time, the rhythmic alternation of cemented and soft silty-sandstone beds is preserved, as it occurred in section 3. In the middle and topmost parts of these sections, as in section 3 (Fig. 5), concretionary horizons of silty sandstone with an

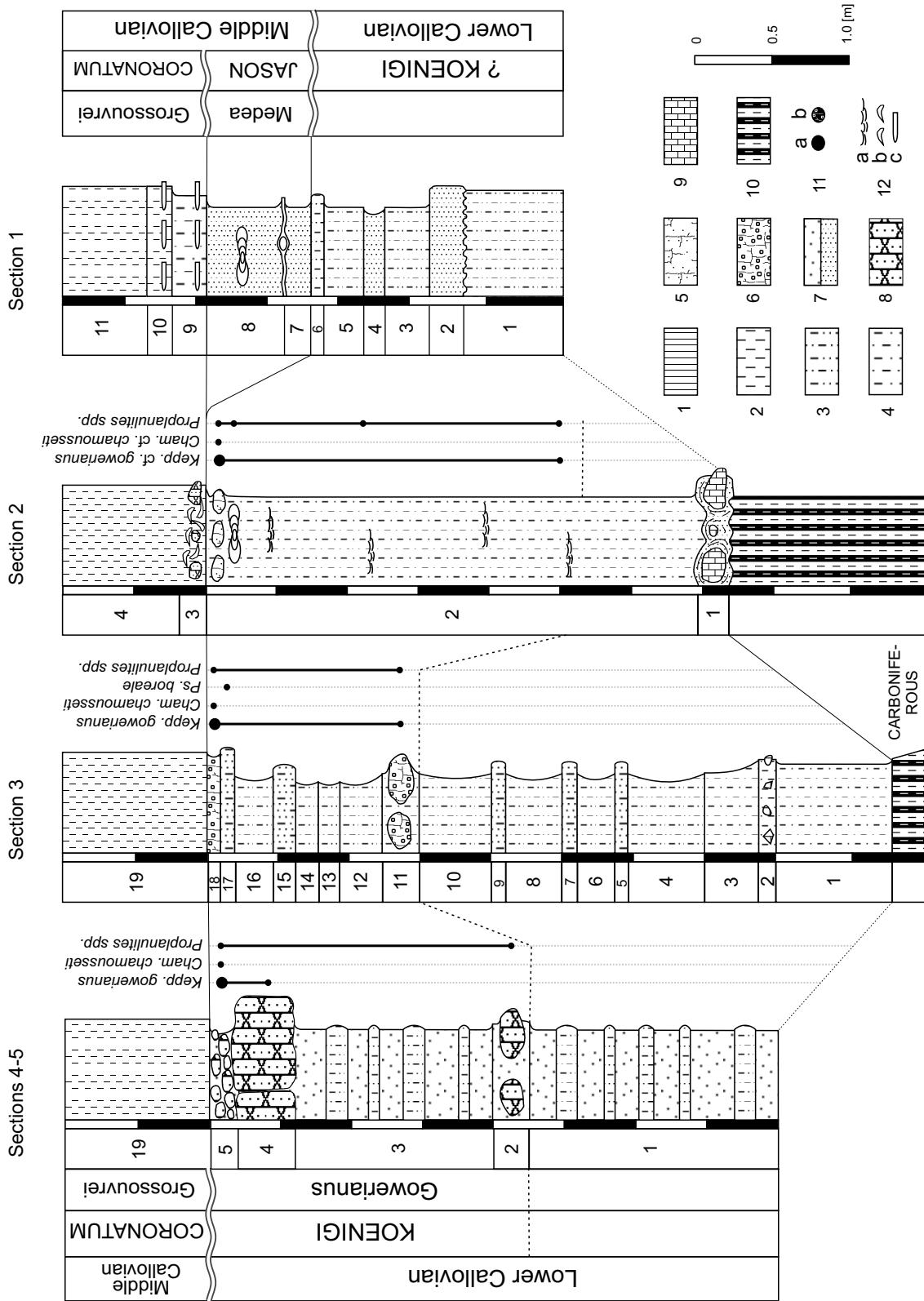


Fig. 5. Distribution of ammonites in the sandy beds of the Lower Callovian and in the boundary beds of the Lower–Middle Callovian in the sections 1–5 of Gorenka quarry

Lithological captions: 1 – fine-laminar clay; 2 – not laminar clay; 3 – sandy clay or sandy silt; 4 – silt; 5 – marlstone; 6 – oolite; 7 – limestone; 8 – sand; 9 – sandstone; 10 – spotty non-marine clay; 11 – phosphorite nodules (a – oolitic, b – not oolitic); 12 – faunal clusters (a – shell detritus, b – bivalve clusters, c – redeposited belemnites horizons). Scale bar 1 m

ammonite assemblage of the Gowerianus Subzone were recorded. Thus, the basal silty sandstone part of the Callovian in Gorenka quarry is everywhere related to the same Gowerianus Subzone. In the other sections, this subzone is completely eroded (sections 3–5) or fossils typical of this subzone occurred in redeposited pebbles (sections 2, bed 3).

The Lower Callovian ammonites of Gorenka quarry are not sufficiently studied, especially in the lower horizons of the sandstone beds, where they are rare and fragmentary. It is not excluded that the lower part of it, where the first *Kepplerites* and *Proplanulites* already appear, can belong to the upper part of the Subpatruus Zone.

The Middle-Upper Callovian and the Lower Oxfordian clayey beds of Gorenka quarry, in general, do not differ from the sections of Mikhaylovtsement quarry either lithologically or biostratigraphically. At the zonal and infrazonal level, complete unity up to a sequence of biohorizons, the number of biostratigraphically fixed gaps and position of stage and substage boundaries is observed. Minor differences are associated only with fluctuation in the thickness of individual beds and biohorizons, as well as the position of concretionary horizons or condensation levels. In the composite section of the Middle-Upper Callovian and Lower Oxfordian of the Mikhaylov area, the Coronatum and Athleta Zones are fully represented. All other zones are not complete to some extent, which is due not only to the presence of internal gaps, but also to insufficient paleontological study in those intervals where ammonites are less common.

AMMONITE STRATIGRAPHY

In the sections of the Mikhaylov region the Middle-Upper Callovian and Lower Oxfordian beds are characterized by a wide variety of ammonites, belonging to seven families: Kosmoceratidae Haug, Cardioceratidae Siemiradzki, Pseudoperisphinctidae Schindewolf, Perisphinctidae Steinmann, Aspidoceratidae Zittel, Oppeliidae Bonarelli and Pachyceratidae Buckman. The most important for correlation within the Boreal and Sub-Boreal provinces are the Boreal and Subboreal families – cardioceratids and kosmoceratids, which are characterized by the highest diversity in the studied succession. The remainder of the ammonites could be used for correlation with Mediterranean and Submediterranean provinces.

The most complete sequence of ammonites was recorded in the Mikhaylovtsement I section, therefore it was adopted as a basis for stratigraphic subdivision. The remaining sections (Mikhaylovtsement II, Mikhaylov-Gorenka) have an auxiliary significance for the detailization of the taxonomic composition of individual ammonite assemblages and the biostratigraphic unit boundaries.

KOSMOCERATIDAE

Kosmoceratids are the main group for the subdivision of the Callovian at the level of zones, subzones and biohorizons within the Boreal-Atlantic (Subboreal) biochorema. For the subdivision of the Middle-Upper Callovian, the macroconch phyletic lineage of *Kosmoceras* with an elegant morphotype, represented by the sequence of subgenera *K. (Gulielmites)* – *K. (Zugokosmoceras)* – *K. (Lobokosmoceras)* is used. The stratigraphic sequence of species in this lineage (*K. (G.) medea* – *K. (G.) jason* – *K. (G.) obductum* – *K. (Z.) posterior* – *K. (Z.) grossouvrei* – *K. (Z.) phaeenum* – *K. (L.) proniae* – *K. (L.) rowlstonense* – *K. (L.) kuklikum* – *K. (L.) geminatum*) was originally established in England and France (Buckman, 1909–1930; Brinkmann, 1929a, b; Callomon, 1955; Tintant, 1963; Tintant, Thierry, 1967; Elmi, 1967; Cariou, 1967, 1971). On the basis of this succession zonal and infrazonal scales have been developed for the Middle and Upper Callovian (Callomon, 1955, 1964, 1968). Later, the suitability of this scale was broadly confirmed for European Russia (Meledina, 1987) and Mangyshlak (Repin, Rashvan, 1996) and further supplemented at the infrazonal level (Kiselev, 2001; Kiselev, Meledina, 2004; Kiselev, Rogov, 2005).

The sections near Mikhaylov contain the upper part of this sequence only (Tab. 1).

The most complete succession of *Kosmoceras*-based biohorizons is observed in the Mikhaylovtsement I section. In other sections, the lower part of this succession is incomplete due to presence of gaps. The thickness of the same biohorizons in different sections is variable because of the facies changes. The full sequence of Middle and Upper Callovian standard zones and subzones of the Subboreal scale was established in the studied sections (Figs 2–5, 8).

The relative thickness of the kosmoceratid subzones in the Mikhaylovtsement I section largely coincides with those in the Oxford Clay Formation of the Peterborough stratotype section (Callomon, 1968, tab. 15): the Proniae Subzone is characterized by maximum thickness while Obductum Subzone is of minimum thickness if compared with other subzones. In the Mikhaylovtsement I section this trend is more pronounced (Fig. 6), but on the whole, the correlation of the thickness of the same subzones in both sections is very high (0.93). Such a close ratio of thicknesses in such remote sections is not accidental and probably reflects real patterns, related to the duration of existence of kosmoceratid species. The absolute thickness of subzones in the Oxford Clay is generally higher than in the Mikhaylovtsement I section, which probably indicates a higher rate of sedimentation in the English basin.

Despite the fact that the entire sequence of *Kosmoceras* has been well studied in various regions of the Boreal-At-

Table 1

The position of the kosmoceratid biohorizons in the sections of the Mikhaylov

biohorizon	section					
	Mikhaylovtsement I		Mikhaylovtsement II		Mikhaylov-Gorenka	
	bed (interval)	m	bed (interval)	m	bed (interval)	m
<i>K. geminatum</i> [a]	bed 10,11	1.00	bed 5c, d	0.3	bed 11 (+1.3–2.4 m)	1.10
<i>K. kuklikum</i> [b]	bed 9	1.30	presumably bed 5b, c	0.8	bed 11 (+0.4–1.3 m)	0.90
<i>K. rowlstonense</i> [b]	bed 8 (+2.0–3.0 m)	1.00	bed 5a	0.2	bed 10 (+4.7–5.0 m)	0.30
<i>K. proniae</i> [b]	bed 7 (+4.0–8.3 m) – bed 8 (+0.0–2.0 m)	4.50	bed 4 (presumably +4.0–7.5 m)	3.5	bed 10 (+3.0–4.7 m)	1.70
<i>K. phaeinum</i> [b]	bed 7c (+1.8–4.0 m)	2.20	bed 4 (+?–4.0 m)	?	bed 10 (+0.8–1.8 m)	1.00
<i>K. grossouvrei</i> [b]	bed 7b (+0.75–1.8 m)	1.05	bed 4 (+0.0–0.8 m)	0.8	bed 10 (+0.6–0.8 m)	0.20
<i>K. posterior</i> [b]	bed 7a (+0.0–0.75 m)	0.75	bed 4 (+0.0–0.3 m)	0.3	bed 9	0.23
<i>K. crassum</i> [b]	bed 6	0.30	–	–	–	–
<i>K. obductum</i> [b]	bed 5	0.20	bed 3	0.5	–	–

m – thickness of the biohorizon, in meters; [a] – biohorizon of alternative sequence; [b] – biohorizon of basic sequence

lantic region (England, Germany, France, Poland, European Russia, Mangyshlak), the upper part corresponding to the *K. (L.) rowlstonense* – *K. (L.) kuklikum* – *K. (L.) geminatum*, is described here for the first time.

K. (L.) rowlstonense (Young et Bird) in the Mikhaylov sections occurs in the upper part of the Proniae Subzone together with the last species of the genus *Funiferites*. In England, the *K. (L.) rowlstonense* biozone includes the «upper part of the Proniae Subzone or the lower part of the Spinosum Subzone» (Callomon, Wright, 1989: p. 832). These differences in our opinion reflect lack of data about the details of kosmoceratid distribution in the Athleta Zone of England due to condensation of the most important sections of the Hackness Rock and Oxford Clay Formation. In particular, the stratotype of the Proniae and Spinosum Subzones in Calvert and Woodham, as well as the Hackness Rock sections, contain gaps in the lower part of the Athleta Zone (Calvert, Hackness Rock), in the middle part (Hackness Rock), and in the upper part (Woodham) (Arkell, 1939; Call-

lomon, 1968; Cox, 1988; Callomon, Wright, 1989). Apparently, the existence of numerous gaps makes it difficult to establish the succession of kosmoceratid species within the Proniae and Spinosum Subzones. However, it is noted (Callomon, Wright, 1989: p. 832) that *K. (L.) rowlstonense* is not known from the stratotype section of the Spinosum Subzone (Woodham, Lower Spinosum Clay, bed E [by Arkell, 1939]). In these beds a younger species *K. (L.) kuklikum* (Buckman) occurs, thus the *rowlstonense* biohorizon should be located in the Proniae Subzone.

According to the data from the Mikhaylov and Peski sections, we have established that the characteristic ammonite fauna of the Spinosum Subzone appears directly above the *K. rowlstonense* biozone. The basis for the inclusion of the *rowlstonense* biohorizon in the Proniae Subzone is the joint occurrence of *K. rowlstonense* with a number of important key ammonite species of the Proniae Subzone, in particular the *Funiferites patruus*, as well as a number of opeliids.

K. (L.) kuklikum (Buckman) in sections of the Mikhaylov region (Pl. 2: 4), as in other sections of the Ryazan and Moscow areas (Pl. 3: 5), occurs between the Proniae Subzone and the Lamberti Zone. This interval is equivalent to the Lower Spinosum Clay of England and contains a similar ammonite assemblage, so we referred it to the “Spinosum” Subzone (=Kuklikum Subzone herein). The diagnosis of this species and its systematic position are understood ambiguously by different specialists, so it needs to be revised. According to one point of view (Callomon, Wright, 1989: p. 832) this species is closest to *K. rowlstonense*, and, accordingly, should belong to the same group (*Lobokosmoceras* in this article). According to another approach (Page, 1994: p. 127), this species belongs to *Kosmoceras* with a coarse-ribbed morphotype, i.e. to *Kosmoceras* s. str. In the paper of Page, it is noted that “The inner whorls of *K. kukli-*

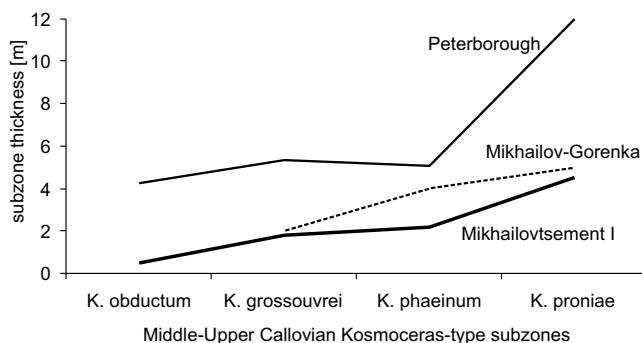


Fig. 6. Relative thickness of the Middle-Upper Callovian subzones, established by the phyletic lineage of the genus *Kosmoceras*, in the Peterborough sections (according to Callomon, 1968, tab. 15) and Mikhaylov sections

kum closely resemble those of *K. spinosum* sensu stricto" (ibid.). This point of view seems erroneous. On the holotype of the species (Buckman, 1926 in Buckman, 1909–1930, pl. DCXXVIa), it is clearly seen that in all stages of morphogenesis the shell is covered with dense and elegant ribbing, which is much closer to that of *K. rowlstonense* (Pl. 3: 6), than to *K. spinosum* (Pl. 3: 1). Thus, the discussed species should be considered as closely allied to *K. (L.) rowlstonense*. The succession of these species leads to the recognition of the *rowlstonense* and *kuklikum* biohorizons, which should refer to the standard infrazonal sequence of the Upper Callovian (see section "Stratigraphic units and correlation").

Another group of macroconchiate *Kosmoceras*, characterized by a coarse-ribbed morphotype – *Kosmoceras* s. str., includes species of the lineage *K. (K.) pollucinum* – *K. (K.) bigoti* – *K. (K.) fibuliferum* – *K. (K.) gemmatum* – *K. (K.) rotundum* – *K. (K.) spinosum*. Their distribution in the Mikhaylov section is as follows (Tab. 2):

The distribution of *K. (K.) pollucinum* in the Mikhaylov section is almost the same as in the other sections where the change of kosmoceratid faunas was studied in detail. In the famous Peterborough section the biozone of this species includes an interval 200–800 cm from the base of the Oxford Clay Formation (Brinkmann, 1929b, tab. 8, 126), which corresponds to the Obductum Subzone (+136–560 cm) and Grossouvrei Subzone (+561–1093 cm) (according to Callomon, 1964, 1968). The only image of a specimen of this species from the Peterborough section (Tintant, 1963, pl. XLIII, f. 1) comes from the interval +540 cm, which corresponds to the upper part of the Obductum Subzone and, probably, to the *crassum* biohorizon. A similar distribution of this species was noted by Brinkmann (1929b, tab. 126) for Popilani (Lithuania). In Germany this species was recorded together with *K. obductum* (ibid., tab. 127).

Distribution of the species *K. (K.) gemmatum* looks quite different. In the section of Peterborough the biozone of this species lies at 2500–2800 cm above the base of the Forma-

tion (ibid., tab. 8), which corresponds to the upper part of the Proniae Subzone (Callomon, 1968). The same is true for the Scarborough Castle (Yorkshire), Hackness Rock Member, where the neotype of this species occurs (Arkell, 1939: p. 189: fig. 4). The Hackness Rock Member in this section ranges from the uppermost Phaeinum Subzone to the lowermost Spinosum Subzone (Callomon, Sykes, 1980; Callomon, Wright, 1989), i.e. exclusively in the Upper Callovian. In the Mikhaylov section, this species appeared earlier, and is also known from the Phaeinum Subzone (Pl. 4: 1) and the Grossouvrei Subzone (Pl. 1: 6, 7) i.e. here it ranges from latest Middle to Late Callovian.

Later species of *Kosmoceras* s. str., completing the phylogenetic sequence of this group, are referred to the closely related species *K. (K.) rotundum* (Quenstedt) (Pl. 3: 2–4) and *K. (K.) spinosum* (Sow.) (Pl. 3: 1). The first of these species is distributed in the Kuklikum Subzone (= "Spinosum" Subzone auct.), and the second one is typical of the Lamberti Zone of the Mikhaylov sections and other sections of European Russia. In English sections only *K. spinosum* is mentioned from both the Spinosum Subzone and in the Lamberti Zone (Arkell, 1939; Callomon, 1968; Callomon, Sykes, 1980). Thus the assignment of the *Kosmoceras* from the Lower Spinosum Clay of the English sections to the species *K. spinosum* seems to be doubtful. Study of the detailed distribution of *Kosmoceras* (*Kosmoceras*) in the Upper Callovian of European Russia has revealed a distinct morphological difference in the middle and adult whorls of specimens from the Athleta Zone compared with those from the Lamberti Zone. The early forms of *Kosmoceras* of this group are characterized, as a whole, by a lower rib ratio and a smaller number of loop-like ribs. Representatives from the Lamberti Zone differ from older ones by their lower density of primary ribs, relatively high number of ventrolateral tubercles and a higher coefficient of rib looping (Fig. 7b). As was previously shown by R. Brinkmann (1929b), the increase of the rib looping value is a characteristic trend in the development of kosmoceratids during the Late Callovian.

Distribution of *Kosmoceras* s. str. in the Mikhaylov section

Zone	Subzone	Biohorizon	<i>K. (K.) pollucinum</i>	<i>K. (K.) bigoti</i>	<i>K. (K.) fibuliferum</i>	<i>K. (K.) gemmatum</i>	<i>K. (K.) rotundum</i>	<i>K. (K.) spinosum</i>
Coronatum	Obductum	<i>K. obductum</i>						
		<i>K. crassum</i>	+					
	Grossouvrei	<i>K. posterior</i>	+	+	+			
		<i>K. grossouvrei</i>	+		+	+		
Athleta	Phaeinum	<i>K. phaeinum</i>			+	+		
	Proniae	<i>K. proniae</i>				+		
	Kuklikum	<i>K. kuklikum</i>					+	
Lamberti	Henrici	<i>L. henrici</i>						+
	Lamberti	<i>L. praelamberti</i>						+
		<i>L. lamberti</i>						+

Table 2

Brinkman investigated only the initial phylogenetic stage of the looped morphotype development, which occurred in the Middle – Late Callovian transition, including the interval of the Phaeinum Zone in the Peterborough section. The change of the “*Bündelungsziffer*” coefficient in this interval, in general, ranged from 1 to 2. According to our data, in *Kosmoceras* s. str. in the Proniae Subzone this ratio reaches values of 3.0–4.5. In *Kosmoceras* of the same group in the Spinosum Subzone, the looping coefficient decreases sharply by 1 to 1.7 (*K. rotundum*), but in the Lamberti Zone this value again rises to 4.5 (*K. spinosum* and *K. balticum*) (Fig. 7c). Thus, *Kosmoceras* s. str. from the Spinosum Subzone and the Lamberti Zone, undoubtedly, are discrete and should be referred to different species.

In this work, only the late forms of *Kosmoceras* (*Kosmoceras*) found in the Lamberti Zone are assigned to *K. spinosum*. The earliest species of this group from the upper part of the Athleta Zone is determined as *K. rotundum* (Quenst.) (Lectotype: Buckman, 1924 in Buckman, 1909–1930, pl. DIV). It should be noted that the type specimens of *K. spinosum* (Sowerby, 1826: p. 78, pl. DXL: 2), “Casts in Pyrites are met with near Weymouth” (ibid.) originates from the Lamberti Zone (topotype: Arkell, 1939: pl. XI, f. 1). *K. (K.) tidmoorensis* Arkell (holotype: Arkell, 1939: p. 189, f. 3), originating from the same zone, is practically not distinguished from this species, therefore, it should be probably considered as the younger synonym of *K. spinosum*.

A similar conclusion about the difference between *Kosmoceras* s. str. in the Athleta and Lamberti Zones was made by K. Page (1994: p. 127). He believes that *Kosmoceras* s. str. from the Spinosum Subzone should be separated from *K. spinosum*, and determined it as *Kosmoceras kuklikum* (Buckman). We consider this definition to be erroneous (see above); nevertheless, the discreteness of the *Kosmoceras* faunas in the Spinosum Subzone and the Lamberti Zone is no longer in doubt.

Specimens assigned by us to as *K. rotundum* are very close (and, probably, identical) to the species *K. zeissi* Dietl (holotype: Dietl, 1993: pl. 1: 1), described from the terminal part of the Spinosum Subzone of the Ornatenton Formation of Germany (*punctulatum* biohorizon).

Thus, the lack of reliable findings of *K. spinosum* in the upper part of the Athleta Zone (the “Spinosum Subzone”) gives grounds for the proposal of a new index-species for this stratigraphic interval (see section “Stratigraphic units and correlation”).

CARDIOCERATIDAE

Cardioceratids are especially significant for the correlation of the Callovian and Oxfordian in the Panboreal Superrealm. In the sections of the Mikhaylov region they are the most diverse in comparison with other families and are represented by three subfamilies with approximately the same amount of species and genera (Tab. 3):

Cadoceratinæ Hyatt in the sections are typical of the lower part of the Middle Callovian and occur in the Medea Subzone (*Cadoceras* (*Rondiceras*), *Pseudocadoceras*) as well as in the Coronatum and Athleta Zones (*C. (Eichwaldiceras)*, *Funiferites*, *Longaeviceras*). Among them, the genus *Funiferites* is of greatest importance for stratigraphical value as it has been used for detailed subdivision of the Middle–Upper Callovian (Kiselev, 1999; Kiselev *et al.*, 2003). In the Mikhaylov area, especially in the Mikhaylov section I, the distribution of the species of the genus *Funiferites*, which form one phylogenetic lineage, is traced in the most detailed way, compared with other sections of Russia and Western Europe: *F. allae allae* (bed 7a–c, Pl. 5: 1–3, Pl. 6: 1, 2) – *F. allae compressum* (bed 7d; Pl. 5: 4–6) – *F. patruus* (beds 7d, 8; Pl. 5: 7–10) – *F. funiferus* (beds 8, 9; Pl. 6: 3, 4). Their distribution is mainly limited to the Athleta

Fig. 7. Distribution of *Kosmoceras* s. str. on the ribbing parameters. The calculations were carried out according to measurements made on the middle and adult whorls preceding the last body chamber

a – sculptural features and abbreviations used; b – correlation between the total rib ratio (T_v/R_p), the rib loop index (R_v/T_v), and the stratigraphic age of *Kosmoceras* s. str.; c – distribution of *Kosmoceras* s. str. on the same correlation diagram as in Fig. b. Abbreviations: ht – holotype, nt – neotype, lt – lectotype

Explanation: loop-like ribs are a kind of secondary sculpture and are formed by convergence of two ribs on the ventral tubercle. Ordinary (non loop-like) secondary ribs, when passing through the ventral side, form two rows of ventral tubercles. The number of pairs of these tubercles corresponds to the number of secondary ribs. The appearance of loop-like ribs reduces the number of ventral tubercles by at least two. Therefore, the relative number of ventral tubercles, expressed by the ratio R_s/T_v , can be an effective indicator of the convergence of the secondary sculpture B_c (the *Bündelungsziffer* parameter by R. Brinkmann, 1929b or the Bundling coefficient by Raup and Crick, 1982). The index shows how many secondary ribs on average converge into the ventral tubercle. For $B_c = 2$, the loop-like ribs are double, with $B_c = 3$ – triple. A value of $B_c < 1$ means that not all secondary ribs converge on the half-whorl.

The consequence of the convergence of secondary ribs is a decrease in the effect of divergence of primary ribs, *i.e.* branching. This phenomenon can be expressed in terms of the final rib ratio R_f , calculated by the ratio T_v/R_p . It is similar to the usual branching coefficient ($R = C_s/C_l$), but takes into account the reduction of it due to the convergence of the ribs. The value of R_f , on the one hand, reflects the branching coefficient R , and on the other hand, what part of the convergence the primary ribs takes. In particular, for $R_f < 1$, loop-like ribs are formed not only by secondary, but also by primary ribs.

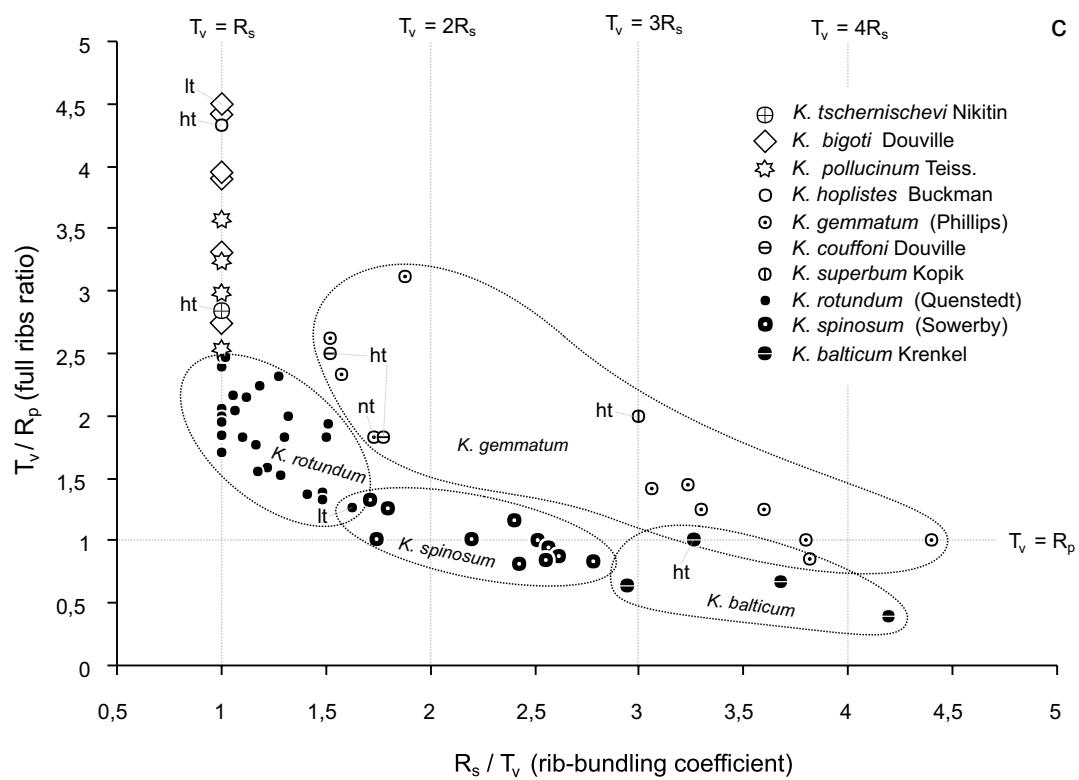
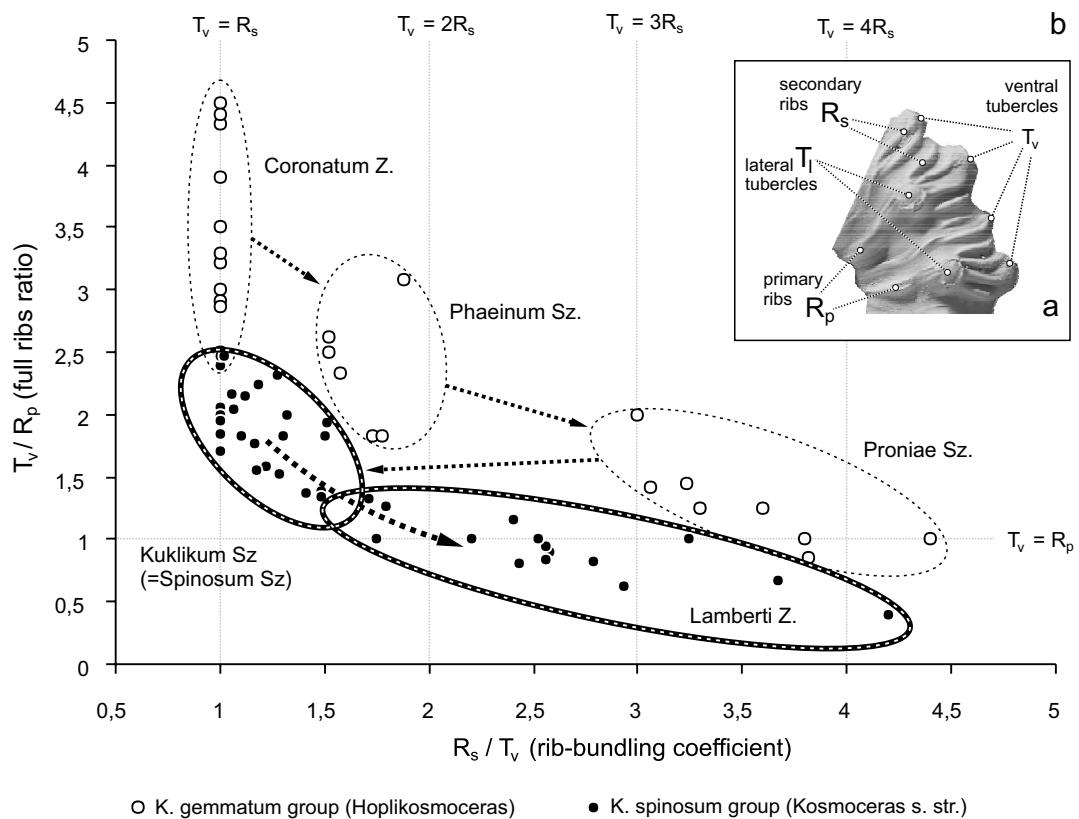


Table 3
**Ammonite diversity of the family Cardioceratidae Siemiradzki, 1891
in the Middle Callovian – Lower Oxfordian in the Mikhaylov region**

Subfamily	Number of species, subspecies and variations, incl. in the open nomenclature	Number of genera
Cadoceratinae Hyatt	15	4
Quenstedtoceratinae Meledina	11	4
Cardioceratinae Siemiradzki	15	4
Total	41	12

Zone. This gives grounds for the recognition of the biohorizons *allae allae*, *allae compressum*, *patruus* and *funiferus*. The minuteness of this succession of biohorizons is comparable with those based on the kosmoceratid succession in the Athleta Zone, which makes it applicable for correlation, at least within European Russia (for more details see the sections “Stratigraphic units and correlation” and “Description of ammonites”).

The first two species of this lineage (*F. allae* and *F. patruus*) are endemic species for the central regions of European Russia, while the latest species *F. funiferus* (Philips) is known in Western Europe, including England (lectotype: Callomon, Wright, 1989: pl. 92: 4), Northern France (=*Ammonites galdrinus* d'Orb., neotype: Fischer, 1994: pl. 65: 2). The type specimen of the species comes from the Hackness Rock Formation, the Proniae Subzone (Callomon, Wright, 1989: p. 815). A specimen of *F. funiferus* from Scarborough is figured in conjunction with *Kosmoceras cf. rowlstonense* (ibid., pl. 93: 2). In the Mikhaylov area most of the *F. funiferus* records were collected from the *rowlstonense* biohorizon, and only few came from the lowermost part of the overlying “*Spinosum*” Subzone (=Kuklikum Subzone, *kuklikum* biohorizon), thus the *funiferus* biohorizon corresponds to the *rowlstonense* biohorizon and the lower part of the *kuklikum* biohorizon.

The genus *Longaeceras* Buckman was found in the Mikhaylov section I only. It is represented by the earliest and latest species of the lineage. *Longaeceras praestenolobum* Kiselev et Meledina (holotype: Kiselev, Meledina, 2004, pl. 2: 1–4), which is an oldest species of this lineage (according to Kiselev, 2005), is known from bed 5 at the base of the Obductum Subzone (*obductum* biohorizon). In addition to this section, this species is known in the Orenburg region and the Sysola River only, i.e. its occurrences are restricted to European Russia. The following member of the lineage *L. stenolobum* (Keys.) emend. (Nik.) – *L. alpha* Kiselev – *L. lahuseni* Bodyl., which are typical for the Middle-Upper Callovian (*crassum-proniae* biohorizons) of European Russia are rare or absent in this section. However, *Longaeceras* has been recorded from regions relatively close to the Mikhaylov area: *L. stenolobum* is

known from the Obductum Subzone of the Ryazan region (Elatma) while *L. alpha* was collected from the Grossouvrei Subzone of the Kostroma region (Burdovo) (Kiselev, 2001).

The latest *Longaeceras* assemblage includes the species *L. placenta* (Leck.) and *L. longaeum* (Leck.) in England and *L. keyserlingi* (Sok.) (=*L. nikitini* (Sok.)) in North European Russia and the Arctic. In the Mikhaylov section I only *L. placenta* (Pl. 7: 1, 2, Pl. 9: 6) was found in bed 9 (Kuklikum Subzone). The holotype of *L. placenta* (Leckenby, 1859, pl. II, f. 1; refigured by Buckman, 1920 in Buckman, 1909–1930, pl. CXLVIII) came from the Hackness Rock, Scarborough, Yorkshire. The precise stratigraphic position of this specimen is unknown, but presumably, the holotype came from the upper half of the lower part of Hackness Rock Member (the author of the species pointed to the origin of this specimen from the Lower Callovian Kelloway Rock Formation, but this was a misunderstanding of the local stratigraphy (Callomon, Wright, 1989)). S. Buckman (1923 in Buckman, 1909–1930) noted that the matrix of the holotype of *L. placenta* was grey and coarsely oolitic («*Ornatum Zone*»), and the matrix of *L. longaeum* was “brown, somewhat sandy, occasionally oolitic; mixed with iron sand. Matrix and fossils much iron-stained” («*Athleta Zone*»). Thus, both species, according to Buckman, came from different beds and different zones, though this has not been the view of subsequent authors, and Callomon and Sykes noted (Callomon, Sykes, 1980) the presence of *L. placenta* in the English sections of the East Midlands in the Proniae Subzone along with *Kosmoceras rowlstonense*. Later, J. Callomon pointed to the presence of *L. nikitini* in the Middle Athleta Zone (=Proniae Subzone) of the Peterborough section (Callomon, 1985: text-fig. 8, f. P). Thus, *Longaeceras* in the English successions ranges mainly in the middle part of the Athleta Zone.

Our observations in the Mikhaylov section I quite clearly show the presence of *L. placenta* in the Kuklikum Subzone, i.e. in the most upper part of the Athleta Zone. In the Adzva River basin (tributary of the Pechora River) *L. placenta* occurs in the same beds as *L. nikitini* and *Kosmoceras kuklikum* (unpublished data), which confirm the age of this species in the Mikhaylov section.

Subfamily Quenstedtoceratinae Meledina. In the Mikhaylov area the subfamily is represented mainly by the genera *Quenstedtoceras* Hyatt, *Lambertoceras* Buckman and *Eboraciceras* Buckman. They characterize the Lamberti Zone throughout the Boreal-Atlantic region. The modern zonal and infrazonal subdivision of the Lamberti Zone by species from this subfamily has been developed in Western Europe (Callomon, 1964; Fortwengler, Marchand 1994; Thierry et al., 1997; Fortwengler et al., 2012) and European Russia (Mitta, 2003; Kiselev, Rogov, 2005a; Kiselev et al., 2013). In the Mikhaylov area the Lamberti Zone is charac-

rized by small thickness and the presence of numerous gaps: in the Mikhaylovtsement I section its thickness is 1.15 m (bed 10–12); in the Mikhaylovtsement II – 1 m (bed 5, upper part); in the Mikhaylov-Gorenka – 1,3 m (bed 11 upper part and 12). In the Lamberti Zone, the *henrici* and *praelamberti* biohorizons and, correspondingly, the Henrici and Lamberti Subzones are established by species of the genus *Lamberticeras*. Ammonites from the *paucicostatum* biohorizon in all the sections are represented mainly by microconchs (*Quenstedtoceras paucicostatum* (Lange), Pl. 8: 5), and only in Mikhaylovtsement II did this horizon contain also *Lamberticeras pseudolamberti* (Sintzow) (=*Q. irinae* Sasonov, 1957) (Pl. 8: 2, 3). At present, *L. pseudolamberti* is known only from the Russian Platform (Alpatyevo, Tarkhanovskaya Pristan, Dubki, Mikhaylov) and the North Caucasus (Mitta, 2003; Kiselev *et al.*, 2013).

The *lamberti* biohorizon was not found in any studied sections. Above the *paucicostatum* biohorizon in all sections the *scarburgense* biohorizon is recorded, which determines the presence of a continuous Callovian–Oxfordian boundary here.

The subfamily *Cardioceratinae* Siemiradzki characterizes exclusively the Lower Oxfordian in the studied sections: bed 12, 13 (Mikhaylovtsement I); beds 6–11 (Mikhaylovtsement II) and bed 13 (Mikhaylov-Gorenka). The Oxfordian of all these sections is poorly characterized by ammonites, and therefore the boundaries between zones and subzones are often conditional. Among the ammonites, the genera *Cardioceras* Neumayr et Uhlig (with the subgenera *Scarburgiceras* Buckman and *Scotiocardioceras* Buckman), *Goliathiceras* Buckman, *Protocardioceras* Schirardin and *Vertebriceras* Buckman are dominant. The lower half of Oxfordian in the Mikhaylovtsement I section (bed 12) contains an assemblage with *C. (Scarburgiceras)* and *Protocardioceras*, which allows us to establish here the *scarburgense*, *alphacordatum* and *praecordatum* biohorizons of the Quenstedtoceras mariae Zone.

The most problematic part of this sequence is the *praecordatum* biohorizon. It has been recognized in the Mikhaylovtsement I section only, in the middle part of bed 12, where the ammonites are preserved as crushed moulds. Among them, *Protocardioceras praecordatum* (Douville) (Pl. 11: 2, 3) is dominant species. The diagnosis of this species is very controversial for a number of nomenclatural reasons, and therefore requires special discussion. The neotype of this species (Douville, 1913: pl. 7: 7; Arkell, 1946 in (Arkell, 1935–48), text-fig. 104, f. 7) is an unquestionable microconch and does not contain features that are often attributed to this species as diagnostic: a macroconchic shell type with involute whorls, reaching the stage of a smooth body chamber (Maire, 1937; Arkell, 1946; Knyazev, 1975) and

rebranching of the ribs in the keel zone (Knyazev, 1975). Other specialists adhere to the practice of referring both micro and macroconchs to this species (Marchand, 1986; Page, 1994). With this approach, the diagnosis of the species is completely blurred, and only one of the features of the sample specimen is used in fact – its stratigraphic position. We consider here *Pr. praecordatum* in the narrow sense, *i.e.* in accordance with the characteristics of the neotype. Specimens from the bed 12 (Mikhaylovtsement I) differ very little from the neotype of this species, with the exception of better preservation of the aperture, which has an obvious microconch character.

Pr. praemartini (Spath) – the index species of the *praemartini* biohorizon, situated at the base of the Praecordatum Subzone of France (Fortwengler, Marchand, 1991; 1994) and later established in European Russia (Kiselev *et al.*, 2013) also refers to a microconch. Ammonites close to *Pr. praemartini* were found in the Mikhaylovtsement I (bed 12b) and Mikhaylov-Gorenka (bed 13) sections (Pl. 9: 14–16). Ammonites in this interval are extremely rare, which does not yet allow reliable recognition of the *praemartini* biohorizon in these sections. However, its presence here is very likely.

The uppermost beds of the Mikhaylov area (Mikhaylovtsement I, bed 13, Mikhaylovtsement II, beds 8–11, Mikhaylov-Gorenka, bed 13, top) contain cardioceratid assemblages which have never been described in other sections of the Lower Oxfordian of European Russia. Most of them are represented by species and variations (intraspecific morphs allocated by Arkell) of *Cardioceras* and *Vertebriceras*, well known in English sections: *Cardioceras (Cardioceras) costicardia* var. *vulgare* Arkell (Pl. 10: 11, 12); *Vertebriceras quadrarium* var. *quadrarium* (Buckman) (Pl. 10: 8, 10); *V. quadrarium* var. *biplicatum* Arkell (Pl. 10: 4); *V. gracile* Arkell (Pl. 10: 5, 7, 9); *V. quadrarium* var. *anglogallicum* Arkell (Pl. 10: 13). In England, they occur mainly in the Red Nodule Beds, and in the Lower Calcareous Grit Formation (Arkell, 1946), which refer, in part or in whole, to the Bukowskii and Costicardia subzones (Arkell, 1941, 1944; Wright, 1980). From the same subzone, a similar fauna is described from Staffin Bay, Isle of Skye (Wright, 2013). A similar complex of *Vertebriceras* is described from the Bukowskii Subzone of the Villers-sur-mer section, Calvados, France (Marchand, 1986: pl. 13: 1–7). By the presence of *C. costicardia* and the closely related species *C. percaelatum* Pawlow (Pl. 9: 17) (according to V.G. Knyazev (1975) these are synonyms), the beds under consideration are attributed to the Costicardia Subzone. The presence of the Bukowskii Subzone in the studied sections remains questionable.

PELTOCERATINAE

The greatest diversity of Peltoceratinae is observed in the sections of the Tethys-Panthalassa Superrealm, as a result of which this subfamily is of particular importance for the correlation within Tethys-Panthalassa (Bonnot *et al.*, 2002) as well as for Boreal-Tethyan correlation. In the Mikhaylov area peltoceratins occurred in some levels only. They make it possible to clarify the correlation between Boreal and Tethyan scales and the pattern of invasions of ammonite faunas of various origins.

Pseudopeltoceras chauvinianum (d'Orbigny) – Mikhaylovtsen I section, bed 7c (Pl. 12: 4), Athleta Zone, Phaeinum Subzone. In European Russia all known *Pseudopeltoceras* findings are restricted to the Phaeinum Subzone, for example, in Alpatyevo (Moscow region) and Burdovo (Kostroma Region) (Kiselev, 2001). In France, where typical specimens of the species occur (lectotype: Fischer, 1994, pl. 65: 1), its mass occurrence is characteristic of the upper part of the Rota Zone of the Submediterranean scale – the “*Pseudopeltoceras*” biohorizon Bourquin et Contini, 1968 (Thierry *et al.*, 1997). In this regard, in the Mikhaylovtsen I section, it is possible to establish a biohorizon based on *Pseudopeltoceras*, which is proposed to be designated by the species name *chauvinianum*.

Peltoceras athleta (Phillips) – Mikhaylovtsen I section, beds 7d, 8, 9 (bottom), the interval from the Proniae Subzone (upper part) to Kuklikum Subzone (lower part in beds 7, 8). Specimens of this species are rare and are represented by deformed clayey moulds, and in bed 9 – by marlstone nuclei of internal whorls. In the Moscow region (Peski, Gzhel, Alpatyevo) this species is known from the concretions of the *rowlstonense* and *kuklikum* biohorizons (Pl. 13: 4). In Submediterranean Europe, the species is distributed in the middle part of the Athleta Zone – the Trezeense Subzone, in the *leckenbyi* and *athleta* (=trezeense) biohorizons. Moreover, in the *athleta* biohorizon this species is especially common (Bonnot, 1993; Bonnot *et al.*, 2002). The Trezeense Subzone corresponds to the Sub-Boreal Proniae Subzone (Thierry *et al.*, 1997). In the Mikhaylovtsen I section, the distribution of *P. athleta* covers only the upper half of the subzone, roughly corresponding to the *patruus* and *funiferus* biohorizons. Probably, this interval corresponds only to the *athleta* biohorizon of the Submediterranean standard scale (Fig. 2D) and is not equivalent to the *leckenbyi* biohorizon, which should correspond only to the lower part of the Proniae Subzone (*allae compressum* biohorizon). The *athleta* biohorizon is an acme-interval of the species *P. athleta*, which has a wider geographical distribution than the index species of the underlying biohorizon, and encompasses not only Submediterranean Province, but also Boreal regions. French specialists distinguish two

morphs of *P. athleta* – an *athleta* morph and a *baylei* morph (Bonnot, 1993). In the French sections, they occupy a different stratigraphic position: the *athleta* morph is found in the lower part of the *athleta* biohorizon, and the *baylei* morph is in the middle part and the top, immediately below the Collotiformis Subzone and the first occurrence of *Kosmoceras ex gr. geminatum* (most likely *K. kuklikum*) (Bonnot *et al.*, 1992). Probably, in the Russian sections, the first morph occurs in the *proniae* biohorizon, and the second one in the *rowlstonense* biohorizon, but it is not yet possible to confirm this on the available material.

In England, according to K. Page, *P. athleta* (neotype: Spath, 1931, pl. CVI: 3, pl. CVI: 5, Hackness Rock Member, Scarborough) occupies a wider interval including the upper part of the Phaeinum Subzone and the Proniae Subzone (acme-level) (Page, 1994). In this case *P. athleta* s. str. (morpha *athleta*), as in France, occupies the lower stratigraphic level – the Phaeinum Subzone, while in the Proniae Subzone the younger morphotype *P. trifidum* (Quenst.) (=morfa *baylei*) is determined. The distribution of this species in the sections of the Mikhaylov area corresponds more to the French range of the *P. athleta* species.

Peltoceras retrospinatum Gerard et Contaut sensu Bonnot occurs in the Mikhaylovtsen I section, bed 9 (upper part); Mikhaylovtsen II, bed 5 (b/c interval), Kuklikum Subzone, *kuklikum* biohorizon (Pl. 13: 1) and in the Lamberti Zone, in the base of the *henrici* biohorizon (Pl. 12: 1, Pl. 13: 2). In European Russia, this species is determined for the first time and currently it is known from the Mikhaylov area only. In France, it is distributed in the top of the Athleta Zone – i.e. in the Collotiformis Subzone and the *collotiformis* biohorizon (Bonnot, 1995; Bonnot *et al.*, 2002). The holotype of the species (Gerard, Contaut, 1936: pl. XIX, Montreuil-Bellay, la Folie, Palluau, Athleta Zone, subzone B) is represented by the mature shell, which has almost no internal whorls. Specimens from Mikhaylov, on the contrary, retain their internal whorls, so we have determined this species following the interpretation of Bonnot, who provides it figured at all stages of morphogenesis. In Mikhaylov *P. retrospinatum* is especially common in the upper part of the *kuklikum* biohorizon and is very rarely found at the base of the *henrici* biohorizon. In France it occupies an interval equivalent to the *kuklikum* biohorizon, as it is associated with *Longaeceras* and *Kosmoceras* (*Kosmoceras*) *gr. spinosum* (Louesme section, bed 90, 92 – Courville, Bonnot, 1998). Since this species is proposed as the index of a biohorizon of the *Peltoceras* scale, which is an alternative to the Submediterranean standard scale (Bonnot *et al.*, 2002), the new biohorizon is established in the Mikhaylovtsen I, II sections (Fig. 2D).

The species of “*Metapeltoceras*” described by A. Jeannet in the section of Herznah (Switzerland) are very close to

or synonymous with *P. retrospinatum*: *Peltoceras brunnschweileri* (Jeannet) (holotype: Jeannet, 1951: pl. 91: 1) and *P. helveticum* (Jeannet) (holotype: Jeannet, 1951: pl. 90: 2). Both species originate from the upper part of the Athleta Zone – bed C3, which overlaps the C2 bed with *P. athleta* and directly underlies the “Lamberti-Schichten”. They are associated with *Kosmoceras rotundum* (Quenst.) (=*K. dun-canii* (Sow.) and *K. spinosum* (Sow.) by Jeannet, 1951: pl. 26: 1, 3, 6), so bed C3 should be assigned to the Kuklukum Subzone.

Peltoceras cf. subtense (Leckenby) occurrences are known from the Mikhaylovtsement I section, bed 10; Mikhaylovtsement II, bed 5c, Lamberti Zone, Henrici Subzone. This species is very rare and usually fragmentary preserved, thus being only a little suitable for precise identification. However, the presence of this species in Mikhaylovtsement seems very likely. In the Dubki section (Saratov region), this species is widespread in the *henrici*, *praelamberti* and *lamberti* biohorizons (Kiselev *et al.*, 2013). In France, it is typical of the lower part of the Lamberti Zone only – the Poculum Subzone, within it the Subtense Subzone and the *subtense* biohorizon are distinguished (Bonnot *et al.*, 2002).

Peltoceratinæ of the Lower Oxfordian in the Mikhaylov sections are rare (except in the uppermost part of the section) and usually were found loose. Therefore, in this paper they are not specifically considered. Some exceptions are represented by ammonites close to *Peltoceratooides athletoides* (Lahusen), known from the horizon with large ammonites with phosphatized whorls in Mikhaylovtsement I section, bed 12 and Mikhaylovtsement II, bed 6 (Lower Oxfordian, Praecordatum Subzone, *alphacordatum* biohorizon). This species was erected by I. Lahusen (1883: pl. X: 5–8) for specimens collected in the sections on the Pronya River, not far from Mikhaylov. However, the neotype was not designated and the type series is lost due to pyrite decay. Study of this species in the sections of South-Eastern France (Bonnot, Cariou, 1999) showed that it is typical of the Mariae Zone and Scarburgense Subzone. For this stratigraphical interval the Athletoides Zone has been proposed along with the *athletoides* horizon in the middle part of this zone. In the Mikhaylov area this species occurs in a higher interval of the Lower Oxfordian.

ASPIDOCERATINAE

Aspidoceratins are mainly typical of the Tethys-Panthalassa Superrealm, but their records are also known in the uppermost Callovian Lamberti Zone of the Mikhaylov region (Fig. 5, 6). These ammonites are relatively uncommon and represented by *Euaspidoceras ferrugineum* Jeannet [M] and *Mirospinctes* aff. *inaquespinosum* [m] only. Surprisingly,

aspidoceratins were not recorded from the Lower Oxfordian part of the studied sections.

OPPELIIDAE

Although oppeliids are ammonites common in Mediterranean and Submediterranean areas, during the Middle-Late Callovian they became permanently established in the Subboreal successions. In contrast to the other ammonite groups considered above, oppeliids are rarely used as index taxa of zonal and infrazonal units. Moreover, oppeliid-based biohorizons are “inserted” within the succession based on non-oppeliid taxa, and all Callovian oppeliid biohorizons introduced so far (except Lower Callovian ones) have been based on taramelliceratins (Dietl, 1993, 2011) which are virtually missing in the Callovian of the Russian Platform: until now only one specimen of *Taramelliceras* of uncertain age (perhaps *praelamberti* horizon of the Lamberti Zone according its matrix) has been found loose at Mikhaylovtsement (Pl. 19: 8). Taramelliceratins became much more numerous above, in the upper part of the Lower Oxfordian, where their mass occurrence (in the Saratov region) or relatively infrequent records from the northern part of the Russian Platform permits the recognition of the *baccatum* horizon in the Cordatum Zone (Kiselev *et al.*, 2013).

The majority of oppeliids occurring in the Callovian – Lower Oxfordian of the Russian Platform belong to the Hecticoceratinæ subfamily. In addition to these ammonites infrequent Oppeliinae [genus *Alcidia* Rollier – for a long time this name has been considered as a junior homonym of *Alcidia* Westwood, 1879 (Lepidoptera), *Alcidia* Bourguignat, 1889 (Gastropoda) and *Alcidia* Monterosato, 1890 (Gastropoda); however, as recently has been shown by Özdi̇kmen (2013), all abovementioned senior names are invalid, thus this generic name is a proper one for oppeliid ammonites. Moreover, *Paralcidia* Spath, 1928, proposed as replacement name for *Alcidia* Rollier, 1913 is itself became junior homonym of the genus *Paralcidia* Warren, 1906 (Lepidoptera)] are known from the uppermost Lower Callovian to Upper Callovian (cf. Rogov, 2002). At Mikhaylovtsement a single specimen of *A. mazetieri* (Petitclerc) has been recorded from the Proniae Subzone (Pl. 19: 6), and two partially preserved specimens referred *A. nurraensis* were found in the Coronatum Zone (Pl. 16: 22).

The first infrequent hecticoceratins appeared in the Russian Platform in the latest Early Callovian (Enodatum Chron, *Rossiensiceras daghestanicum* (Neumayr et Uhlig)). In the Jason Zone hecticoceratins are also relatively uncommon, and the only one specimen of this subfamily is recorded from the Jason Zone of Mikhaylovtsement (*Rossiensiceras uhligi* (Neumayr), Pl. 19: 7).

Much more diverse and abundant hecticoceratins are known from the Coronatum and Proniae zones of the Russian Platform. Among these ammonites are a few lineages belonging to the genera *Brightia* and *Orbignyiceras* which could be used in future for introducing phylogenetic biohorizons. However, our knowledge of the evolutionary patterns in hecticoceratins need to be improved further. It should be noted that nearly all species recorded in the Mikhaylov region (including the new taxa described below) are known from the Western European Subboreal and Sub-mediterranean successions, thus the correlational potential of this ammonoid group is still underestimated.

Above the Athleta Zone oppeliids became uncommon in the Ryazan region and adjacent areas of the Moscow Synclise, and only in the southern parts of the Russian Platform (e.g. Dubki section, Kiselev *et al.*, 2013) do their occurrences in the Lamberti Zone and lowermost Oxfordian remain relatively numerous.

PACHYCERATIDAE

Pachyceratids appeared suddenly at the beginning of the Middle Callovian Coronatum Chron and instantly dispersed throughout the Subboreal, Submediterranean and Mediterranean areas. Their southern Middle Callovian occurrences were described from India (Krishna, Thierry, 1987). In the Russian Platform, pachyceratids, represented by genera *Erymnoceras* and *Rollierites* became abundant at the beginning of the Coronatum Chron, but quickly declined further, totally disappearing here before the beginning of the Late Callovian. The pachyceratids of this region are still insufficiently known. They show clear size dimorphism with microconch diameter 5–10 cm and macroconch diameter up to 30–40 cm. However, these dimorphs lack any clear mature modifications and generally cannot be distinguished from each other by their inner whorls. Thus traditionally pachyceratid micro- and macroconchs are not separated at either genus or species level.

DYNAMICS OF AMMONITE DIVERSITY

In the studied sections a wide diversity of ammonites was identified at all taxonomic levels. Among the ammonite families, the most diverse were Cardioceratidae, whose

Table 4
Diversity of ammonites of the Middle Callovian – Lower Oxfordian in the Mikhaylov area

Family	Number of species, subspecies and variations, incl. in the open nomenclature	Number of genera
Kosmoceratidae Haug	27	2
Cardioceratidae Siemiradzki	41	12
Pseudoperisphinctidae Schindewolf	10	5
Perisphinctidae Steinmann	4	2
Aspidoceratidae Zittel	9	6
Oppeliidae Bonarelli	38	5
Pachyceratidae Buckman	3	2
Total	131	33

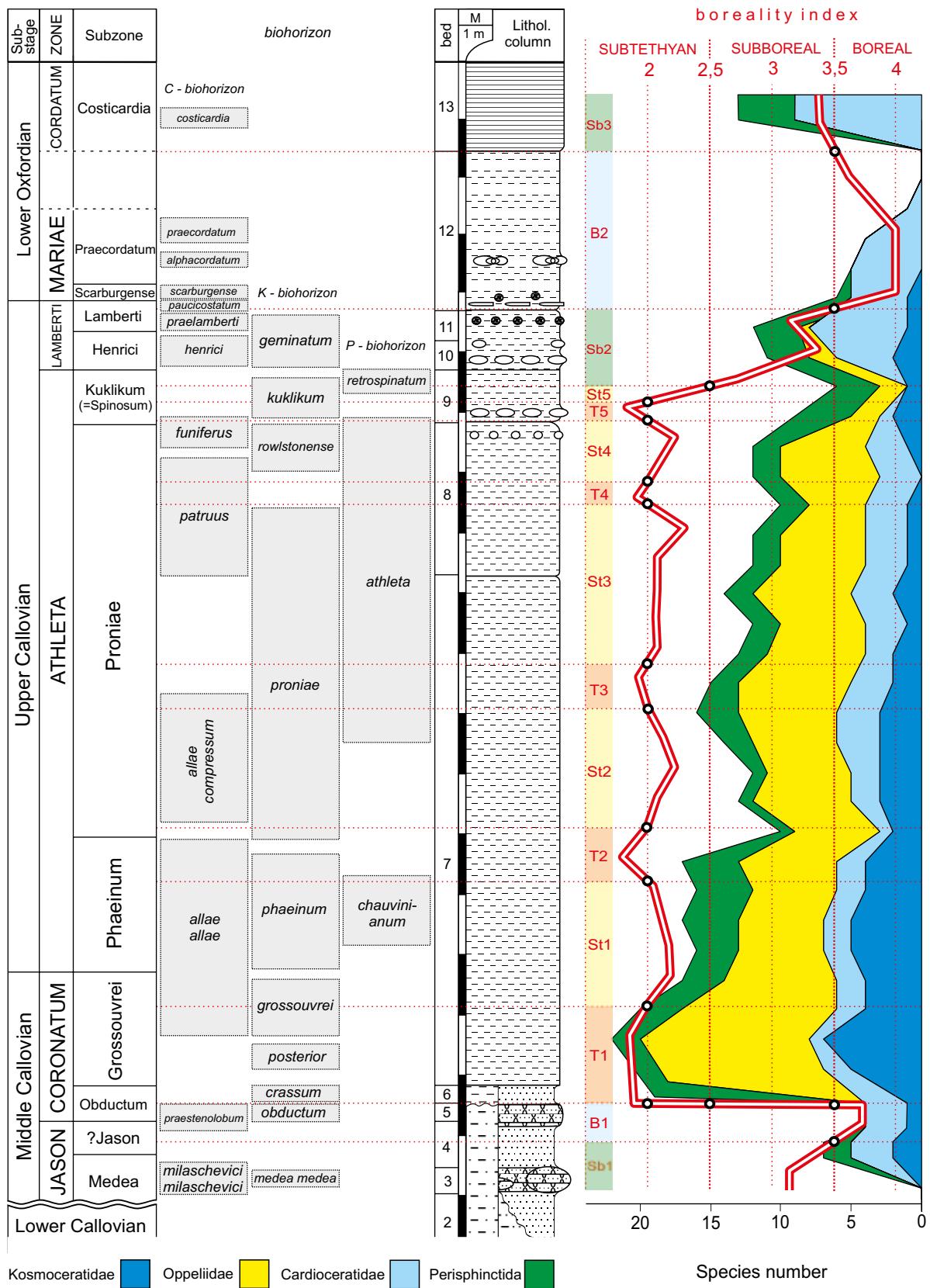
presence agrees with the Boreal affinity of the ammonite assemblages (Tab. 4):

A study of the diversity dynamics shows (Fig. 8) that the maximum number of ammonite taxa occurs in the Middle Callovian Grossouvre Subzone (22 species), and the minimum in the Lower Oxfordian *praecordatum* biohorizon (1 species). In general, the highest diversity is characteristic of the Middle-Upper Callovian, in the interval belonging to the Coronatum – Proniae subzones. Here, the largest number of ammonite families is known from the late Middle Callovian, with especially high oppeliid diversity. The maximum diversity of oppeliids (12 species) and kosmoceratids (7 species) occurs in the Grossouvre Subzone. Two peaks of diversity are observed for cardioceratids, the first in the Lamberti (7 species) and the second in Costicardia (9 species) subzones. Perisphinctida (Pseudoperisphinctidae and Perisphinctidae) occupy a subordinate position over most of the stratigraphic interval. They became relatively numerous only in the middle and upper parts of the *kuklikum* biohorizon. In general, in the studied sections several successive phases of dominance of ammonite families can be recognized:

1. The first phase of Cardioceratidae dominance: *medea medea* – *obductum* hemerae;
2. Phase of Oppeliidae dominance: *crassum* – *rowlstonense* hemerae;
3. Phase of Perisphinctida dominance: *kuklikum* hemera;
4. The second phase of Cardioceratidae dominance: Henrici–Costicardia subchrons.

Fig. 8. Ammonite diversity in the Mikhaylov section I. The ammonite paleobiodiversity calculated according to the number of species belonging to different families is shown on the cumulative diagram

The red double line shows the Boreality index graph; the horizontal red dotted lines labelled critical levels corresponding to the boundaries of the Boreality index episodes (B – Boreal, Sb – Sub-Boreal, St – Sub-Tethyan and T – Tethyan). On the vertical color scale the sequence of the episodes is given. For explanations, see the text



Undoubtedly, the changes in ammonite assemblages reflect the structure of ammonite immigration events for each time interval and, as a consequence, changes in the paleobiogeographic pattern during the Callovian and Oxfordian. To assess the overall ratio of species of different paleobiogeographical origin, we use the Boreality index I_b , calculated by the ratio of species according to the formula

$$I_b = (4B + 3Sb + 2St + T) / (B + Sb + St + T),$$

where:

B – the number of Boreal taxa (Cardioceratidae),
 Sb – the number of Sub-Boreal taxa (Kosmoceratidae),
 St – the number of Sub-Tethyan (Submediterranean) taxa (Aspidoceratidae and Perisphinctidae),
 T – the number of Tethyan taxa (Oppeliidae and Pachyceratidae).

At a value of $I_b = 1$ the ammonite assemblage is completely Tethyan, $I_b = 2$ – Sub-Tethyan, $I_b = 3$ – Sub-Boreal, $I_b = 4$ – Boreal. Accordingly, the range of the Tethyan is between values of 1 to 1.5, Sub-Tethyan interval of 1.5–2.5, Sub-Boreal – 2.5–3.5 and Boreal – 3.5–4.0.

For the whole Middle Callovian – Lower Oxfordian interval of the Mikhaylov succession the average Boreality index is 2.60 for genera and 2.51 for species. This means that despite the predominance of Boreal taxa among the ammonites studied, there is a significant admixture of the Tethyan and Sub-Tethyan taxa, which, on the whole, characterizes the ammonite assemblage as a transitional between the Sub-Boreal and Sub-Tethyan. The dynamics of the Boreality index through the studied succession (Fig. 8) makes it possible to distinguish three phases:

1. The first Boreal phase corresponds to the interval *medea medea* – *obductum* hemerae. Boreality index here varies from 3.14 to 3.75.
2. Sub-Tethyan phase corresponds to *crassum-kuklikum* hemerae, with the Boreality index ranged from 1.80 to 2.30 (the average value of 2.04), which is close to those of Submediterranean successions.
3. The second Boreal phase corresponds to the Henrici-Costicardia Chrons. The Boreality index here significantly exceeds 3.00, ranging from 3.36 in the Henrici Subchron to 4.00 in the Praecordatum Subzone (4).

It is unclear how relative changes in the diversity and abundance of ammonites of different paleobiogeographical origin were associated with changes in the temperature of sea water. It is possible that their distribution was largely controlled by features of the paleogeography and other (including biotic) factors. In any case, for the Oxfordian-Kimeridgian interval of the European part of Russia, sharp changes in ammonite assemblages occurred against a background of paleotemperatures which remained nearly constant (Wierzbowski *et al.*, 2018).

During the Boreal phases there were some oscillations of the Boreality index, this varying from Subboreal ($I_b = 2.5$ –3.5) to Boreal ($I_b > 3.5$). In the first Boreal phase, two episodes are distinguished: the Sub-Boreal episode (Sb1) and the Boreal episode (B1) (Fig. 8). During the second Boreal phase, two Sub-Boreal episodes can be recognized (Sb2 and Sb3) along with one Boreal episode (B2).

During the Sub-Tethyan phase, the Boreality index increases several times towards “Tethyan” values, thus this phase can be divided into 5 Tethyan and 5 Sub-Tethyan episodes (Tab. 5).

Table 5

Relative duration of phases and episodes identified by the Boreality index

Phase	Episode	Stratigraphic interval		
		Kosmoceratid biohorizons	Cardioceratid biohorizons	Peltoceratin biohorizons
First Boreal	Sb1	<i>medea medea</i>	<i>milaschevici milaschevici</i>	
	B1	<i>obductum</i>	<i>praestenolobum</i>	
Sub-Tethyan	T1	<i>crassum-grossouvrei</i>		
	St1	<i>grossouvrei-phaeinum</i>	<i>allae allae</i>	<i>chauvinianum</i>
	T2	<i>phaeinum-proniae</i>	<i>allae allae</i>	
	St2	<i>proniae</i>	<i>allae compressum</i>	<i>athleta</i>
	T3	<i>proniae</i>	<i>allae compressum</i>	<i>athleta</i>
	St3	<i>proniae</i>	<i>patruus</i>	<i>athleta</i>
	T4		<i>patruus</i>	<i>athleta</i>
	St4	<i>rowlstonense</i>	<i>patruus-funiferus</i>	<i>athleta</i>
	T5	<i>kuklikum</i>		
	St5	<i>kuklikum</i>		<i>retrospinatum</i>
Second Boreal	Sb2	<i>kuklikum-geminatum</i>	<i>henrici-praelamberti</i>	
	B2		<i>paucicostatum-praecordatum</i>	
	Sb3		<i>costicardia</i>	

Episodes identified by the Boreality index are characterized by different durations. The shortest duration characterizes episodes of the middle part of the Sub-Tethyan phase, which occupies most of the Athleta Zone. The minimum value here is less than one hemera. The maximum duration is typified by episode B2, which corresponds to at least 5 hemerae.

The values of the Boreality index depend to a great extent upon the number of Oppeliidae in the ammonite assemblage (correlation coefficient 0.85). In particular, all the Tethyan episodes coincide with peak values in the number of species of the Oppeliidae. The degree of influence of Kosmoceratidae and Perisphinctida on the Boreality index is significantly smaller (correlation coefficient 0.59 and 0.52 respectively). Surprisingly the influence of cardioceratid occurrences on the Boreality index is especially small (0.32). Probably, the change in the composition of the ammonite assemblages depended mainly on the invasion of Tethyan ammonites.

It is curious that coherent changes in the species diversity are peculiar only for Kosmoceratidae and Oppeliidae (correlation coefficient 0.52). There is no correlation between the remaining families in the fluctuation of the number of taxa (the correlation coefficient is less than 0.1). This suggests that the invasions of both Kosmoceratidae and Oppeliidae in the central part of the Middle Russian Sea possibly were caused by the same reasons, while all other families appeared in the area relatively independently of each other, probably from different paleoaquatories.

The faunal spectra, based on counting the relative frequencies of taxa belonging to each family (Fig. 9), on the whole show a similar pattern as the diagram of paleobiodiversity in Fig. 8. Its comparison with the ammonite spectra of the Upper Callovian – Lower Oxfordian in Western Europe shows that changes of the Boreal and Sub-Boreal families (Cardioceratidae and Kosmoceratidae) in some sections (Bonnot *et al.*, 1984, 1992; Jardat, 2010) occur in the same way as in the Mikhaylov region (and other sections of the European Russia). But changes of the relative abundance of Sub-Tethyan and Tethyan families (Oppeliidae, Perisphinctidae, Aspidoceratidae, etc.) show a completely different pattern in different areas.

The first and second Boreal phases are characterized by a sharp increase in the number of Cardioceratidae, which indicates the invasion of this family at the beginning of the Middle Callovian and in the Early Oxfordian. In the Sub-Tethyan phase, not only an invasive increase in the diversity and abundance of the Oppeliidae occurs, but also new endemic taxa evolved, some of them so far established in European Russia only (Rogov, 2000). In Boreal phases, all ammonite taxa are characterized by Circumboreal, Circumarctic or Boreal-Atlantic distribution.

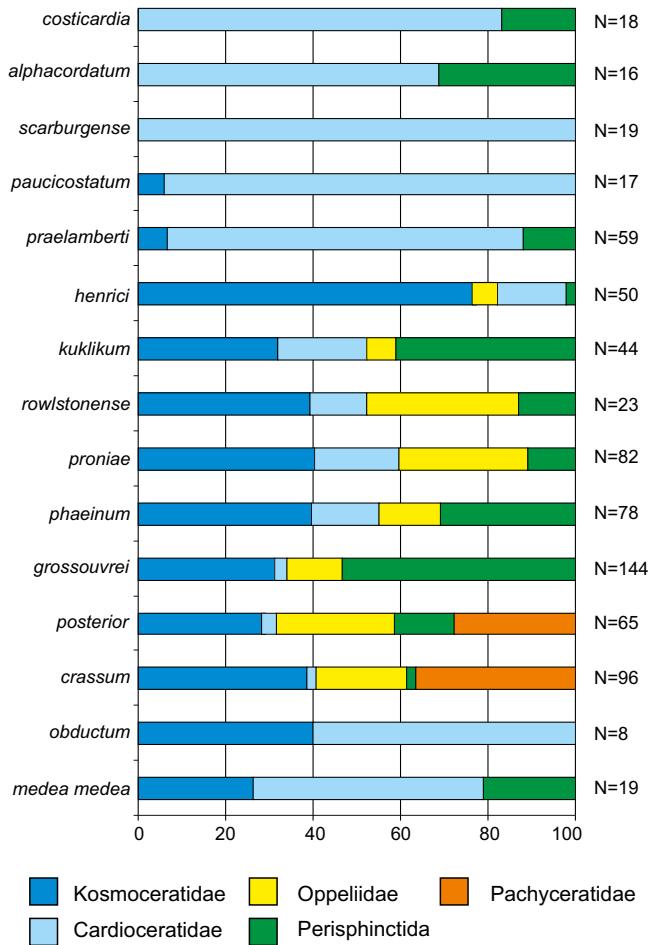


Fig. 9. Relative frequency (time averaged to biohorizons) of different ammonite families in the Mikhaylov section I

N – number of specimens

The following species and subspecies are among the possible endemic taxa of the Sub-Tethyan phase: *Cadoceras intermedium* sp. nov., *Funiferites allae allae* Kiselev, *F. allae compressum* subsp. nov., *F. patruus* (Eichw.), *Longaevierceras praestenolobum* Kiselev et Meledina, *Pseudocadoceras macellum* Kiselev, *Pseudocadoceras* sp. nov., *Brightia (B.) lominadzei* sp. nov., *B. (B.) nodosiformis* Rogov.

Of the nine above-mentioned names, 2 refer to the Oppeliidae, i.e. to the group of Tethyan origin. Endemic taxa are distributed throughout the interval of the Coronatum Zone and the Athleta Zone. Their number ranges from 3 to 9 for each subzone: Obductum – 2, Grossouvrei – 6, Phaeinum – 3, Proniae – 9. As can be seen, the number of endemic forms grows towards the end of the Sub-Tethyan phase and then abruptly terminates.

The abundance of endemic taxa in the Sub-Tethyan phase and the predominance of Circumboreal taxa in the

Boreal phases could be explained by the influence of eustatic events. As a working hypothesis, it can be assumed that during the eustatic sea-level fall, the connection of the Middle-Russian Sea with high-Boreal areas decreased, but its connection with Submediterranean regions remained unchanged. This led to the dominance of Submediterranean taxa, which gave rise to several new local species and subspecies. All these processes correspond to the Sub-Tethyan phase. At this time endemic taxa also evolved in the Boreal ammonite groups such as the genus *Funiferites*, and just as in the Oppeliidae, at the end of the Athleta phase these ammonites invaded Western Europe (*Funiferites funiferus*, *Brightia (B.) progzhellensis*, *B. (B.) gzhellensis*).

With a sea level rise the connection of the Middle Russian Sea with Boreal basins increased, which led to an intensification of the Boreal spread (Kiselev, 2004) and invasion of Boreal ammonite taxa. Boreal ammonites, presumably, were opportunistic with respect to the Submediterranean ammonites, which they displaced almost completely, remaining the dominant group of ammonites in Boreal and Sub-Boreal basins.

The position of the regressive phase in the Middle-Late Callovian and the transgressive phase at the beginning of the Early Oxfordian is shown in many publications (Hallam, 1988, 2001; Ramajo, Aurell, 2008; Haq, 2017). The peak value of the Late Callovian regression is noted differently for different territories, but for the Boreal regions, in particular England (Norris, Hallam, 1995) and European Russia (Sahagian *et al.*, 1996) it falls in the Athleta Chron.

STRATIGRAPHIC SUBDIVISION AND CORRELATION

Below a description of the biostratigraphic units of the Middle and Upper Callovian of Central Russia is provided. It is assumed that the proposed scale lacks biostratigraphically recognizable horizons at the infrazonal level, therefore it could be proposed as zonal and infrazonal standard for European Russia. Most of the zonal and infrazonal subdivisions of this scale are defined on the basis of species from the cardioceratid and kosmoceratid lineages which evolved within the single Boreal-Atlantic Realm. Therefore, the stratigraphic scale of the Middle-Upper Callovian of European Russia does not fundamentally differ from those of the Boreal Europe (primarily England and North-West France) (Fig. 10). At the level of zones and subzones these schemes coincide. However, on the infrazonal level these schemes significantly differ from each other: of 28 Middle Callovian-Lower Oxfordian biohorizons of European Russia, only 9 are common not only by name, but also by position on the scale, with those of the Western Europe. Such strong differences reflect not only the real distinction in the ammonite

assemblages of European Russia and North-West Europe, but also the nomenclatural and technical problems of the recognition and correlation of infrazonal units (Rogov *et al.*, 2012). These problems are associated with the varied understanding of the taxonomic differences in ammonites by different specialists, and with other subjective factors. Due to these reasons, there is a discrepancy between the substage and stage boundaries in the stratigraphic scales of these regions, in particular the Lower-Middle Callovian and Callovian-Oxfordian boundaries. At present this discrepancy does not exceed one biohorizon.

Most of the units of this stratigraphic scale are identified by index-species of the genera *Kosmoceras*, *Cardioceras* and *Quenstedtoceras* and are already established, since they were proposed earlier and in another region. Provincial units, characteristic mainly for European Russia, are distinguished by species of the genus *Funiferites*.

This scale was developed mainly on the basis of sections of the Moscow and Ryazan regions, which are key areas for the Callovian-Oxfordian of the southern part of the Moscow synecline. The most complete sections, which are stratotypes of biohorizons, are considered as reference sections. These include sections of the Mikhaylov area, characterized by the greatest completeness in the Middle-Upper Callovian, where 7 stratotypes are proposed, and the famous section near Elatma, with the most complete sequence at the top of the Lower Callovian and the Middle Callovian (3 stratotypes). Continuous successions of biohorizons across the substage boundaries were traced in two sections for the Lower-Middle Callovian boundary (Elatma and Alpatyovo) and in three sections for the Callovian-Oxfordian boundary (Mikhaylov, Peski and Dubki). The infrazonal subdivision of the upper part of the Lamberti Zone and the Mariae Zone is developed on the basis of the Dubki section in the Saratov region (Kiselev *et al.*, 2013) and Khanskaya Gora (list of all localities from the European Russia mentioned in this paper is provided in Supplement 1) (Orenburg region).

MIDDLE CALLOVIAN

Jason Zone d'Orbigny, 1852 emend. Callomon 1964

Medea Subzone Callomon, 1955

=*K. (Gulielmites) medea* (Subzone): Callomon, 1955: p. 256, 257

=*medea* (sous-zone): Tintant, 1963: p. 54, 55

=*medea* (Subzone): Callomon, 1964: p. 278, 279; Cariou *et al.*, 1967: p. 690, 691; Callomon, 1968: p. 271, 272; Mangold, 1971: p. 346; Callomon *et al.*, 1987: p. 32, 33; Cox, 1988: p. 8; Thierry *et al.*, 1997: p. 70; Kiselev, 1999: p. 92, 93; 2001: p. 23

Index-species. *Kosmoceras (Gulielmites) medea* Callomon. The holotype was figured by Callomon (1955, pl. 2: 1). England, Kidlington, bed 12.

Stratotype. England, Kidlington, Oxfordshire (beds 9–14). The hypostratotype is located in Peterborough, Cambridgeshire (beds 5–9, 21–55 cm [Callomon, 1964, 1968]).

Characteristic ammonites. In England, predominantly kosmoceratids (Callomon, 1955; 1968) – index species, *K. (Kosmoceras) nodosum* Call., *Gulielmiceras (Gulielmiceras) gulielmi* (Sow.). Less common are *Cadoceras* s.str. (ibid.), *Indosphinctes patina* (Neumayr), *Reineckeia (Reineckeia) anceps* (Rein.) and *Cadoceras (Rondiceras) milaschevici compressum* (Nik.) (Page, 1994). A similar ammonite assemblage is described from Northern Germany (Lange, 1973; Mönnig, 1995).

In Western France (Poitou) ammonites are dominated by the index species, Reineckeidae and Oppeliidae (Cariou et al., 1967): *Reineckeia tyranniformis* Spath, *R. substeinmanni* Lemoine, *R. cf. indosabauda* Par. et Bon., *R. gr. ravana* Spath, *R. (Reineckeites) aff. douvillei* Steinm., *Rossiensiceras mathayense* (Kilian), *R. rossiene* (Teiss.), *Zieteniceras* cf. *tuberculatum* (de Tsyt.), *Z. aff. regulare* (Till), *Orbignyiceras pseudopunctatum* (Lah.), *Eulunulites lunula* (Rein.), ?*E. cf. richei* (Lem.), *Phlycticeras polygonium* (Zieten), *Phlycticeras lachati* Par. et Bon., *Phl. pustulatum* (Rein.), *Phl. cristagalli* (d'Orb.), *Oecotrausters (Thraxites) conjugens* (Waagen). Less common are *Oeocptychius refractus* (Rein.), *Pleurocephalites*, *Indosphinctes* and *Choffatia*. In Southern Germany (Swabia, Franconia), the index species is uncommon and ammonite assemblages are dominated by Sub-Tethyan taxa (Callomon et al., 1987; Niederröfer, Dietl, 2014): *Choffatia* aff. *waageni* (Teiss.), *Grossouvria* sp., *Homoeoplanulites funatus* Oppel sensu Mangold, *Macrocephalites* spp., *Reineckeia anceps anceps* (Rein.) sensu Cariou, *R. aff. substeinmanni* Lemoine.

In European Russia, Kosmoceratidae and Pseudopersphinctinae predominate in the central regions (Ryazan, Moscow, Bryansk regions), while in the more northern regions (Kostroma Region, Komi Republic), cadoceratins became more numerous, sometimes attaining up to 100% of the whole assemblage. Oppeliids (*Rossiensiceras uhligi*) are known to date from the Mikhaylov area only, and they are very rare.

Biohorizons: *medea medea* and *medea magnum*.

Key sections in European Russia: Makaryev, Chermenino (Kostroma Region); Mikhaylov, Nikitino, Elatma (Ryazan Region); Alpatyev (Moscow region); Malinoviy Ovrag (Saratov region).

Geographic range. Russia (Central Russia, the Lower Volga region), England, France, Germany.

***medea medea* biohorizon** Callomon, Dietl, Page, 1988
emend. Kiselev, 2001

=*Medea* α (faunal horizon): Callomon, Dietl, Page, 1988: p. 363;
Mönnig et al., 2018: p. 234

=*Medea medea* (biohorizon): Kiselev, 2001: p. 23

Stratotype. Kidlington (beds 11, 12), Oxfordshire, England.

Index-species. Early chronosubspecies of the subzonal index-species.

Characteristic ammonites. Index-species, *K. (Kosmoceras) nodosum* Call., *Gulielmiceras (Gulielmiceras) gulielmi* (Sow.), *Cadoceras (Rondiceras) milaschevici milaschevici* (Nik.), *Pseudocadoceras cuneatum* Sas., *Indosphinctes mutatus* (Trd.), *Anaplanulites submutatus* (Nik.), *Grossouvria variabilis* (Lah.), *Rossiensiceras uhligi* (Neum.).

Key sections in European Russia: 1) Makaryev (bed 4 in Kiselev, 2001); 2) Chermenino (bed 3/9 in Kiselev, 2013); 3) Alpatyev (sands and sandstones of bed 6); 4) Mikhaylov (Mikhaylovtsenement I, bed 3; Mikhaylovtsenement II (bed 2, interval 350–400 cm above the base); Mikhaylov-Gorenka, (beds 7, 8); 5) Elatma (bed 6, in Kiselev, 2001).

Geographic range. Central Russia, England, France (Burgundy), Germany.

Correlation. Equivalent the *bannense* biohorizon of Cariou (1974) of the Submediterranean scale.

***medea magnum* biohorizon** Kiselev, 2001

=*Medea magnum* (biohorizon): Kiselev, 2001: p. 23

Stratotype. Makaryev (bed 5 in Kiselev, 2001)

Index-species. *Kosmoceras (Gulielmites) medea magnum* Kiselev. Late chronosubspecies of the subzonal index-species. The holotype is figured by Tintant (1963, pl. XXV: 1). England, Peterborough.

Characteristic ammonites. Index-species, *K. (Kosmoceras) baylei* Tint., *Gulielmiceras (Gulielmiceras) gulielmii* (Sow.), *G. (Spinikosmoceras) tschegemensis* (Tschichatshev), *Cadoceras (Rondiceras) milaschevici* (Nik.), *C. (Cadoceras) sp.*, *Pseudocadoceras cuneatum* Sas., *Ps. (Percacosticeras) sp.*, *Indosphinctes mutatus* (Traut.), *Anaplanulites submutatus* (Nik.), *Grossouvria cf. variabilis* (Lah.)

Key sections in European Russia: 1) stratotype; 2) Chermenino (bed 3/10 in Kiselev, 2013); 3) Alpatyev (presumably, bed 7); 4) Mikhaylov (presumably), 5) Nikitino (in some condensed concretions).

Correlation. An exact correlation with the West European scale is unclear. Probably, the biohorizon corresponds to beds 13, 14 of the holostroatype of the subzone and to the *medea* β biohorizon of Germany.

Subboreal Province						Submediterranean Province		
ZONE	Subzone	biohorizon			biohorizon	Subzone	ZONE	
		England	N-W. France	European Russia				
Lower Oxfordian	MARIAE	Cordatum	cordatum			Cordatum	CORDATUM	ATHLETOIDES
		Costicardia	costicardia		costicardia			
		Bukowskii	bukowskii		baccatum	mazuricus		
					bukowskii	claromontanus		
		Praecordatum	praecordatum		praecordatum			
			alphacordatum		alphacordatum	alphacordatum		
			praemartini		praemartini	praemartini		
		Scarburgense	aff. scarburgense	woodhamense		woodhamense		
			scarburgense	scarburgense		athletoides		
			woodhamense					
			redcliffense					
Upper Callovian	LAMBERTI	Lamberti	pauci. γ, <i>Peltomorphites</i>	thuouxensis			LAMBERTI	ATHLETA
			paucicostatum γ					
			paucicostatum β	paucicostatum		paucicostatum		
			paucicostatum α					
			Quenstedtoceras sp.1		mojarowskii			
			lamberti	lamberti	lamberti	lamberti		
			praelamberti	praelamberti	praelamberti	praelamberti		
		Henrici	henrici	henrici		schroederi	CORONATUM	GRACILIS
			messiaeni			subtense		
		"Spinosum"	(kuklikum)	kuklikum		nodulosum		
Middle Callovian	JASON	Proniae	proniae	rowlstonense	funiferus	colliformis		
				proniae	patruus	piveteaui		
		Phaeinum	phaeinum	phaeinum	allae compressum	athleta	ANCEPS	CORONATUM
					allae allae	leckenbyi		
		Grossouvrei	grossouvrei	grossouvrei		"Pseudopeltoceras"		
			posterior	posterior		rota / regulare		
		Obductum	obductum (crassum)	crassum		waageni		
		Jason	(jason jason) (jason sedgwickii)	jason	obductum	leuthardti		
					jason jason	baylei	CORONATUM	GRACILIS
		Medea	?		jason sedgwickii	villanyensis		
Lower Callovian	CALLOVI-ENSE		medea α	medea medea		richei		
			?	enodatum aeeta	blyensis	Tyranniformis		
		Enodatum	enodatum γ		medea magnum	turgidum	GRACILIS	CORONATUM
			enodatum β		medea medea	bannense		
			difficilis		enodatum aeeta	posteriorius		
			enodatum α		enodatum enodatum			
					enodatum crispatum			
					fracidus			
					pamprouxensis			
					boginense			

Fig. 10. Biostratigraphic subdivision of the Middle Callovian – Lower Oxfordian of Central Russia

A. England (according to Callomon, 1964; Callomon, Sykes, 1980; Callomon *et al.*, 1988; Page, 2004); Subboreal and Submediterranean France (Cariou, 1984; Mönnig, 1993, 1995; Niederhöfer, Dietl, 2014; Dietl, Mönnig, 2016; Mönnig *et al.*, 2018). Units with grey patterns correspond to the intervals established in the ammonites, black arrows – by Sub-Tethyan and Tethyan ammonites. In parentheses are the biohorizons that can be established from biostratigraphic data,

B

European Russia				Germany			
Sub-stage	ZONE	Subzone	biohorizon	biohorizon	Subzone	ZONE	Sub-stage
Lower Callovian	CALLOVIENSE	JASON	CORONATUM	Cordatum Costicardia Bukowskii	MARIAE	CORDATUM	
					scarburgense		
Middle Callovian			ATHLETA	LAMBERTI "Spinosum" Proniae Phaeinum	LAMBERTI		
					henrici		
Upper Callovian				Lamberti	paucicostatum mojarowskii lamberti praelamberti henrici kuklikum rowlstonense proniae phaeinum	LAMBERTI	
					allae compressum allae allae grossouvrei posterior crassum obductum jason jason jason sedgwickii medea magnum medea medea enodatum aeeta enodatum enodatum enodatum crispatum fracidus		
					funiferus patruus allae interpositum / zugium obductum posterior (crassum) obductum anterior jason β jason α medea β medea α incisum enodatum γ parallelum enodatum β enodatum α	ATHLETA	
						JASON	CORONATUM
						CALLOVIENSE	Middle Callovian
							Lower Callovian
							Lower Oxfordian
							Lower Oxfordian
							Lower Oxfordian

and its comparison with the biostratigraphic scales of Subboreal and Submediterranean Europe

Fortwengler, Marchand, 1994, 1997; Thierry *et al.*, 1997; Cariou *et al.*, 1997; Bonnot *et al.*, 2002); **B.** Germany (Callomon *et al.*, 1987; Dietl, 1993, 2011, 2015; Mikhaylov succession. White arrows show the levels where a direct correlation of the biohorizons is available by the index-species belonging to Boreal which are described in publications

Jason Subzone Callomon, 1955

=*K. (Gulielmites) jason* (Subzone): Callomon, 1955: p. 256, 257

=*jason* (sous-zone): Tintant, 1963: p. 54, 55

=*jason* (Subzone): Callomon, 1964: p. 279; Cariou *et al.*, 1967: p. 690, 691; Callomon, 1968: p. 272; Mangold, 1971: p. 346; Callomon *et al.*, 1987: p. 32, 33; Cox, 1988: p. 8; Repin, Rashvan, 1996, c. 12; Thierry *et al.*, 1997: p. 70; Kiselev, 1999: p. 93; 2001: p. 23, 24

Stratotype. Kidlington, (bed 15–26), Oxfordshire, England. The hypostratotype established in Peterborough, Cambridgeshire (bed 10–13, interval 56–135 cm in Callomon, 1964, 1968).

Index-species. *Kosmoceras (Gulielmites) jason* (Reinecke, 1818). By now, two neotypes have been proposed. The first neotype was selected by R. Brinkmann (Brinkman, 1929a: p. 44) from the originals of S. Buckman (Buckman, 1924 in Buckman, 1909–1930, Pl. DIII, Germany, Württemberg). This specimen is represented by the internal whorls of *Kosmoceras (Gulielmites)* and, in the opinion of J. Callomon (1955: p. 229), practically does not differ from other species of *K. (Gulielmites)*, *i.e.* is unsuccessful. Another neotype was selected by H. Tintant (Tintant, 1963: p. 250) from the collection of A. Orbigny (IPM-R.7164 [coll. d'Orbigny, No. 3169-II-1], Fischer, 1994, pl. 60: 3). This neotype contains adult whorls and corresponds to the generally accepted diagnosis of this species, therefore, according to Tintant, it must be considered a true type of this species. The choice of both neotypes does not fully comply with the rules of ICZN (Zeiss, 1972), since they are not collected from the type locality. According to E. Mönnig, who found and studied the original collection of Reinecke (Mönnig, 1995: p. 16), the type of *Nautilus jason* Reinecke is a microconch of *Catasigaloceras enodatum* (Nik.), *i.e.* *Gulielmiceras anterior* (Brinkmann) or a microconch of *Sigaloceras hylas* (Reinecke) (Dietl, Mönnig, 2016). The type specimen figured by Reinecke (1818: Taf. III: 15, 16), as well as all ammonites from the Goldschneckenkons beds, according to the data of German specialists (Dietl, Mönnig, 2016), should originate from the *parallelum* horizon of the Enodatum Subzone, *i.e.* from the Lower Callovian. Unfortunately, the original specimens from the Reinecke collection were not figured, so in modern publications only possibly morphologically similar specimens are figured, which, in the opinion of German experts, are close to the original (*ibid.*: Taf. I: b–g). Since it is difficult to verify this conclusion, prior to choosing the *Kosmoceras jason* neotype from a type locality, we adhere in this work to the interpretation of the species that is accepted by French specialists. Meanwhile, the type series of *Nautilus jason* has been preserved and, probably, the existing syn-

types will be published in the near future. Thanks to the courtesy of E. Mönnig, we were able to get acquainted with the images of specimens of this type series. It consists of 10 shells ranging in size from 2.5 to 9.0 mm. Among them are the juvenile macroconchs and microconchs of kosmoceratids of the both Middle Callovian and Lower Callovian types. The question of naming (or renaming) the Jason Zone of the Middle Callovian can be solved only after describing this collection and choosing the lectotype.

Characteristic ammonites. In England ammonite assemblages are dominated by kosmoceratids, mostly the index-species. The remaining ammonites are represented by the rare *Indosphinctes patina* (Neum.) (Page, 1994: pl. 22: 4–6), *Cadoceras (Rondiceras) cf. milashevici* (Nik.), *C. (Cadoceras) cf. arcticoides* Kiselev et Meledina (*ibid.*: pl. 17: 3) and *Reineckeia aff. anceps* (Rein.). In Eastern France (Burgundy) (Tintant, Thierry, 1967) ammonites are mainly represented by macrocephalitids, perisphinctids and reineckeids: *Pleurocephalites cuenoti* (Corroy), *P. jacobi* (Corroy), *P. aff. paronai* (Basse), index-species, *Kosmoceras baylei* Tint., *Choffatia*, *Grossouvria*, *Binatisphinctes mosquensis* (Fisch.), *Reineckeia liffolensis* Steinm., *Reineckeites paronai* (Petit.), *R. douvillei* (Steinm.). In the Jura (Mangold, 1967) perisphinctids are dominant in the ammonite assemblage, which includes index-species, Reineckeidae, *Choffatia neumayri* (Siem.), *C. cf. perdagata* (Waag.), *C. prorsocostata* (Siem.), *Grossouvria kontkiewiczi* (Siem.), *G. anomala* (Loczy), *G. variabilifera* (Loczy), *G. leptoides* (Loczy) and *Binatisphinctes scopinensis* (Neum.). In the Central Massif (Cariou, 1967) the Jason Zone is characterized mainly by reineckeids and oppeliids: *Reineckeia (Kellawaysites) multicostata* Petitcl., *R. (Reineckeia) grossouvrei* Petitcl., *R. (R.) reissi* Steinm., *Reineckeites aff. stuebeli* Steinm., *Rossiensiceras metomphalum* (Bon.), *Rossiensiceras* sp., *Orbignyiceras (?) didieri* (Petitcl.), *Brightia (B.) aff. submatheyi* (Lee), *Phlycticeras gr. pustulatum* (d'Orbigny), *Oeptychius refractus* (Rein.) and index-species, *Choffatia* sp., *Grossouvria* sp. In South-West Germany, according to Zeiss (1956), the subzone is represented mainly by the Oppeliidae (about 25 species), which constitute at least 65% of all ammonite species. In European Russia ammonite assemblages are dominated by kosmoceratids and cardioceratids; they are accompanied by very few oppeliids.

Location of sections. 1) Elatma (bed 7); 2) Yaroslavl Region – Rybinsk (Perebori) (grey pyritized clays); 3) Alpatyevo (silty sands up to 1 m), 4) Makaryev, 5) Chermenino (bed 3/12–3/15 in Kiselev, 2013); 5) Mikhaylov (Mikhaylovskiy I, presumably).

Biohorizons: *jason sedwickii* and *jason jason*.

Geographic range. Russia – Central Russia, Komi Republic (Sysola River basin), Lower Volga Region, Orenburg Region (Sukhaya Peschanka River); England (Yorkshire,

Scotland), France (Paris Basin, Rhone River), Germany, Poland, Kazakhstan (Mangyshlak), Georgia (Golotl), Lithuania.

jason sedgwickii biohorizon Buckman emend. Kiselev, Meledina, 2004

=*conlaxatum* (hemera): Buckman, 1923 in Buckman, 1909–1930, pl. 418; 1928: p. 29

=*Jason α* (biohorizon): Dietl in: Thierry et al., 1997: p. 70; Mönnig et al., 2018: p. 234

=*Jason sedgwickii* (biohorizon): Kiselev, Meledina, 2004: p. 163

Index-species. *Kosmoceras (Gulielmites) jason sedgwickii* (Pratt) (holotype: Buckman, 1925 in Buckman, 1909–1930, pl. DXCVIII). Early chronosubspecies of the subzonal index-species.

Stratotype. The biohorizon was first identified in Peterborough (England), in the hypostratotype of the Jason Zone, in the interval 56–79 cm (below the boundary of the abrupt increase in shell diameter in *Kosmoceras (Gulielmites)*) (Brinkmann, 1929b, Abb. 30)). At Kidlington (Oxfordshire), in the holostratotype of the zone, the lower biohorizon of the Jason Subzone occupies about 30 cm of clay, approximately corresponding to the beds 16–19 (Callomon, 1964; 1968).

Characteristic ammonites. Index-species, *K. (Kosmoceras) tschernischevi* Nik., *Gulielmiceras (Gulielmiceras) jen- ceni* (Teiss.), *Gul. (Spinikosmoceras) tschegemensis* (Tschichatschew), *Cadoceras (Rondiceras) pura* Vor., *C. (Cado- ceras) arcticoides* Kiselev et Meledina, *C. (Cadoceras) cf. postelatmae* Sas., *C. (Bryocadoceras) bryocostilatum* Kiselev, *Pseudocadoceras cuneatum* Sas., *Ps. (Costacadoceras) nansenii* (Pomp.), *Anaplanulites* cf. *evolutus* (Mangold), *Grossouvreria* cf. *kontkiewiczi* (Siem.), *Putealiceras ironense* (Tschikhachev).

Key sections in European Russia: 1) Elatma (bed 7), 2) Alpatyevo (presumably bed 8); 3) Rybinsk (Perebory, Konyushino); 4) Uzhovka (the top of a bed of clayey silt below the lower concretionary level); 5) Chermenino (beds 3/12–3/15 in Kiselev, 2013).

Geographic range. European Russia, England, France (Sarthe), Germany, Lithuania (Popilani).

jason jason biohorizon Dietl emend. Kiselev, Meledina, 2004

=*Jason β* (biohorizon): Dietl in Thierry et al., 1997: p. 70; Mönnig et al., 2018: p. 234

=*Jason jason* (biohorizon): Kiselev, Meledina, 2004: p. 163

Index-species. *Kosmoceras (Gulielmites) jason jason* (Rein.) sensu d'Orbigny. Late chronosubspecies of the sub-

zone index-species. Corresponds to the neotype of the species in the interpretation of the French specialists (Fischer, 1994, pl. 60: 3).

Stratotype. Kidlington, Oxfordshire, England. The biohorizon approximately corresponds to beds 20–26 (Callomon, 1964, 1968). In the Oxford Clay of Peterborough (England), it is corresponding to the 80–135 cm (the interval of a stepwise increase in the diameter of the *Kosmoceras (Gulielmites)* shell before the boundary of its abrupt decrease (Brinkmann, 1929b, Abb.30)).

Characteristic ammonites. index-species, *K. (Kosmo- ceras) tschernischevi* Nik., *Gulielmiceras (Gulielmiceras) jen- ceni* Teiss., *Gul. (Spinikosmoceras) tschegemensis* (Tschichatschew), *Cadoceras (Rondiceras) pura* Vor., *C. (Cado- ceras) arcticoides* Kiselev et Meledina, *C. (Cadoceras) cf. postelatmae* Sas., *C. (Bryocadoceras) bryocostilatum* Kiselev, *Pseudocadoceras cuneatum* Sas., *Ps. (Costacadoceras) nansenii* (Pomp.), *Anaplanulites* cf. *evolutus* (Mangold), *Grossouvreria* cf. *kontkiewiczi* (Siem.), *Putealiceras ironense* (Tschikhachev).

Key sections in European Russia: 1) Votcha (bed 6 in Kiselev, 2006); 2) Alpatyevo (bed 9, presumably); 3) Rybinsk (Perebory, Konyushino, Mikhaylovskoye); 4) Uzhovka (the top of the clayey silt bed below the first concretionary level); 5) Mikhaylov (Mikhaylovskoye I, presumably, bed 4).

Geographic range. European Russia, England, France (Sarthe, Blya, Champagne, Bourgogne), Germany, Lithuania (Popilani).

Coronatum Zone d'Orbigny, 1852 emend. Callomon, 1964

Obductum Subzone Brinkmann, 1929 emend. Callomon, 1955

=*Kosm. obductum* (Zone): Brinkmann, 1929b: p. 36 (pars)

=*K. (Zugokosmoceras) obductum* (Subzone): Callomon, 1955: p. 256, 257

=*obductum* (sous-zone): Tintant, 1963: p. 54, 55

=*Obductum* (Subzone): Callomon, 1964: p. 279, 280; Cariou et al., 1967: p. 690, 691; Callomon, 1968: p. 272; Mangold, 1971: p. 347; Callomon et al., 1987: p. 32–34; Cox, 1988: p. 8; Repin, Rashvan, 1996: p. 12; Thierry et al., 1997: p. 70; Kiselev, 1999: p. 93; Kiselev, 2001: p. 24

Index-species. *Kosmoceras (Gulielmites) obductum* (Buckman, 1925). The holotype is figured in the work of S. Buckman (Buckman, 1925 in Buckman, 1909–1930, V, pl. DLIX).

Stratotype. Peterborough (beds 14–16b, level 136–560 cm (Callomon, 1964, 1968)), Cambridgeshire, England.

Biohorizons. Two biohorizons *obductum* and *crassum*, which differ widely in the composition of the ammonite assemblages in European Russia and France (see below). In England the biohorizons differ mainly only by their index-species while the rest of assemblage remains unchanged.

Geographic range. European Russia (Central Russia, the Lower Volga region), England (Yorkshire), France, Germany (Franconia), Poland, Kazakhstan (Mangyshlak), North Caucasus (Dagestan, Georgia), Lithuania.

obductum biohorizon Buckman, 1925

=*obductus* (hemera): Buckman, 1925 in Buckman, 1909–1930: pl. 559; Buckman, 1928 in Buckman, 1909–1930: p. 28

=*Obductum* (biohorizon): Kiselev, 2001: p. 24

Index-species. The same as for the subzone.

Stratotype. This biohorizon was allocated by D.N. Kiselev in the Elatma section in the lower part of bed 8, where the horizon of condensed nodules with ammonites of the *obductum* biohorizon is present. Since the nodules were redeposited within the *crassum* biohorizon, this choice of stratotype is unsuccessful, and neostratotype is proposed herein at Peterborough, England (interval 136–460 cm). The top of the biohorizon (at the level 460 cm) coincides with the sharp jump in the average diameter of the shell of *Kosmoceras* (*Gulielmites*) from 101 mm to 112 mm (Brinkmann, 1929b, Abb. 28). Hypostratotype – Mikhaylovtsenement II, bed 3.

Characteristic ammonites. In European Russia this horizon is dominated by kosmoceratids and cardioceratids: *Kosmoceras* (*Gulielmites*) *obductum* (Buckm.) var. *a* and var. *b*, *K.* (*Kosmoceras*) *bigoti* Douv., *Gulielmiceras* (*Gulielmites*) *complanatum* Tint., *G.* (*Spinikosmoceras*) *castor* (Rein.), *Cadoceras* (*Cadoceras*) aff. *proniense* Sas., *C.* (*C.*) cf. *wosnessenski* (Grew.), *C.* (*Eichwaldiceras*) *carinatiforme* Kiselev, *C.* (*Bryocadoceras*) *schumarovi* (Nik.), *C.* (*B.*) *vetulum* Kiselev, *Longaeviceras* *stenolobum* (Keys.) emend. Nik., *Pseudocadoceras* *macellum* Kiselev, Ps. (*Novocadoceras*) cf. *suraense* (Sas.), Ps. (*Costacadoceras*) *laminatum* Buckm. Other ammonites are represented by *Erymnoceras* *coronatum* (Brug.), *Indosphinctes* *abichi* (Neum.), *Choffatia* *pseudofunata* (Teiss.), *Orbignyiceras* *orbignyi* (Tsytovitch), *Brightia* (*B.*) *eccentrica* sp. nov., *Alcidia* *nurrhaensis* (Wagen), *Zieteniceras* cf. *rarecostatum* sp. nov. In France (Burgundy), kosmoceratids are represented by a similar set of species and occur in nearly equal proportion with the Tethyan groups of ammonites (Tintant, Thierry, 1967: p. 678): index-species, *Gulielmiceras* *complanatum* (Tint.), *G.* *ventricosum* (Tint.), *Spinikosmoceras* *castor* (Rein.), *S.* *pollux* (Rein.), *Brightia* *metomphala* (Par. et Bon.), *Subgrossouvría* *coronaformis* (Loczy), *Erymnoceras* *coronatum* (Brug.), *E.* *baylei* (Jean.), *Rollierites* *minuendum* (Roll.), *Reineckeia* spp.,

Hecticoceratinae (*Lunuloceras*, *Brightia*, *Rossiensiceras*). In the Northern Caucasus the biohorizon is known in Dagestan of the Tsudakhar and Burtanimahi sections (Gavrilov et al., 2015; Ippolitov et al., 2015). Ammonites are represented by the index-species, *Indosphinctes* ex gr. *choffatti* (Parona et Bonarelli), *Gulielmiceras* sp. *Choffatia* sp., *Subgrossouvría* sp., *Anaplanulites* ex gr. *nikitinoensis* (Sasnov), *Rossiensiceras* *evolutum* (Lee), *Brightia* *subnodososa* (Tsytovitch). The following ammonites are also mentioned in the Avar Koisu section (Lominadze, Sakharov, 1969; Lominadze, 1982): index-species, *Gulielmiceras* *castor* (Rein.), *K.* *clavifer* Tint., *K.* aff. *zugium* Buck., *K.* aff. *castorinum* Tint., *Erymnoceras* *coronatum* Brug., *E.* *doliforme* Rom., *E.* *avarensis* Lominadze, *E.* *baylei* Jean., *E.* cf. *chikhachevi* Amann., *Rollierites* *minuendum* Rol., *Rossiensiceras* *metomphalum* (Bon.), *R.* *metomphalum* bonarelli (Chikh.).

Key sections in European Russia: 1) Elatma (bed 8, condensed concretions of sandstone); 2) Alpatyovo (bed 10); 3) Mikhaylov (Mikhaylovtsenement I, bed 5; Mikhaylovtsenement II, bed 3); 4) Polovchinovo and Vasilkovo – the Unzha River (clay with concretions); 5) Uzhovka (the lower bed of oolitic marl up to 0.3 m); 7) Votcha – the Sysola River (bed 8 in Kiselev, 2006); 8) Moscow City (bed 2, middle part).

crassum biohorizon Kiselev, 2001

? =*stutchburii* (hemera): Buckman, 1924 in Buckman, 1909–1930: pl. 531; Buckman, 1928 in Buckman, 1909–1930: p. 29

=*Crassum* (biohorizon): Kiselev, 2001: p. 24

Index-species. *Kosmoceras* (*Zugokosmoceras*) *crassum* Tintant. The holotype was figured by Tintant (1963: pl. XXIX: 2). Blye (Jura).

Stratotype. Earlier (Kiselev, 2001), a stratotype was proposed in the Elatma section (Ryazan Region) in the matrix of bed 8. Since the Middle Callovian is strongly condensed in this section and it is far from the stratotype of the subzone, the neostratotype is proposed at Peterborough, England (interval 460–560 cm, Brinkmann, 1929b, Abb. 28). Hypostratotype – Mikhaylovtsenement I, bed 6.

Characteristic ammonites. Index-species, *Kosmoceras* (*Zugokosmoceras*) *effulgens* (Buckm.), *K.* (*Kosmoceras*) *pollucinum* Teis., *Gulielmiceras* (*Spinikosmoceras*) *castor* (Rein.), *G.* (*S.*) *pollux* (Rein.), *G.* (*S.*) *fuchsi* (Neum.), *G.* (*Gulielmiceras*) cf. *robustum* Tint., *Erymnoceras* cf. *coronatum* (Brug.), *Rollierites* sp., *Rollierites* *renardi* (Nik.), *Okaites* *mosquensis* (Fisch.), *Grossouvría* *nikitini* (Par. et Bon.), *Zieteniceras* aff. *rarecostatum* sp. nov., *Brightia* (*B.*) *eccentrica* Rogov, *B.* (*B.*) *davitashvili* Lominadze, *B.* (*B.*) *subinvoluta* (Bonarelli), *B.* (*B.*) aff. *brightii* (Pratt), *Orbignyiceras* *orbignyi* (Tsyt.), *O.* cf. *lonsdalii* (Pratt), *Lunulocer-*

as fallax (Zeiss), *Rossiensiceras rossiiense* (Teiss.), *Alcidia* cf. *nurrhaensis* (Waagen), *Putealiceras* cf. *punctatum* (Stahl), *Rehmannia* (*Locyceras*) *crassicostata* (Lóczy).

Key sections in European Russia: 1) stratotype; 2) Mikhaylov (Mikhaylovtsement I, bed 6); 3) Moscow City (bed 2, the upper part).

Remarks. While describing the species *Kosmoceras crassum*, Henry Tintant has pointed out (Tintant, 1963: p. 269–276) that its stratigraphic position is above that of *Kosmoceras obductum*, and therefore «Au point de vue stratigraphique, ces formes semblent caractériser un niveau élevé du Callovien moyen, correspondant sensiblement à la sous-zone à Grossouvrei (partie supérieure de la zone à Coronatum), alors que le vrai *K. obductum* caractérise au contraire la sous-zone inférieure de la zone à Coronatum» (ibid.: p. 276). Tintant (1963) was uncertain about the stratigraphic position of this species, probably because the species is much more reminiscent of *K. obductum* than *K. grossourei*. In the description Tintant compares the new species mainly with *K. obductum* (mentioned 18 times).

The specificity of the ammonite complex of the *crassum* biohorizon was shown by Tintant when he described sections in Burgundy (Côte Chalonnaise), from where the following ammonites were mentioned (Tintant, Thierry, 1967: p. 676): *Kosmoceras crassum* (Tint.), *K. pollucinum* (Teiss.), *Gulielmiceras* aff. *pollux* (Rein.), *Phlycticeras pustulatum* (Rein.), *Choffatia* aff. *cardoti* (Petit.), *Choffatia waagensi* (Teiss.), *Grossouvria subtilis* (Neum.), *Erymnoceras doliforme* (Roman), *E. cf. ajax* (d'Orb.), *E. coronatum* (Brug.), *Reineckeia* cf. *fehlmanni* (Jean.), *R. aff. crassicosta* (Loc.), *R. groussourei* (Petit.), *Reineckeites plana* (Lee), *R. stubeli* (Steinm.), *Kellawaysites* aff. *greppini* (Opp.), *K. aff. multicostata* (Petit.), *Rossiensiceras rossiiense* (Teiss.). A similar ammonite assemblage was described in Franconia (Callomon et al., 1987). In the North Caucasus, this biohorizon can be allocated in the Avar Koisu section, where the following ammonite assemblage has been described (Lominadze, Sakharov, 1969; Lominadze, 1982): index-species, *K. trinode* Buck., *K. cf. castorinum* Tint., *K. aff. herakles* Tint., *Gulielmiceras* *pollux* (Rein.), *G. ornatum* (Schl.), *Erymnoceras coronatum* Brug., *E. doliforme* Rom., *E. golothonense* Lominadze, *E. philbyi* Ark., *Rollierites minuendum* Rol., *R. dimidiatum* Rol., *R. romani* Jean., *R. tzudakharenensis* Lominadze, *R. cf. turkmenensis* Amann., *Reineckeia falcata* Tint., *Orbignyiceras pseudopunctatum* (Lahusen) and others.

In the ammonite assemblages of the *crassum* biohorizon of the Elatma and Mikhaylov sections the index-species of any of the standard subzones (*K. obductum* and *K. grossourei*) were not found. Attribution of the discussed biohorizon to the Obductum Subzone is determined by its position in the sections of Elatma and Mikhaylov below the *posterior* biohorizon. The author of the *posterior* biohorizon J. Callomon (1964) has drawn the lower boundary of the Grossouvrei Subzone in Peterborough by the first occurrence of *K. (Z.) posterior* (Brinkmann, 1929b: Taf. 2: 4, Taf. 3: 3, Callomon, 1963: pl. 1: N), therefore any unit of the Coronatum Zone, located below the first occurrence of the species, should be assigned to the underlying Obductum Subzone

Grossouvrei Subzone Callomon, 1955

=*Kosm. obductum* (Zone): Brinkmann, 1929b: p. 36 (pars)

=*K. (Zugokosmoceras) grossourei* (Subzone): Callomon, 1955: p. 256, 257

=*grossourei* (sous-zone): Tintant, 1963: p. 54, 55

=*grossourei* (Subzone): Callomon, 1964: p. 280; Cariou et al., 1967: p. 690, 691; Callomon, 1968: p. 272; Mangold, 1971: p. 347; Callomon et al., 1987: p. 32–34; Cox, 1988: p. 8; Thierry et al., 1997: p. 70; Kiselev, 1999: p. 93, 94; Kiselev, 2001: p. 25; Dietl, 2015

Index-species. *Kosmoceras (Zugokosmoceras) grossourei* Douville, 1915. Lectotype figured by Douville (1915: pl. 12: 1).

Stratotype. Peterborough (beds 17a–22c, interval 561–1093 cm (Callomon, 1964, 1968)), Cambridgeshire, England.

Biohorizons: *posterior* and *grossourei*.

Geographic range. European Russia (Central Russia, the Pechora River basin), England (Yorkshire), France, Switzerland (Herznach), Germany, Poland, Georgia.

***posterior* biohorizon** Callomon, 1964

=*Obductum-Posterior* (horizon): Callomon, 1964: p. 280; Thierry et al., 1997: p. 70

=*Posterior* (biohorizon): Kiselev, 2001: p. 25

Stratotype. Peterborough (interval 561–864 cm (Callomon, 1964, 1968)), Cambridgeshire, England.

Index-species. *Kosmoceras (Zugokosmoceras) posterior* Brinkmann, 1929. The holotype is figured by Brinkmann (1929b: Taf. 2: 4). England, Peterborough, level 560 cm.

Characteristic ammonites. Index-species, *K. (Kosmoceras) pseudogrossourei* Tint., *K. (K.) cf. bigoti* Douv., *Gulielmiceras (Spinikosmoceras) castor* (Rein.), *G. (S.) pollux* (Rein.), *G. (Gulielmiceras) robustum* (Tint.), *G. (G.) fasciculatum* (Tint.), *Longaeviceras alpha* Kiselev, *C. (Bryocadoceras) vetulum* Kiselev, *C. (Eichwaldiceras) sp.*, *Pseudocadoceras meledinae* Kiselev, *Ps. (Percacosticeras) callomoni* Kiselev, *Ps. gulyaevi* Kiselev, *Ps. (Novocadoceras) diffusum* Kiselev, *Erymnoceras doliforme* (Roman), *Binatisphinctes fluctuosus* (Pratt), *Okaites comptoni rossicus* (Siem.), *O. mosquensis* (Fisch.), *Alcidia* sp., *Zieteniceras rarecostatum* sp. nov., *Brightia* (*Brightia*) *eccentrica* Rogov, *B. (B.) progzhel-*

lensis Rogov, *B. (B.) mangoldi* (Lom.), *Orbignyiceras orbignyi* (Tsyty.), *O. lonsdalii* (Pratt), *Lunuloceras fallax* (Zeiss), *Rossiensiceras rossense* (Teiss.).

Key sections in European Russia: 1) Burdovo (bed 2 in Kiselev, 2001); 2) Elatma (bed 9); 3) Mikhaylov (Mikhaylovtsenement I, bed 7a, Michalovtsenement II, bed 4a, Mikhaylov-Gorenka, bed 9); 4) Uzhovka (presumably); 5) Alpatyev (presumably in the top of bed 10); 6) Moscow City (top of the bed 2).

***grossouvrei* biohorizon** Callomon, 1964

=*zugium* (hemera): Buckman, 1923 in Buckman, 1909–1930: pl. 389

=*Grossouvrei* (horizon): Callomon, 1964: p. 280, 288; Thierry et al., 1997: p. 70

=*Grossouvrei* (biohorizon): Kiselev, 2001: p. 25

Index-species. The same as for the subzone.

Stratotype. Peterborough (interval 864–1093 cm (Callomon, 1964, 1968)), Cambridgeshire, England.

Characteristic ammonites. Index-species, *K. (Kosmoceras) aff. pollucinum* (Teiss.), *Gulielmiceras (Spinikosmoceras) aculeatus* (Eichw.), *Funiferites allae allae* Kiselev, *C. (Eichwaldiceras) intermedium* sp. nov., *Pseudocadoceras aff. primigenium* (Par. et Bon.), *Erymnoceras doliforme* (Roman), *Binatisphinctes fluctuosus* (Pratt), *Rossiensiceras cf. rossense* (Teiss.), *Putealiceras virile* (Zeiss), *P. mangoldi* (Lominadze), *Brightia (B.) pseudocracoviense* (Tsytvovich), *B. (B.) aff. progzhellenensis* Rogov, *B. (B.) cf. subinvoluta* (Bonar.), *Zieteniceras rarecostatum* sp. nov., *Orbignyiceras orbignyi* (Tsyty.), *O. cf. michailowense* (Zeiss), *O. lonsdalii* (Pratt), *Brightia (B.) brightii* (Pratt), *B. (B.) rectocostata* (Buckm.), *B. (B.) salvadori* (Par. et Bon.), *Lunuloceras fallax* (Zeiss), *L. sinuicostatum* (Zeiss).

Key sections in European Russia: 1) Elatma (bed 10); 2) Mikhaylov (Mikhaylovtsenement I, bed 7b, Mikhaylovtsenement II, bed 4 [40–80 cm above the base]; Mikhaylov-Gorenka, bed 10b); 3) Alpatyev (upper 0.05 m of bed 10); 4) Moscow City (bed 3).

UPPER CALLOVIAN

Athleta Zone d'Orbigny, 1852

Phaeinum Subzone Callomon 1968

=Elizabethae Zone: Neaverson, 1925: p. 31

=Lower P. athleta Zone: Callomon, 1968: p. 274

=Phaeinum Subzone: Callomon, Sykes, 1980: p. 46; Meledina, 1987: p. 149, 150; Cox, 1988: p. 8; Callomon, Wright, 1989: p. 801; Repin, Rashvan, 1996: p. 14; Thierry et al., 1997: p. 71; Kiselev, 1999: p. 95; Kiselev, 2001: p. 26

Index-species. *Kosmoceras (Zugokosmoceras) phaeinum* (Buckman, 1924). The holotype was figured by Buckman, 1924 in Buckman, 1909–1930: pl. CDXC. England, Wiltshire, Christian Malford. Oxford Clay Formation.

Stratotype. Calvert (Buckinghamshire, England). Oxford Clay Formation, beds 10–12 (Callomon, Sykes, 1980).

Biohorizons. In the European Russia the subzone includes 2 parallel biohorizons based on species belonging to different lineages – *phaeinum* and *allae allae*. In England, the subzone includes the only *phaeinum* biohorizon, while in the Southern Germany (Swabia) two biohorizons – *aculeatus/balticum* and *berckhemeri* are recognized in this subzone.

Geographic range. Central Russia, Lithuania, England, France, Germany, Eastern Greenland (Callomon, 1993).

***phaeinum* biohorizon** Callomon, 1968

=*hoplistes* (hemera): Buckman, 1924 in Buckman, 1909–1930: pl. CDLXXXVIII

=*acutistriatum* (hemera): Buckman, 1924 in Buckman, 1909–1930: pl. CDLXXXVIa, b

=*K. zugium interpositum* (horizon): Tintant, 1963: p. 54

=*phaeinum* (horizon): Thierry et al., 1997: p. 71

Index-species, stratotype, geographic range the same as for the subzone.

Characteristic ammonites. In European Russia – index-species, *K. (Zugokosmoceras) cf. zugium* (Buckm.), *K. (Kosmoceras) fibuliferum* (Buckm.), *K. (K.) gemmatum* (Phill.), *Gulielmiceras (Spinikosmoceras) acutistriatum* (Buckm.), *G. (S.) rimosum* (Quenst.), *G. (S.) aculeatus* (Eichw.), *G. (S.) cf. ornatus* (Schlot.) emend. (Brinkm.), *Funiferites allae allae* (Kiselev), *Pseudopeltoceras chauvinianum* (d'Orb.), *Binatisphinctes fluctuosus* (Pratt), *Okaites comptoni comptoni* (Pratt), *Okaites mosquensis* (Fisch.), *Brightia (Brightia) progzhellenensis* sp. nov., *B. (B.) cf. subinvoluta* (Bonar.), *B. (B.) brightii* (Pratt), *B. (B.) lominadzei* sp. nov., *Orbignyiceras pseudopunctatum* (Lahusen), *O. lonsdalii* (Pratt), *O. cf. michailowense* (Zeiss). In England (Callomon, Sykes, 1980: p. 46) according to the abundance of kosmoceratids, the ammonite assemblage is in many respects similar to those of the Central Russia: index-species, *K. gemmatum* (Phillips), *G. (G.) rimosum* (Quenstedt), *G. (S.) acutistriatum* (Buckman), *G. (S.) aculeatus* (Eichwald), *G. (S.) ornatus* (Schlotheim), *Binatisphinctes comptoni* (Pratt), *B. fluctuosus* (Pratt), *Orbignyiceras lonsdalii* (Pratt), *Brightia (B.) brightii* (Pratt), *B. (B.) rectocostata* (Buckm.). In Germany (Dietl, 2015), Tethyan taxa predominate, mainly *Reineckeia* and *Hecticoceratinæ*, while kosmoceratids are relatively infrequent.

Key sections in European Russia: 1) Burdovo (bed 3); 2) Elatma (bed 11); 3) Mikhaylov (Mikhaylovtsenement I, bed 7c; Mikhaylovtsenement II, bed 4, interval 350–400 cm above the base; Mikhaylov-Gorenka, bed 10b [top], 10c [base]); 4) Alpatyevo (in redeposited nodules); 5) Dyadkovo, top of bed 4; 6) Votcha (in redeposited concretions).

Remarks. Despite the fact that the *phaeinum* biohorizon is the junior synonym of previously proposed biohorizons (see synonyms), its name here is used as the only valid one. This is due to the following reasons: 1) The species *Hoplitesmokeras hoplistes* Buckman, 1924 (in Buckman, 1909–1930: pl. CDLXXXVIII) is regarded as the junior synonym of *K. (K.) gemmatum* (Phill.) (Neotype No. J.4822, Arkell, 1939: p. 189, fig. 4) and therefore it is invalid. The replacement of the name *hoplistes* by *gemmatum* with preservation of the original authorship is also impossible, since the stratigraphic distribution of the species *K. gemmatum* is much wider (see above) than the *phaeinum* biohorizon. 2) The use of the name *acutistriatum* is problematic, since the ammonite assemblage of the *acutistriatum* hemera, mentioned by Buckman (1928: p. 28) differs from that of the *phaeinum* biohorizon and rather corresponds to that of the *obductum* biohorizon. 3) The *K. zugium interpositum* horizon, proposed by Tintant (1963), is not applicable for a variety of reasons. On the one hand, the species *Zugokosmokeras zugium* Buckm. (holotype: Buckman, 1923 in Buckman, 1909–1930: pl. CCCLXXXIX) and *Z. interpositum* Buckm. (holotype: Buckman, 1923 in Buckman, 1909–1930: pl. CDXIX) in our opinion are younger synonyms of the species *K. grossouvrei* Douv. (holotype: Douville, 1915: p. 37, pl. XII: 3, 3a). On the other hand, H. Tintant himself placed this horizon in the Grossouvrei Subzone, therefore, most likely it should correspond to the *grossouvrei* biohorizon. Nevertheless, in the species complex of the *K. zugium interpositum* horizon, Tintant includes *Kosmoceras phaeinum*, the specimens of which were not figured in his work. Such a contradictory characterization of this horizon does not allow its use instead of the *phaeinum* biohorizon.

***allae allae* biohorizon** Kiselev *et al.*, 2003

=*allae allae* (biohorizon): Kiselev *et al.*, 2003: p. 222; Kiselev, Rogov, 2005: p. 128; Rogov *et al.*, 2012: fig. 4

Index-species. *Funiferites allae allae* (Kiselev). Holotype: Kiselev, 1999: pl. 3: 1–3, Middle Callovian (upper part of the Grossouvrei Subzone) of the Mikhaylov section (Mikhaylovtsenement I, the lower part of bed 7).

Stratotype. Mikhaylov (Ryazan Region), Mikhaylovtsenement I, bed 7, level 100–400 cm above the bottom.

Characteristic ammonites. Index-species, *Kosmoceras (Zugokosmoceras) grossouvrei* Douv., *K. (Z.) phaeinum* (Buckm.), *K. (Kosmoceras) fibuliferum* Buckm., *K. (K.) cf.*

gemmatum (Phill.), *Gulielmiceras (Spinikosmoceras) aculeatus* (Eichw.), *G. (S.) cf. ornatum* (Schlot.) emend. (Brinkm.), *Binatisphinctes fluctuosus* Buckm., *Okaites comptoni comptoni* (Pratt), *Rossiensiceras cf. rossiene* (Teiss.), *Putealiceras virile* (Zeiss), *P. mangoldi* (Lominadze), *Brightia (B.) proghellenensis* sp. nov., *B. (B.) lominadzei* sp. nov., *B. (B.) pseudocracoviense* (Tsytovitch), *B. (B.) subinvoluta* (Bonar.), *B. (B.) brightii* (Pratt), *Zieteniceras rarecostatum* sp. nov., *Orbignyceras orbignyi* (Tsyty.), *O. lonsdalii* (Pratt), *O. michailowense* (Zeiss), *L. fallax* (Zeiss), *L. sinuicostatum* (Zeiss).

Correlation. The upper part of the *grossouvrei* biohorizon – Phaeinum Subzone of the standard scale.

Key sections in European Russia: 1) Burdovo (bed 3); 2) Elatma (bed 11); 3) Mikhaylov (Mikhaylovtsenement I, bed 7, 100–400 cm above the bottom, Mikhaylovtsenement II, bed 4, interval 350–400 cm above the bottom; Mikhaylov-Gorenka, bed 10a–c, 0–270 cm above the bottom); 4) Votcha (in redeposited concretions).

Geographic range. European Russia – Central Russia (Ryazan, Moscow and Kostroma regions), the Komi Republic (the basins of the Sysola River and the Usa River), (?) Lithuania.

Proniae Subzone Brinkmann, 1929 emend. Callomon, 1968

=*Duncani*-zone: Neaverson, 1925: p. 33

=*Proniae* (Zone): Brinkmann, 1929b: p. 36

=Middle *P. athleta* Zone: Callomon, 1968: p. 275

=*Proniae* Subzone: Callomon, Sykes, 1980: p. 46; Meledina, 1987: p. 149–151; Cox, 1988: p. 8; Callomon, Wright, 1989: p. 801; Repin, Rashvan, 1996: p. 14; Thierry *et al.*, 1997: p. 1971; Kiselev, 2001: p. 17; Kiselev, Rogov, 2005: p. 130

Index-species. *Kosmoceras (Lobokosmoceras) proniae* Teisseryre. Lectotype (Brinkmann, 1929a): Teisseryre, 1883: tab. III, fig. 15 (refigured herein, Pl. 20: 2), the Upper Callovian basin of the Pronya River (Ryazan region).

Stratotype. Calvert (Buckinghamshire, England). Oxford Clay Formation, beds 13 a–b (Callomon, Sykes, 1980).

Biohorizons. Five biohorizons in European Russia, of which two are based on kosmoceratids – *proniae* and *rowlstonense*, and three are based on cardioceratids – *allae compressum*, *patruus*, *funiferus*. The *rowlstonense* biohorizon is established for the first time by the index-species, belonging to the same phylogenetic line as *Kosmoceras proniae*. In South-West Germany the subzone includes a sequence of 3 biohorizons – *Complanatoides*, “*Evexa*” alpha, and “*Evexa*” beta, which have been proposed by G. Dietl (Thierry *et al.*, 1997 – these biohorizons were mentioned on the basis of the unpublished data of Dietl, but they have not yet been formally described).

Remarks. Brinkmann (1923, 1927, 1929b) while studying the kosmoceratid succession in the Popilani sections, showed, in particular, that the species *K. proniae* and *K. rowlstonense* do not occur together in most of the sections. Similar results were published by Callomon and Wright (1989: p. 802). They describe the sequence of ammonite complexes in the lower part of the Hackness Rock Member, which is represented by two beds of iron-oolitic rocks corresponding to the upper half of the Phaeinum Subzone, the Proniae Subzone and the lower half of the “Spinosum” Subzone. The lower part of the succession is separated here from the upper part by a gap, which corresponds to the middle part of the Proniae Subzone. The lower part contains *K. gemmatum*, *K. proniae*, *K. duncani*, *P. athleta*, the upper part – *K. rowlstonense*, *K. rimosum*, *K. spinosum*. On the basis of this sequence, Callomon and Wright assumed the possibility of allocating two biohorizons, but it was noted that “now it is not possible to separate these two horizons in the field”.

In the sections of Central Russia the discrete vertical distribution of the species *K. proniae* and *K. rowlstonense* – two segments of the evolutionary sequence of “gracile Kosmoceras” – is fairly clearly traced. Thus the *proniae* and *rowlstonense* biohorizons can be recognized, the first of which was previously established in England, and the second one is described herein for the first time.

Geographic range. European Russia, England, France, Germany, Poland, Lithuania and the North Caucasus.

proniae biohorizon Buckman, 1923

=*proniae* (hemera): Buckman, 1923 in Buckman, 1909–1930: pl. CDXXXVI; Buckman, 1928 in Buckman, 1909–1930: p. 28

=*Proniae* (horizon): Thierry *et al.*, 1997: p. 71

=*Proniae* (biohorizon): Kiselev *et al.*, 2003: p. 222; Kiselev, Rogov, 2005: p. 128

Index-species. The same as in the subzone.

Stratotype. The same as for the subzone.

Characteristic ammonites. In European Russia – index-species, *K. (Kosmoceras) gemmatum* Phill., *K. (K.) gracile* Kopik, *Gulielmiceras (Spinikosmoceras) cf. ornatus* (Schlotheim), *Funiferites patruus* (Eichw.) emend. (Nik.), *F. allae compressum* subsp. nov., *Cadoceras (Eichwaldiceras) intermedium* sp. nov., *Pseudocadoceras* sp. nov., *Pseudopeltoceras* sp., *Peltoceras athleta* (Phillips), *Binatisphinctes* ex gr. *binatus* (Leckenby), *B. welschi* (Gerard et Contaut), *Okaites comptoni rossicus* (Siem.), *Orbignyiceras lonsdalii* (Pratt), *O. diversicostatum* (Ger. et Cont.), *Brightia (Brightia) proghellenensis* sp. nov., *B. (B.) cf. subinvoluta* (Bonar.), *B. (B.) lominadzei* sp. nov., *B. (B.) pseudocracoviense* (Tsytovitch),

B. (Glyptia) tenuicostata Rogov. In England (Callomon, Sykes, 1980: p. 46) Boreal taxa predominate – *K. (L.) proniae* Teisseyre, *K. (L.) rowlstonense* (Young & Bird), *K. duncani* (Sowerby), *K. (K.) bigoti* (Douville), *K. (K.) aff. spinosum* (Sow.), *Gulielmiceras*, *(G.) rimosum* (Quenstedt), *Longaeviceras placenta* (Leckenby), *Longaeviceras* spp., *Peltoceras athleta* (Phillips), *Peltoceras* spp. Fauna 6 (Mangold, 1967: p. 685) corresponds to this biohorizon in France (Jura), characterized by the prevalence of the Tethyan taxa and characterized by occurrences of *K. (L.) proniae* (Teiss.), *K. (K.)* spp., *Orbignyiceras trezeense* (Ger. et Cont.), *Alcidia* cf. *diversicostata* (Gér. et Cont.), *Taramelliceras* ex gr. *suevicum* (Opp.), *Collotia angustilobata* (Brasil), *Collotia* sp., *Collotites* sp., *Choffatia* gr. *evoluta* (Neum.), *Subgrossouvreria orion* (Opp.), *Orionoides indicus* Spath, *O. lanquinei* Gér. et Cont., *O. termieri* Gér. et Cont., *Grossouvreria* cf. *variabilis* (Lah.), *G. sulcitera* (Opp.), *Binatisphinctes* sp., *Peltoceras athleta* (Phill.), *P. trifidum* (Qu.), *Pseudopeltoceras* cf. *chauvinianum* (d'Orb.), *Ps. rollieri* (Jeannet), *Ps. cf. retrorsum* Spath, *Ps. leckenbyi* (Bean), *Euaspidoceras* sp., *Rursiceras* sp.

In South-West Germany, the biohorizon can be allocated at the base of the Ornatenton FM, where it is represented by a rich ammonite assemblage (Hahn *et al.*, 1971). Among them, there are about 5 species of Kosmoceratidae, 3 species of Pseudoperisphinctidae, 4 species of Peltoceratinidae, 3 species of Reineckiidae and 11 species of Oppeliidae.

rowlstonense biohorizon Kiselev & Rogov, 2005

=*rowlstonense* (biohorizon): Kiselev, Rogov, 2005: p. 128; Rogov *et al.*, 2012: fig. 4.

Index-species. *Kosmoceras (Lobokosmoceras) rowlstonense* (Young et Bird). Neotype: Callomon, Wright, 1989: pl. 96: 4. Castle Hill, Scarborough (England), Hackness Rock Member.

Stratotype. Mikhaylov (Ryazan region): Mikhaylovtsement I, bed 8, 180–280 cm above the base. Hypostratotype: Scarborough (Yorkshire), Hackness Rock.

Characteristic ammonites. Index-species, *K. (Kosmoceras) cf. rotundum* (Quenst.), *Funiferites funiferus* (Phill.), *F. patruus* (Eichw.), *Pseudopeltoceras* aff. *leckenbyi* (Bean), *Brightia (Brightia) nodosa* (Quenstedt), *B. (B.) nodosiformis* Rogov, *B. (B.) glypta* (Buckman), *B. (B.) gzhellensis* Rogov, *B. salvatori* (Parona et Bonar.), *B. (Glyptia) tenuicostata* Rogov.

Key sections in European Russia: 1) Mikhaylov (Mikhaylovtsement I, bed 8, 180–280 cm above the base; Mikhaylovtsement II, bed 5a; Mikhaylov-Gorenka, bed 10c [top] –11a); 2) Peski (bed 1); 3) Guryevo (Tula region, Venev district), presumably.

Correlation. See the subsection „Kosmoceratidae” in the „Ammonite stratigraphy” section of this article.

Geographic range. Central Russia (Ryazan, Moscow and Tula regions), England, the Lithuania (Popilani), East Greenland (Milne Land).

***allae compressum* biohorizon** Kiselev & Rogov, 2005

=*allae* subsp. (biohorizon): Kiselev *et al.*, 2002: p. 82; Kiselev *et al.*, 2003: p. 222

=*allae compressum* (biohorizon): Kiselev, Rogov, 2005: p. 128; Rogov *et al.*, 2012: fig. 4.

Index-species. *Funiferites allae compressum* subsp. nov.

Stratotype. Mikhaylov (Ryazan region), Mikhaylovtsement I, bed 7c, 400–620 cm above the base.

Characteristic ammonites. Index-species, *Kosmoceras (Lobokosmoceras) proniae* Teiss., *K. (Kosmoceras) gemmatum* (Phill.), *Gulielmiceras (Spinikosmoceras)* cf. *ornatus* (Schlotheim), *G. (S.) aculeatus* (Eichw.), *Pseudopeltoceras* aff. *chauvinianum* (d'Orb.), *Binatisphinctes fluctuosus* Buckm.

Correlation. Corresponds to the lower part of the Proniae Subzone of the standard scale.

Geographic range. Central Russia (Mikhaylov).

***patruus* biohorizon** Kiselev *et al.*, 2003 emend. herein

=*Patruus* (biohorizon): Kiselev *et al.*, 2003: p. 222; Kiselev, Rogov, 2005: p. 128

Index-species. *Funiferites patruus* (Eichw.) emend. (Nik.). Holotype: Eichwald, 1868: pl. 34: 6. No. 2/2030, Paleontological-Stratigraphic Museum of St. Petersburg State University. Upper Callovian of the Koltsovo section (Tver Region).

Stratotype. Mikhaylovtsement I, beds 7, 8, 520–1020 cm above the base of bed 7.

Characteristic ammonites. Index-species, *Kosmoceras (Lobokosmoceras) proniae* Teiss., *K. (L.) rowlstonense* (Young et Bird), *K. (K.) gemmatum* (Phill.), *Gulielmiceras (Spinikosmoceras)* cf. *ornatus* (Schlotheim), *G. (S.) aculeatus* (Eichw.), *Binatisphinctes fluctuosus* Buckm., *Okaites mosquensis* (Fischer), *Peltoceras athleta* (Phill.), *Longaeciceras lahuseni* (Bodyl.), *Brightia (Brightia) nodosa* (Quen.), *B. (B.) glypta* (Buckm.), *B. (B.) gzhellensis* Rogov.

Correlation. Corresponds to the upper part of the Proniae Subzone – the lower part of the Spinosum Subzone of the standard scale.

Key sections in European Russia: 1) Mikhaylov (Mikhaylovtsement); 2) Alpatyovo (horizon of oolitic marl concretions); 3) Peski (bed 1); 3) Burdovo (bed 4).

Geographic range. Central Russia (Ryazan, Moscow, Tver and Kostroma regions).

***funiferus* biohorizon** Kiselev *et al.*, 2003

=*Funiferus* (biohorizon): Kiselev *et al.*, 2003: p. 222; Kiselev, Rogov, 2005: p. 128; Rogov *et al.*, 2012: fig. 4

Index-species. *Funiferites funiferus* (Phillips). Holotype: specimen J.16381 (Museum of Oxford University), Phillips, 1829: pl. 6: 23, refigured in Callomon, Wright (1989: pl. 92: 4). Upper Callovian, Athleta Zone of England (Yorkshire, Hackness Rock Member).

Stratotype. Mikhaylovtsement I, bed 8 (level 220 cm above the base) and bed 9 (the lower nodules horizon).

Characteristic ammonites. Index-species, *Kosmoceras (Kosmoceras) rotundum* (Quenst.), *K. (Lobokosmoceras) rowlstonense* (Young et Bird), *Gulielmiceras (Spinikosmoceras) ornatus* (Schlotheim), *Okaites mosquensis* (Fischer), *Peltoceras athleta* (Phill.), *Longaeciceras lahuseni* (Bodyl.), *Brightia (Brightia) nodosa* (Quen.), *B. (B.) glypta* (Buckm.), *B. (B.) gzhellensis* Rogov.

Correlation. The upper part of the Proniae Subzone and the lower part of the Spinosum Subzone (= Kuklikum Subzone herein) of the standard scale.

Key sections in European Russia: 1) Mikhaylov (Mikhaylovtsement I, bed 8 [top] and bed 9 [bottom], Mikhaylovtsement II, bed 5a, Mikhaylov-Gorenka, bed 10 [top] and bed 11 [bottom], 2) Peski (bed 1); 3) Gzhel (Moscow region).

Geographic range. Central Russia (Ryazan and Moscow region), England (Yorkshire), France (Normandy, province of Calvados).

Kuklikum Subzone Brinkmann, 1929 emend.
Callomon 1968

=*Kosmoceras spinosum* (Subzone): Brinkmann, 1929b: p. 36

=Upper *P. athleta* Zone: Callomon, 1968: p. 276

=Spinosum Subzone: Callomon, Sykes, 1980: p. 46, 47; Meledina, 1987: p. 134; Cox, 1988: p. 8; Callomon, Wright, 1989: p. 801; Repin, Rashvan, 1996: p. 12, 14; Thierry *et al.*, 1997: p. 71

=“Spinosum” (Subzone): Kiselev, Rogov, 2005: p. 128, 130; Dietl, 2011: s. 35

Index-species. *Kosmoceras (Lobokosmoceras) kuklikum* (Buckman). Holotype: Buckman, 1926 in Buckman, 1909–1930: pl. DCXXVIA, b. Upper Callovian of England (Oxford, Oxford Clay Formation).

Stratotype. Woodham (Buckinghamshire, England). Oxford Clay Formation, beds E-D1.

Biohorizons. In the European Russia the subzone includes the *kuklikum* biohorizon of the kosmoceratid scale

and the *funiferus* biohorizon of the cardioceratid scale. A threefold subdivision of the subzone was proposed in South Germany (Dietl, 1993), where three biohorizons were identified on the basis of Tethyan index species: *Collotia* (*Fraasi* biohorizon), *Taramelliceras* (*Prorsosinuatum* and *Punctulatum* biohorizons).

Remarks. The Kuklikum Subzone is characterized by specific ammonite assemblages, both in Russia and in Western Europe, so the independence of this stratigraphic unit is beyond doubt. Nevertheless, the definition of the boundaries of the subzone is complicated by a number of questions connected with the ambiguity of its index-species.

It seems unjustified to use *Kosmoceras spinosum* as an index of this subzone. According to the British authors (see synonyms), this species in English sections is widespread, occurring both in the upper part of the Athleta Zone and in the lower part of the Lamberti Zone. In the stratotypic section of Woodham, this interval corresponds to the so-called Spinosum Clay, represented by clays and siltstones. Its lower part (Lower Spinosum Clay, layer E) is entirely related to the Spinosum Subzone of the British scale. This interval is characterized by numerous finds of small pyritized shells of *Kosmoceras* (Arkell, 1939; Callomon, 1968; Hollingworth, Wignall, 1992), among which *K. spinosum* (Sow.) and *K. tidmoorensis* Arkell predominate. The upper part of this member (Upper Spinosum Clay, bed D (2)) belongs to the Henrici Subzone of the Lamberti Zone (Callomon, 1968), however, *K. spinosum* is also noted from this part of the succession. This species is also mentioned from the overlying interval represented by the marlstones and limestones of the Lamberti Limestone (Lamberti Zone). As Arkell (1939: p. 187) noted “The syntypes came from “near Weymouth”, from the Lamberti clays of Tidmoor Point”

Thus, the indexation of the Spinosum Subzone does not correspond to the actual distribution of the index-species and appears to be a formal action. Its meaning, evidently, was to fix the features of the Spinosum Clay – the abundance of pyritized ammonites of the genus *Kosmoceras*. This action is not a biostratigraphic procedure and should not be used for the name of biostratigraphic units. For this reason, the name “Spinosum” was replaced by the name “Kuklikum” (which was also proposed in Kiselev, Rogov, 2005: p. 128) by the species of *Kosmoceras*, which, on the one hand, is distributed exclusively within the stratigraphic interval inherent only in the Lower Spinosum Clay, on the other hand, continues the *Kosmoceras* (*Lobokosmoceras*) lineage which is used for subdivision of the lower part of the Proniae Subzone (see the section “Ammonite stratigraphy”).

Geographic range. European Russia, England, France, Germany, Poland, Lithuania, the North Caucasus, Eastern Greenland (Callomon, Birkelund, 1980).

***kuklikum* biohorizon Buckman, 1926**

=*duncani* (hemera): Buckman, 1920 in Buckman, 1909–1930: pl. CXLVIII; Buckman, 1928 in Buckman, 1909–1930: p. 28

=*kuklikum* (hemera): Buckman, 1926 in Buckman, 1909–1930: pl. DCXXVIa, b; Buckman, 1928 in Buckman, 1909–1930: p. 28

=*kuklikum* (biohorizon): Kiselev, Rogov, 2005: p. 128, 130

Index-species. *Kosmoceras* (*Lobokosmoceras*) *kuklikum* (Buckman). Holotype: Buckman, 1926 in Buckman, 1909–1930: pl. DCXXVIa, b. Upper Callovian of England (Oxford, Oxford Clay Formation).

Stratotype. Mikhaylovtsen I, bed 9.

Characteristic ammonites. Index-species, *K.* (*Kosmoceras*) *rotundum rotundum* (Quenst.), *K.* (*Kosmoceras*) *rotundum subspinosum* Nikolaeva et Rozhd., *Longaeviceras placenta* (Leck.), *Peltoceras ex gr. athleta* (Phillips), *Rurisceras* sp., *Sublunuloceras cf. dynastes* (Waagen), *Brightia* (*Glyptia*) *canaliculata canaliculata* (Quenstedt).

Correlation. It corresponds to the Spinosum Subzone of Western Europe and the Collotiformis Subzone of the Sub-mediterranean scale.

Key sections in European Russia: 1) Mikhaylov (Mikhaylovtsen I, bed 9; Mikhaylovtsen II, bed 5 [b/c interval]; Mikhaylov-Gorenka, bed 11b, c); 2) Peski (bed 2); 3) Guryevo (Tula region, Venev district); 4) Berdyanka River, Belyaevka village (base of bed 4); 5) Rybinsk (Perebor); Yoda River (Rybinsk district).

Geographic range. European Russia (Ryazan, Moscow and Tula regions), England.

A description of the higher stratigraphic units of the Lamberti Zone and the Lower Oxfordian, was published by us previously (Kiselev *et al.*, 2013).

SYSTEMATIC PALAEONTOLOGY

The principles of taxonomy used in this work. At present, there are no generally accepted criteria for the allocation and delimitation of ammonite taxa, which often leads to confusion in the understanding of diagnoses and the ranges of genera and species. Especially complicating the recognition of suitable taxa of lower rank is the usage of the sexual dimorphism concept in the systematics of Jurassic ammonites. Thus here we briefly outline the particular rules or principles on the basis of which the ammonite taxa are determined in this work (Tab. 6).

1 principle. The concept of sexual dimorphism should not be manifested in the taxonomy of ammonites in the form of any specific criteria for allocating or combining species,

subgeneric and generic taxa that could replace the morphological criteria.

The use of the concept of sexual dimorphism in ammonoid taxonomy, which follows the situation when one taxon, established to the microconch, is considered as a synonym of a macroconchiate taxon (or *vice versa*), seems an unsuccessful solution, regardless of the state in which the current systematics of the group under discussion is. First of all, the sexual nature of ammonoid dimorphism and thus micro- and macroconchs will never be established reliably because of the specific properties of the paleontological material. All modern concepts of sexual dimorphism in ammonites (Makowski, 1962; Callomon, 1963) or polymorphism (Matyja, 1986, 1994) are nothing more than models that explain examples of diversity in ammonites, but providing no evidence of its sexual nature. To some extent, an indirect confirmation of the sexual nature of the “classical” dimorphism in ammonoids is provided by a few examples of pseudohermaphroditism with the transfer of certain characteristics from one putative sex to another (Parent *et al.*, 2008). In most cases, it is impossible to unambiguously correlate micro- and macroconch taxa at the species level. In fact, the only joint occurrence is used for the combination of micro and macroconchs into pairs (Howarth, 2017). It is well known that in many lineages the rates of morphogenesis in micro- and macroconchs are different (Kiselev, 1996; Rogov, 2017) and the supposed micro- and macroconchs in some cases are characterized by significant differences in morphology since their earliest ontogenetic stages and clear differences in their faecal distribution (Kiselev, 1996).

So far, the results of methodically irreproachable (using morphometric and statistical methods) comparative morphological studies in which the morphological similarity and difference of micro- and macroconchs are shown are rarely described in the literature. Without such studies, any attempts to unite these morphological groups into one taxon remain an unproven declaration.

2 principle. Microconchs and macroconchs are considered as independent taxa, therefore they are separated both at the species and generic levels, but for those groups which are characterized by weak dimorphism (such as pachyceratids, which lack mature apertural modifications and are characterized by the close proximity of micro- and macroconchs in all features except the final conch size) micro- and macroconchs are distinguished at the species level only. It should be noted that the variability of many Callovian ammonites has not yet been sufficiently studied, and the interpretation of co-occurring morphotypes is not quite clear in many cases.

Family CARDIOCERATIDAE Siemiradzki, 1891

Subfamily QUENSTEDTOCERATINAE Meledina, 1977

Genus *Lamberticeras* Buckman, 1920

Type species: *Ammonites lamberti* Sowerby (Sowerby, 1821: p. 73, pl. 242: 1–3). Upper Callovian of England.

Diagnosis: Macroconchs with a final shell diameter up to 25 cm, platiconic or discoconic on middle and late whorls, moderately involute or involute, less often semi-evolute. The maximum whorl height is observed at middle whorls (Wh/Wb always exceeds 1 and reaches 1.5), at late whorls the cross section remains high or becomes isometric (Wh/Wb = 1) and rarely low (Wh/Wb < 1). The cadiconic stage is absent. The ribs are prorsiradiate, falcate-shaped. Bifurcate ribs alternate with simple and intercalatory secondary ribs in different ratios. On the middle whorls, the ribs connecting on the ventral side and form a cord-like blunt keel. On adult whorls the keel is absent and the ventral side is rounded.

Composition: *Lamberticeras lamberti* (Sow.); *L. henrici* (Douv.) (Douville, 1912: p. 55, pl. 4: 34–37), *L. praelamberti* (Douv.) (Douville, 1912: p. 57, pl. 4: 39–42), *L. gregarium* (Leckenby) (Buckman, 1918 in Buckman, 1909–1930: pl. CXVIIb); *L. pseudolamberti* (Sintzow) (Lahusen, 1883: pl. 4: 4) (= *Q. irinae* Sasonov (Sasonov, 1957: pl. 10: 1)).

Remarks. The species referred here to as *Lamberticeras* are traditionally regarded as characteristic representatives of the genus *Quenstedtoceras*, but the use of *Quenstedtoceras* (in the traditional sense) is complicated due to nomenclatural contradictions. The sequence of accumulation of these contradictions coincides with the appearance of the following nomenclatural innovations:

- 1821. Description *Ammonites lamberti* (Sowerby, 1821: p. 73, pl. 242: 1–3) and *Amm. leachi* (*ibid.*: c. 73, pl. 242: 4).
- 1877. Designation of the genus *Quenstedtoceras* (as *Quenstedioceras* – Hyatt, 1877: p. 390) without description, but with a single mentioned species *Q. leachi*.
- 1881. Recognition of the “*Lamberti* group” in the genus *Amaltheus* (Nikitin, 1881: p. 264), to which the species *Amaltheus lamberti* (Sow.), *A. leachi* (Sow.) (non *Q. leachi* (Sow.) sensu Arkell, 1939) are assigned. Only macroconchs are shown in Nikitin (1881: pl. 1): *A. sutherlandiae* (Murch.), *A. rybiskianus* Nik. and *A. mologae* Nik.
- 1884. The first diagnosis of the genus *Quenstedtoceras* (as *Quenstedioceras* – Nikitin, 1884: p. 58) as “*Quenstedioceras* nov. gen.”.
- 1886. Nikitin (1886) first used the *Quenstedticeras* for *Quenstedioceras*.
- 1900. Hyatt (1900) confirmed replacement of *Quenstedioceras* by *Quenstedtoceras*.

Table 6

List of ammonite genera and subgenera used in the study

Family, subfamily		Genera, subgenera		
		Macroconch taxa		Microconch taxa
CARDIOCERATIDAE Siemiradzki, 1891	Cadoceratinae Hyatt, 1900	<i>Cadoceras</i> Fischer, 1882	<i>Cadoceras</i> Fischer, 1882 (type species <i>Ammonites sublaevis</i> J. Sowerby, 1814)	<i>Pseudocadoceras</i> Buckman, 1918
			<i>Rondiceras</i> Troitskaya, 1956 (type species <i>Stephanoceras milaschevici</i> Nikitin, 1881)	
			<i>Eichwaldiceras</i> Buckman, 1920 (type species <i>Ammonites carinatus</i> Eichwald, 1868)	
			<i>Longaeviceras</i> Buckman, 1918 (type species <i>L. longaeicum</i> Buckman, 1918)	<i>Novocadoceras</i> Sasonov, 1975 (type species <i>N. suraense</i> Sasonov, 1975)
			<i>Funiferites</i> Kiselev et al., 2003 (type species <i>Ammonites funiferus</i> Phillips, 1829)	<i>Percacosticeras</i> Kiselev, 1996 (type species <i>Longaeviceras polonicum</i> Callomon & Wright, 1998)
CARDIOCERATIDAE Siemiradzki, 1891	Quenstedtoceratinae Meledina, 1977	<i>Cardioceras</i> Neumayr et Uhlig, 1881	<i>Lamberticeras</i> Buckman, 1920 (type species <i>Amm. lamberti</i> Sowerby, 1821)	<i>Quenstedtoceras</i> Hyatt, 1877 (type species <i>Ammonites leachi</i> Sowerby, 1819)
			<i>Eboraciceras</i> Buckman, 1918 (type species <i>Ammonites dissimilis</i> Brown, 1849)	
			<i>Pavloviceras</i> Buckman, 1920 (type species <i>Quenstedtoceras pavlovi</i> R. Douville, 1912)	
			<i>Cardioceras</i> Neumayr et Uhlig, 1881 (type species <i>Ammonites cordatus</i> Sowerby, 1813)	<i>Vertebriceras</i> Buckman, 1920 (type species <i>V. dorsale</i> Buckman, 1920)
			<i>Scarburgiceras</i> Buckman, 1924 (type species <i>Ammonites scarburgense</i> Young et Bird, 1828)	<i>Protocardioceras</i> Schirardin, 1958 (type species <i>Quenstedtoceras praecordatum</i> Douville, 1912)
KOSMOCERATIDAE Haug, 1887	Kosmoceratinae Haug, 1887	<i>Kosmoceras</i> Waagen, 1869	<i>Scotioceratoceras</i> Buckman, 1925 (type species <i>Ammonites excavatus</i> Sowerby, 1815)	<i>Korythoceras</i> Buckman, 1920 (type species <i>K. korys</i> Buckman, 1920)
			<i>Goliathiceras</i> Buckman, 1919 (type species <i>Nautilus ammonoides</i> Young et Bird, 1828)	
			<i>Pachycardioceras</i> Buckman, 1926 (type species <i>P. robustum</i> Buckman, 1926)	
			<i>Kosmoceras</i> Waagen, 1869 (type species <i>Ammonites spinosus</i> Sowerby, 1829)	<i>Spinikosmoceras</i> Buckman, 1924 (type species <i>S. acutistriatum</i> Buckman, 1924)
			<i>Lobokosmoceras</i> Buckman, 1923 (type species <i>Cosmoceras proniae</i> Teisseryre, 1887)	<i>Gulielmiceras</i> Buckman, 1920 (type species <i>Ammonites gulielmi</i> Sowerby, 1821)
ASPIDOCERATIDAE Zittel, 1895	Peltoceratinae Spath, 1924	<i>Pseudopeltoceras</i> Spath, 1928 (type species <i>Ammonites chauvinianus</i> Orbigny, 1847)	At the genera level is not separated	
			<i>Peltoceras</i> Waagen, 1871 (type species <i>Amm. athleta</i> Phillips, 1829)	<i>Rursiceras</i> Buckman, 1919 (type species <i>Amm. reversus</i> Leckenby, 1859)
	Aspidoceratinae Zittel, 1895	<i>Peltoceratooides</i> Spath, 1924 (type species <i>P. semirugosum</i> Waagen, 1875)	<i>Parawedekindia</i> Schindewolf, 1925 (type species <i>Amm. arduennensis</i> d'Orbigny, 1848)	
			<i>Euaspidoceras</i> Spath, 1930 (type species <i>Amm. perarmatus</i> Sowerby, 1822)	<i>Mirospinctes</i> Schindewolf, 1926 (type species <i>Perisphinctes mirus</i> Bukowski, 1887)
			<i>Choffatia</i> Siemiradzki, 1898 (type species <i>Perisphinctes cobra</i> Waagen, 1875)	<i>Grossouvría</i> Siemiradzki, 1898 (type species <i>Amm. sulciferus</i> Oppel, 1857)
PSEUDO-PERISPINCTIDAE Schindewolf, 1925	<i>Binatisphinctes</i> Buckman, 1921 (type species <i>Amm. binatus</i> Leckenby, 1859)		<i>Okaites</i> Sasonov, 1965 (type species <i>Amm. mosquensis</i> Fischer, 1843)	
	<i>Orionoides</i> Spath, 1931 (type species <i>Perisphinctes pseudoorion</i> Waagen, 1875)		Not definitely defined	
			<i>Properisphinctes</i> Spath, 1931 (type species <i>Perisphinctes bernensis</i> Loriol, 1898)	

Table 6 cont.

Family, subfamily	Genera, subgenera	
	Macroconch taxa	Microconch taxa
PACHYCERATIDAE Buckman, 1918	<i>Erymnoceras</i> Hyatt, 1900 (type species <i>Amm. coronatus</i> Bruguiere, 1789)	<i>Erymnoceras</i> Hyatt, 1900 (type species <i>Amm. coronatus</i> Bruguiere, 1789)
	<i>Rollierites</i> Jeannet, 1951 (type species <i>Stephanoceras renardi</i> Nikitin)	<i>Rollierites</i> Jeannet, 1951 (type species <i>Stephanoceras renardi</i> Nikitin)
OPPELIIDAE Bonarelli, 1894	<i>Orbignyiceras</i> Gerard et Contaut, 1936 (type species <i>Harpoceras pseudopunctatum</i> Lahusen, 1883) <i>Sublunuloceras</i> Spath, 1928 (type species <i>Harpoceras lairense</i> Waagen, 1875) <i>Zieteniceras</i> Zeiss, 1956 (type species <i>Hecticoceras zieteni</i> Tsytovitch, 1911) <i>Rossiensiceras</i> Gerard et Contaut, 1936 (type species <i>Harpoceras rossense</i> Teissreyre, 1883) <i>Alcidia</i> Rouillier, 1913 (type species <i>Ammonites subdiscus</i> d'Orbigny) <i>Chanasia</i> Rouillier, 1921 (type species <i>Hecticoceras chanasiense</i> Parona et Bonarelli, 1895)	<i>Brightia</i> Rollier, 1922 (type species <i>Amm. hecticus nodosus</i> Quenstedt, 1849) <i>Putealiceras</i> Buckman, 1922 (type species <i>Amm. putealis</i> Leckenby, 1859) <i>Lunuloceras</i> Bonarelli, 1894 (type species <i>Amm. lunula</i> auct. = <i>A. onticola</i> Menke, 1830) <i>Eulunulites</i> Elmi, 1967 (type species <i>Hecticoceras (Lunuloceras)</i> <i>pompeckyi</i> Parona et Bonarelli, 1895)

1918. Confirmation of a type species of *Quenstedtoceras* by S. Buckman (1918 in Buckman, 1909–1930: p. xi), which is the only species mentioned by the author of the genus type *Q. leachi* (Sow.): “Genus, *Quenstedtoceras*, Hyatt, 1876: Type, *Q. leachii*, Hyatt (*Am. leachi*, J. Sowerby, Min. Conch., Aug. 1819, ccxlii, f. 4)”. Buckman also includes one more species in this genus, *Q. williamsoni* Buckman, 1918 in Buckman, 1909–1930 (pl. CXVIIb).
1918. The designation of the genus *Vertumniceras* (Buckman in Buckman, 1909–1930, 1918: p. 14) with a type species *Am. vertumnus* (holotype: Leckenby, 1859: pl. I: 3, Buckman, 1918 in Buckman, 1909–1930: pl. CXVIa–c).
1920. Establishment of the genus *Lamberticeras* with a detailed diagnosis and designation of the type species *L. lamberti* (Buckman, 1920 in Buckman, 1909–1930: p. 14, 15: pl. CLIV): «*Lamberticeras*, g.n. Genoholotype, *L. lamberti*, J. Sowerby sp. – a topotype so identified, in Mr. Tutcher's Coll. (Pl. CLIV)».
1920. Establishment of the genus *Bourkelamberticeras* (Buckman, 1920 in Buckman, 1909–1930: p. 17): «*Bourkelamberticeras* instead of *Lamberticeras* – the species was named after Aylmer Bourke Lambert (J. Sow. Ill, 73)».
1937. The first use of the name *Bourkelamberticeras* as the subgenus of *Quenstedtoceras* (Maire, 1937). The genus includes 5 species and 11 variations.
1939. The designation of the neotype for *Quenstedtoceras leachi* (Sow.), a type species of the genus *Quenstedtoceras* by W.J. Arkell (1939: p. 168: pl. X: 5). The morphological features of the neotype fully correspond to the diagnosis of the genus *Vertumniceras* Buckman, 1918 in Buckman, 1909–1930, which automatically makes the latter genus invalid. For this reason, Arkell considers the genus *Vertumniceras* as a junior synonym of the genus *Quenstedtoceras*. In this same work, Arkell used *Bourkelamberticeras* as the subgenus of *Quenstedtoceras*.
1949. The first indication of the double authorship of the genus *Quenstedtoceras* as “*Quenstedticeras* Hyatt, 1977, emend. Nikitin, 1884” (Krimholtz, 1949: p. 200).
1955. Addition of the genus *Lamberticeras* to the “Official list of generic names in zoology”: «*Lamberticeras* Buckman (S.), 1920 (gender: neuter) (type species, by original designation: *Ammonites lamberti* Sowerby (J.), 1819)» (ICZN, 1955, opinion 324j: p. 230).
1957. The use of the name *Lamberticeras* as subgenus of *Quenstedtoceras* in the Treatise (Arkell et al., 1957: p. L304). The name *Bourkelamberticeras* is considered as an objective synonym. The same approach is used in the new version of the Treatise (Howarth, 2017).
1958. The designation of *Ammonites lamberti* (Sowerby) as a type of the genus *Quenstedtoceras* (with the writing of the genus *Quenstedticeras*) in Krimholtz et al. (1958: p. 79). Wherein, the genus *Vertumniceras* is regarded as a junior synonym of the genus *Quenstedtoceras*.
- The main contradictions in the diagnosis of the genus *Quenstedtoceras* are related to the choice of a type species. Historically, there were two different solutions to this problem:
- The first variant** (Buckman, 1918 in Buckman, 1909–1930; Arkell, 1939): type of genus by monotype is *Amm. leachi* (Sowerby) and, accordingly, the genus *Quenstedtoceras* is the senior synonym of the genus *Vertumniceras* Buckman. As the neotype of *Q. leachi* selected by W. Arkell is a microconch, therefore, *Quenstedtoceras* s. str. should be considered as a microconch taxon. This approach was also followed by N.T. Sasonov (1965).
- The second variant** (Nikitin, 1881, 1884, Krimholtz, 1949; Meledina, 1977): type of genus is *Amm. lamberti* (Sowerby) – macroconch, so *Quenstedtoceras* s. str. is

a macroconch taxon, and the names *Lamberticeras* and *Bourkelamberticeras* should be considered as its junior synonyms.

The most optimal solution to the problem would be the use of the nomenclature approach based on the diagnosis of *Quenstedtoceras* proposed by S.N. Nikitin. This would reduce the number of taxa with a dubious nomenclature and preserve the microconchiate genus *Vertumniceras*. However, the genus *Quenstedtoceras* with the type species *Amm. leachi* (Sowerby) has all the features of suitability according to ICZN rules. The rule of the First Reviser (ICZN, Article 24) does not apply to the action of Nikitin, since in the establishment of the genus A. Hyatt (1877) gave an indication on the species group name (*ibid.*, Article 12 (b) (5), explaining the word “indication” for the names published until 1931). After the designation of the *Q. leachi* neotype understanding of this species has became clear and, in a narrow sense, the genus *Quenstedtoceras* should be understood as a microconch taxon.

With this approach, difficulties arise from the choice of the generic name for ammonites of the *Amm. lamberti* group of two names: *Lamberticeras* and *Bourkelamberticeras*. It is shown above that the confusion in this question was caused by the author of these genera S. Buckman, who erected the genus *Lamberticeras* in March 1920, but few months later, in June of the same year proposed to abandon his name and replace it with *Bourkelamberticeras*. This Buckman decision led to the fact that both names became unstable in use. Thus, W. Arkell (1939) originally used the name *Bourkelamberticeras*. This name was also used by V. Maire (1937), J. Schirardin (1958) and N.T. Sazonov (1965). Later, Arkell replaced this generic name by *Lamberticeras* (Arkell *et al.*, 1957). It was fixed as valid by the decision of the International Commission on Zoological Nomenclature (ICZN, 1955, opinion 324-j). In the preliminary addition to the official list of generic names, Arkell (1951: p. 225) motivated his decision as follows: «The name *Lamberticeras* was first published as a *nomen nudum* by Kilian in 1910 (*Lethaea geognostica. Z* (No. 1) (*Lief. 2*): 194). Possessing no status in zoological nomenclature, the name *Lamberticeras* Kilian, 1910, does not invalidate the later name *Lamberticeras* Buckman, 1920. On erroneous information that the opposite was the case Buckman (1920, Type Ammonites 3: 17) renamed his genus *Bourkelamberticeras*. Both the *nomen nudum* *Lamberticeras* Kilian, 1910, and the junior objective synonym *Bourkelamberticeras* Buckman (S.), 1920, should now be relegated to the Official Index of Rejected and Invalid Generic Names in Zoology».

Subfamily CADOCERATINAE Hyatt, 1900

Genus *Funiferites* Kiselev, Gulyaev et Rogov, 2003

group of *Amaltheus funiferus* Phill. (pars): Nikitin, 1878: p. 109

group of *Lamberti* (pars): Nikitin, 1881: p. 264–272

Cadoceras Fisch. (pars): Nikitin, 1884: p. 67, 68; 1885: p. 51, 52; Spath, 1932: p. 58–64; Sazonov, 1957: p. 100–103

Longaeviceras (pars): Buckman, 1918 in Buckman, 1909–1930: p. xiv

Chamousetia (pars): Douville, 1912: p. 19–23; Sasonov, 1965: p. 36–38; Callomon, Wright, 1989: p. 803

Chamousetia (*Platychamousetia*) (pars): Repin, 2002: p. 35, 36

Cadoceratinae indet. (gen. nov.?): Mitta, 2000: p. 59, 60

Funiferites: Kiselev *et al.*, 2003: p. 223, 224; Howarth, 2017: p. 73

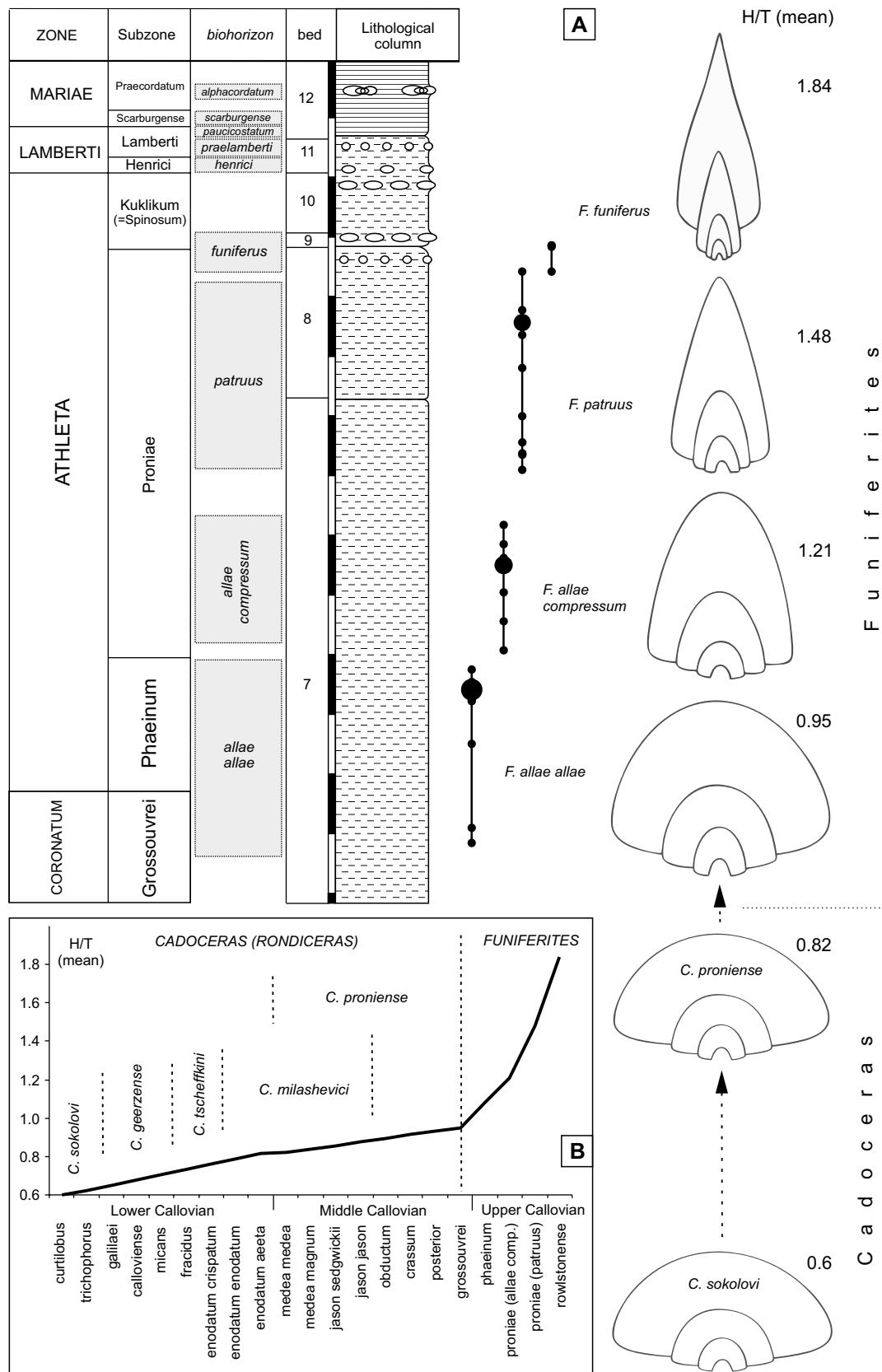
Type species. *Ammonites funiferus* Phillips, 1829 (Phillips, 1829: pl. 6: 23). Lectotype (OUM J 16381) from the Phillips collection has been figured by Callomon and Wright (1989: pl. 92: 4); England, Hackness Rock, Upper Callovian, Athleta Zone.

Diagnosis. Macroconchs with discoconic or oxyconic adults whorls and cadiconic or discoconic middle whorls. Cross-section is broad or isometric with a rounded venter in early species of the genus, but became highly oval, subtriangular, or keeled in younger species. The relative height of the whorls tends to a constant value at middle and late whorls. The adult shell is smooth, the sculpture is present only in the early and middle whorls. The ribs are sinusoidally curved, with a bend on the venter. With age, the ribbing disappears starting from the lateral sides, and is retained only on the venter, especially in the keeled species.

Phylogeny. Ammonites of the genus *Funiferites* appear in the Athleta Chron almost suddenly, without any apparent direct connection with other taxa, and also disappear in the same chron (Callomon, Wright, 1989). There are several points of view on the origin of this group. Most researchers associate it with *Chamousetia* (Douville, 1912, Callomon, Wright, 1989, Repin, 2002), although they can not indicate transitional forms in the stratigraphic interval that separates the groups. In the opinion of V.V. Mitta (2000) ammonites of the “*Ammonites*” *funiferus* group can originate from *Rondiceras stenolobum* (Keys.) emend. Nikitin,

Fig. 11. Distribution of species and change in the proportions of the whorl cross-section in the *Cadoceras* – *Funiferites* lineage

A. In the Mikhaylovskiy section; B. In relation to the Callovian infrazonal scale. H/T (mean) is the average value of the proportion factor as the ratio of the whorl height to the whorl width



distributed in the lower parts of the Coronatum Zone of the Middle Callovian. However, this species (in our opinion it is the first representative of the genus *Longaeviceras*) differs from ammonites close to *F. funiferus* by the shape of the last whorls, which are much wider, not keeled and have a rounded venter. This feature is also retained in later *Longaeviceras*, which co-occur together with “*Ammonites*” *patruus* and “*A.*” *funiferus*.

D.N. Kiselev (1999) suggested that the youngest species of the group “*Ammonites*” *funiferus* can derive from the species *Cadoceras allae* Kiselev. This point of view was confirmed by a detailed study of the Middle and Upper Callovian sections of the Mikhaylov area. Here, in the clayey succession within a thickness of about 8–10 m, a phyletic lineage, ending with the species *Funiferites funiferus*, was traced (Fig. 11, see also Rogov *et al.*, 2012: fig. 4). The earliest species of this genus is *F. allae*, whose chronosubspecies are distributed from the upper part of the Grossouvrei Subzone to the lower part of the Proniae Subzone. In this stratigraphic interval the shape of their shell varies from cadiconic, through pachyconic to discoconic. This trend can be traced already within the species *F. allae*, which makes it possible to distinguish the chronosubspecies *F. allae* s. str. and *F. allae compressus* subsp. nov. The next evolutionarily successive species *F. patruus*, distributed at the top of the Proniae Subzone and the lower parts of the Kuklikum Subzone, already has a flattened discoconic shell, transitional to oxyconic. Its undoubted descendant *F. funiferus* from the Kuklikum Subzone is characterized by an oxyconic shell with a slightly depressed keel on the last whorl. This species disappears without leaving descendants shortly before the top of the Kuklikum Subzone.

The main trend in the evolution of *Funiferites* is a gradual lateral flattening of the shell during the Middle and Late Callovian from *F. allae allae* to *F. funiferus*. It is expressed in a smooth change in the relative height of the whorls (parameter Wh/Wb) from the wide and isometric to the high and ultrahigh (Fig. 12a). Significant variability of this feature is observed, which leads to a significant overlap of the morphological fields of neighboring taxa within this lineage, up to 46% for subspecies and 15.5–40.0% for species (Fig. 12b). During the morphogenesis, the relative height of whorls changes insignificantly or does not change at all, while it varies very clearly through the evolution of this genus. This is seen both from the shift of the trend line of each species (Fig. 12a) and from the change in the average value of H/T: 0.95 for *F. allae allae*; 1.21 for *F. allae compressus*; 1.48 for *F. patruus* and 1.84 for *F. funiferus* (Fig. 11).

During the evolution of the genus *Funiferites* the lateral flattening of the shell is accompanied by a correlatively related decrease of the umbilical diameter (Fig. 12b). On average, the relative height of the whorl increases from species

to species (and subspecies) at each phyletic stage (*F. allae allae*, *F. allae compressus*, *F. patruus* and *F. funiferus*) by 1.24 times, and the umbilical diameter decreases by 1.22 times. We can assume that in the evolution of *Funiferites* these two parameters change coherently. As a result, the evolving parameters of the shell vary from *F. allae allae* to *F. funiferus* approximately twice: H/T in 1.92 and U% in 1.78 times.

The most probable ancestor of the genus *Funiferites* and, accordingly, its earliest subspecies *F. allae allae*, is *Cadoceras proniense* Sasonov – a species which is known in the Middle Callovian of the Ryazan region and widely distributed in the central part of European Russia. The holotype of the species originates from the Coronatum Zone of the Nikitino section (Sazonov, 1965: pl. 14: 3), the paratypes – partly from the same zone and section (ibid.: pl. 13: 3) and from the Jason Zone of the Elatma section (ibid.: pl. 10: 4). We have found this species mainly in the Jason Zone (Pl. 6: 5–7). This species stratigraphically precedes the early *Funiferites* and occurs up to the top of the Obductum Subzone. Morphologically, it is also very close to *F. allae allae* both in shell shape and ribbing. Its sculpture consists of rectiradiate ribs with a rib ratio of 2.5–3.0, ribs are often sinusoidally curved, which is typical feature of *Funiferites*. The cross section of *C. proniense* whorls is wider (0.82) than in *F. allae allae* (Fig. 11). The overlap of the morphological fields of both species averages about 55%, which exceeds the relative overlap of the morphological fields between the neighbouring members of the *Funiferites* lineage. This means that the rate of morphological changes in the evolution of the *C. proniense* – *Funiferites* lineage is sharply accelerated after the appearance of *F. allae allae*, which indicates a change in the trend of morphological changes during the evolutionary transition of *Cadoceras* into *Funiferites*.

The systematic position of *Cadoceras proniense* is debatable. Morphologically, *C. wosnessenskii* (Grewingk), described from the Callovian of Southern Alaska (Grewingk, 1850: pl. 4: 1; Pompeckj, 1900: pl. 5: 5) is hardly distinguishable from this species. This similarity is most likely caused by parallelism. In this regard, both species should be considered as approximately isochronous vicarious analogs.

Most likely *Cadoceras proniense* originated from the group of Middle Russian cadoceratins, belonging to the *Cadoceras* (*Rondiceras*) lineage, which is widely distributed in the Lower and Middle Callovian of European Russia. The earliest member of this group – *Cadoceras sokolovi* Kiselev is characterized by the middle whorls which are quite comparable to that of *C. proniense*, including rectiradiate ribbing, but the cross-section of *C. sokolovi* is noticeably lower (Wh/Wb [mean] = 0.6). The general trend of phylogenetic changes in *Cadoceras* (*Rondiceras*) is a gradual increase in the cross-section height of adult whorls. Probably, this pro-

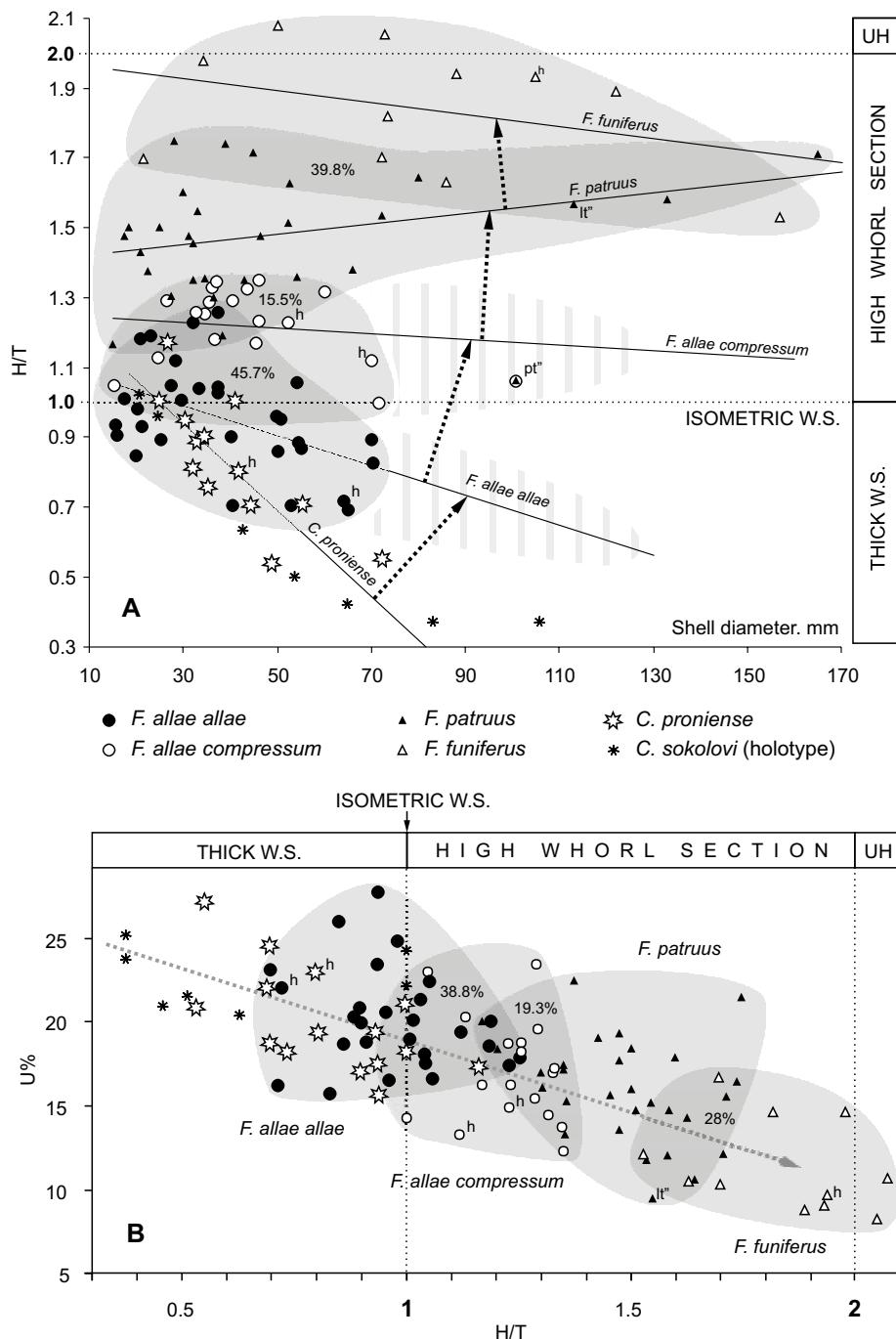


Fig. 12. Distribution of species and subspecies of the genus *Funiferites* and phylogenetically related *Cadoceras* species according to the shell shape

A. According to the proportions of the cross-section H/T (height/thickness of whorl section) in relation to the diameter of the shell; **B.** By the proportions of the cross-section H/T and the relative umbilical diameter ($U\%$). Gray fillings indicate the morphological fields of *Funiferites*, the figures show the relative overlap between species; the trend lines are shown by a solid line, the morphological boundaries labelled by a dashed line. Arrows indicate the direction of phylogeny. Abbreviations: h – holotype; lt – lectotype, pt – paratype (double comma points are type specimens with reconstructed values of features according to regression formulas); UH – ultrahigh whorl section

cess was parallel in different groups of this lineage, and one of them gave rise to *Funiferites*. The shell flattening in this group occurs at a faster rate than in the ancestral *Cadoceras* (Fig. 11b), which allows us to confidently demarcate these genera by the appearance of *F. allae*.

Comparison. The morphotype of *Funiferites*, which is most pronounced in *F. funiferus*, appeared independently three times during the evolution of the cardioceratids (Bajocian-Kimmeridgian): in the Early Callovian (Koenigi Chron) – the genus *Chamousettia*, in the Late Callovian (Athleta Chron) – *Funiferites*, and in the Early-Middle Oxfordian – the genus *Cardioceras*. There are no direct phyletic transitions between these groups, and the morphological similarity between them should be considered as a manifestation of parallelisms and iterative evolution in cardioceratids. Therefore, it is unnecessary to analyze the differences between these taxa.

The greatest difficulties arise when distinguishing between *Funiferites* and ancestral cadoceratins of the *Cadoceras* (*Rondiceras*) lineage. The main difference between these groups lies in the type of morphogenesis: in *C. (Rondiceras)* the difference between the early pre-cadiconic and adult cadiconic stages (according to Ivanov, 1960) is very sharp. In the middle whorls (the pre-cadiconic stage), the relative whorl height reached its maximum, and later gradually decreases to an isometric and, subsequently, a low cross-section (the cadiconic stage). This is clearly seen in the example of *C. sokolovi* (Fig. 11a): a change in whorl proportions forms a trend with a high correlation coefficient (0.87). In *Funiferites*, the proportions of whorls do not change in morphogenesis (the correlation coefficient is in the range of 0.0095–0.2300).

Composition. Three species: type species, *F. patruus* (Eichwald) and *F. allae* (Kiselev).

Remarks. Yu.S. Repin (2002) described a new subgenus *Chamousettia* (*Platychamousettia*), into which he placed two species: *C. (P.) dertevi* Repin (type species) and *C. (P.) funifera* (Phillips). Study of the holotype of *C. (P.) dertevi* (Museum VNIGRI, No. 859/42, figured in Repin, 2002: fig. 1) shows that it does not come from the Adzva River, as the author of the species indicates. Most likely it comes from an erratic boulder from the banks of the Pechora River and does not have an exact location. Nodules with *Chamousettia chamousetti* (d'Orb.), identical in matrix and with the fossils in the same preservation, are often found in Quaternary sediments that are exposed along the right bank of the middle reaches of the Pechora River. The holotype of *C. (P.) dertevi* refers to the flattened morph of *C. chamousetti*, which is confirmed by the presence of an imprint of a microconch *Pseudocadoceras boreale* (Buckm.) on the body chamber of this specimen. Thus, *Platychamousettia* should be considered the junior synonym of the genus *Chamousettia*.

Distribution. Middle Callovian, Coronatum Zone, Grossouvrei Subzone, *grossouvrei* biohorizon – Upper Callovian, Athleta Zone of European Russia and Lithuania; the Athleta Zone of England, France, Germany.

Funiferites allae allae (Kiselev, 1999)

Pl. 5: 1–3, Pl. 6: 1, 2; Tab. 7

1987. *Eboraciceras* sp. nov.; Rotkyte: p. 17, pl. IV: 6

1999. *Cadoceras allae*; Kiselev: p. 96, pl. 3: 1–3, 9, 8 (only)

Holotype. No PIN 4839/19; Ryazan Region, Mikhaylovtsen'ye-I section, bed 7 (lower part); Middle Callovian, Coronatum Zone, Grossouvrei Subzone.

Diagnosis. The final diameter of the shell is unknown. Whorls are semi-involute and flattened. Wh/Wb ratio rarely exceeds 1, mainly at D = 30–35 mm. The stage of the high whorls, with Wh/Wb ratio of about 1 at the beginning and end of the stage, occurs at D = 20–30 mm. The end of this stage is marked at D = 35–55 mm. In this stage the cross-section has a characteristic subquadrate-oval shape: the umbilical walls are low and subvertical, with a round edge; lateral sides are flat and completely parallel to the spiral plane, occupying about a little more than half the lateral height of the whorl, and passing, with rounded bend, into the wide ventral side. There is no ventral sharpening. This shape of the cross-section remains for a long time, up to D = 50 mm, while the lateral sides are gradually transiting to the ventral side.

The sculpture is weakly expressed, begins relatively late (D = 10–12 mm) and ends relatively early (D = 35–40 mm), it consists of low, monotonous ribs. The ribs are well differentiated (the branching coefficient is 2.57–3.10), simple ribs are absent, and triplicate ribs are dominant. The ribs are prorsiradiate, with a slight inclination, and have a sinusoidal shape. Both lateral and ventral sides have a strong arching in the direction of the aperture. The apex of the lateral sinus is at the branching point of the ribs, in the lower third of the height of the whorl. The ventral sinus is acute and sometimes form the impression of a false acuity of the venter. With age, all elements of the sculpture disappear synchronously or with some delay of the ventral ribs. Striated growth lines at late whorls also have a sinusoidal shape.

Comparison. The main difference of this subspecies from the stratigraphically preceding descendant species *Cadoceras proniense* Sasonov and its vicarial counterpart *C. wosnessenskii* (Grew.) is the lack of a cadiconic stage in the adult whorls and a noticeable sinusoidal curvature of the sculpture at middle whorls. The cross-section of the middle whorls in these taxa may be almost the same, but the average is higher (Fig. 12a) in *F. allae allae*. A homeomorphic analogue of this subspecies at the high-whorl stage (or the pre-cadiconic stage) or at the beginning of the cadiconic

Table 7

Measurements (in mm) and it ratios (in %)

No.	D	Wh	Wb	U	Wh/ Wb	U%
PIN 4839/19 holotype	64.3	33.4	46.5	14.1	0.70	22.02
7/2 paratype	50.8	24.5	25.7	10.4	0.90	20.58
7/9	20.3	9.1	9.31	5.02	0.98	24.77
M7/315	53.0	23.6	33.4	8.5	0.70	16.03
M/42	49.7	24.0	25.0	8.2	0.96	16.49
	37.4	19.0	18.2	6.6	1.04	17.64
MC7-6	70.2	36.0	40.3	14.6	0.89	20.79
	54.6	26.5	30.0	11.1	0.88	20.33
MC7-5	70.4	35.0	42.4	11.05	0.82	15.69
	54.1	31.2	29.5	9.0	1.05	16.63
MC7-7	50.2	24.2	28.2	9.4	0.86	18.72
	40.2	19.4	21.2	8.0	0.90	19.90
MC7-10	37.5	17.5	17.0	8.0	1.03	21.33
	27.4	13.0	12.4	6.15	1.05	22.44
A125	33.2	15.6	15.0	6.0	1.04	18.07
A127	28.3	14.0	12.5	5.5	1.12	19.43
MC7-8	21.0	10.3	8.7	4.2	1.18	20.00
	29.6	14.4	14.3	5.6	1.01	18.92
MK319	20.0	9.0	10.6	5.2	0.85	26.00
	15.5	7.2	7.7	4.3	0.90	27.74
ZN530	21.3	9.7	10.4	5.0	0.93	23.47
M7-20	17.4	8.3	8.2	3.5	1.012	20.11
M.360	16.0	6.8	7.5	3.0	0.90	18.75
M.300	37.4	19.1	15.2	6.7	1.25	17.91
	32.2	15.6	12.7	5.6	1.22	17.39
	23.2	10.7	9.0	4.3	1.18	18.53

stage is the Lower Callovian (Enodatum Subzone) species *C. (Rondiceras) tcheffkini* (d'Orbigny). In the general proportions of the shell and the expression of the sculpture they could be almost indistinguishable. The described subspecies at the same morphogenetic stage is distinguished by a noticeable sinusoidal curvature of the ribs.

Distribution. Middle Callovian, Coronatum Zone, Grossouvre Subzone – Upper Callovian, Phaeinum Subzone of the central regions of European Russia and Lithuania (Popilani).

Material. 31 specimens from Mikhaylov (Ryazan Region); 1 specimen from Moscow City.

Funiferites allae compressus Kiselev, subsp. nov.

Pl. 5: 4–6; Tab. 8

1999. *Cadoceras allae*; Kiselev: p. 96, pl. 3: 4–7 (only)

2000. "Ammonites" *patruus* (pars); Mitta: pl. 55: 2, 3, 9

Derivatio nominis: from *compressus* (Latin) – compressed.

Holotype. Specimen No YPU-MC7-1; Mikhaylov, Mikhaylovtsement-I section, bed 7 (middle part); Upper Callovian, Athleta Zone, Proniae Subzone (lower part).

Diagnosis. The maximum diameter of the shell is measured before the beginning of the final uncoiling of umbilical spiral in a single specimen (MCEBC collection [Moscow]) and it attains 128 mm. The reconstructed final diameter of the shell on the terminal body chamber is about 205 mm. Whorls are semi-involute, discoconic. The cross-section of whorls is high, it is rarely isometric and is never low on middle and adult whorls. The high-whorls stage is stretched and comes at $D = 10\text{--}15$ mm, ends up to $D = 70$ mm or does not end at all. At this stage, the cross-section has a characteristic subtriangular-oval shape: the umbilical walls are low and steep, with a slightly rounded bend; lateral sides inclined, high, smoothly turning into a rounded ventral side. A similar shape of the cross-section remains unchanged during the all stages of morphogenesis. Sculpture is the same as in *F. allae*.

Table 8

Measurements (in mm) and it ratios (in %)

No.	D	Wh	Wb	U	Wh/ Wb	U%
7/8	32.6	16.25	12.94	6.13	1.25	18.80
2/20	37.0	18.6	15.2	7.0	1.22	18.90
M7-10	40.5	20.0	15.5	9.5	1.29	23.40
A34	46.2	23.5	17.4	5.7	1.35	12.30
	37.0	19.0	14.1	5.1	1.34	13.70
MC7-2	71.5	37.0	37.0	10.2	1.00	14.26
MC7-1 holotype	70.0	35.2	31.5	9.3	1.11	13.28
	52.4	27.0	22.0	7.8	1.22	14.88
MC7-4	46.2	24.15	19.6	7.5	1.23	16.23
	36.2	19.0	14.3	6.25	1.32	17.26
MC7-11	45.4	23.5	20.1	7.4	1.16	16.29
	34.6	18.2	14.5	6.3	1.25	18.21
MC8-3	60.0	31.1	23.6	8.7	1.31	14.50
	43.5	21.6	16.3	7.4	1.32	17.01
M550	15.2	6.6	6.3.0	3.5	1.04	23.02
MC 467	24.6	11.3	10.0	5.0	1.13	20.32
B285	35.5	18.0	14.0	5.5	1.28	15.49
	26.5	13.3	10.3	5.2	1.29	19.62

Comparison. The new subspecies differs from the nominal subspecies by having higher whorls at all stages of morphogenesis.

The subspecies structure of *F. allae* is the same as that of the Middle Callovian species *Cadoceras (Rondiceras) milaschevici* (Nikitin), which also has two subspecies – *C. (R.) milaschevici* s.str. (with a low cross-section) and *C. (R.) milaschevici compressum* (Nikitin) (with a more compressed shell). The first subspecies can be considered as a homeomorphic analogue of *F. allae* s. str., and the second – of *F. allae compressus*. This similarity is an undoubtedly demonstration of parallelism, however, the shells can be so similar at the same diameter of the shell, that this can lead to erroneous diagnosis. The main difference between these species is the presence or absence of the cadiconic stage: in *Funiferites* it is missing, while in *C. (Rondiceras)* it is typical. The high-whorl stage of *C. (R.) milaschevici* is distinguished from that of *F. allae compressus* by the reduction of the sculpture on the lateral side on the entire shell, which is not typical for *Funiferites*.

Most species of the genus *Stenocadoceras* (Imlay) are also homeomorphic to *F. allae compressus*. Undoubtedly, the described subspecies is one of several Middle Russian vicariate subspecies of this Arctic genus. The similarity between them is sometimes so large in the general course of morphogenesis (including the absence of the cadiconic stage) and shell shape (high subrectangular or subtriangular cross section with rounded, not sharpened, venter) that dis-

tinguishing these taxa is almost impossible. Especially there is a strong similarity of species with less relief sculpture in the middle whorls, for example in *S. multicostatum* (Imlay) (Imlay, 1953: pl. 44: 1–16). The main difference of *F. allae compressus* from this species is sinusoidally curved shape of ribs, while in all *Stenocadoceras* the ribs are falcate-prorsiradiæ. The *Stenocadoceras*-like morphotype repeatedly appeared during the Callovian in different groups of cadoceratines (*Cadochamousetia*, *Cadoceras (Rondiceras)*, *Longaeviceras*, *Stenocadoceras* and *Funiferites*), which filled a special adaptive zone in ammonite communities in various paleobiogeographical regions.

Distribution. Upper Callovian, the Athleta Zone, the Proniae Subzone (the lower part) of the central regions of European Russia.

Material. 15 specimens from Mikhaylov sections (Ryazan Region); 2 specimens from Burdovo section (Kostroma region).

Funiferites patruus (Eichwald, 1868) emend. (Nikitin, 1885)

Pl. 5: 7–10; Tab. 9

1865–68. *Ammonites patruus*; Eichwald: p. 1061, pl. 34: 6

1885. *Cadoceras patruum*; Nikitin: p. 60, pl. (XI)XIII: 59, 60

1999. *Cadoceras (Cadoceras) patruum*; Kiselev: p. 97, pl. 3: 10–12; pl. 4: 1–5

2000. “*Ammonites*” *patruus* (pars); Mitta: p. 60–61, pl. 55: 1, 4–8; pl. 56: 1, 2; pl. 57: 1.

Lectotype. A specimen figured by Eichwald (1865–68: pl. 34: 6; re-figured by Mitta (2000: pl. 55: 1)). Upper Callovian in Central Russia (Koltovo Village, Tver Region). This specimen is stored in the Paleontological-Stratigraphical Museum of the Saint-Petersburg State University (Saint-Petersburg), specimen no. 2/2030.

Description. The final diameter of shell is not known. We have only one specimen with a fragment of the terminal body chamber with the reconstructed diameter 178 mm. Accordingly, the final diameter of this shell can reach up to 200 mm. Whorls are very involute in the middle and late stages of morphogenesis. The largest relative diameter of the umbilicus is observed at early whorls and later it is gradually decreases. The cross-section of the whorls is high since the earliest stages. Wh/Wb attains 1 already at $D = 7\text{--}10$ mm, and further increases. The cross-section in the early and middle whorls is subrectangular with a low and steep umbilical wall, and later became subtriangular keeled, with the umbilical wall becoming flattened and rounded.

The sculpture is fully developed at $D = 20\text{--}30$ mm, then disappears at the umbilical edge, later on the lateral sides and at $D = 80\text{--}100$ mm ribbing disappears on the ventral side and the shell becomes completely smooth. The ribbing is differentiated: bifurcate ribs are almost absent, triplicate ribs predominate, with rib ratio 2.6–2.8. Bifurcate ribs predominate only at $D = 10\text{--}15$ mm. Ribs are low prorsiradiate. The shape of the ribs at all whorls is almost straight, with a barely noticeable sinusoidal curve, consisting of a lateral and

a ventral arch. The latter one is expressed more strongly and forms a rounded sinus.

Comparison. This species differs from *F. allae compressus* at all stages of morphogenesis by its straightened sculpture, higher and involute whorls. Similarly, as well as having a more differentiated sculpture at all stages of morphogenesis and the sinusoidal curvature of the ribs, it differs from *Stenocadoceras*.

Remarks. The lectotype (Mitta, 2000: pl. 55: 1) and the paralectotype (*ibid.*: pl. 55: 1) radically differ in the proportions of the cross-section: the paralectotype corresponding to the adult stage of morphogenesis is characterized by Wh/Wb = 1.08, which is not typical for this species. At Wh = 54 mm in the paralectotype (a whorl fragment) its reconstructed diameter (according to the regression formula $D = 1.9943 H - 1.3173$) attains 106.3 mm. The specified proportion of the cross section for a such a diameter is not included in the range of *F. patruus* variability and corresponds to *F. allae compressus* adult whorls (Fig. 12a). Therefore, the paralectotype of the species, as well as several specimens, figured in the work of Mitta (2000) (see above), we considered as belonging to *F. allae compressus*.

Distribution. The Upper Callovian, the Athleta Zone, the Proniae Subzone (the upper part) of the central regions of European Russia (Ryazan, Moscow, Tver and Kostroma regions).

Material. 21 specimens from Mikhaylov sections (Ryazan Region), 2 specimens from Alpatyevo section (Moscow region).

Table 9
Measurements (in mm) and its ratios (in %)

No.	D	Wh	Wb	U	Wh/Wb	U%
M7/890	46.4	23.6	16.0	6.3	1.47	13.57
MC1/485	36.6	18.2	14.0	6.2	1.30	16.93
	27.4	13.3	10.2	4.4	1.30	16.05
MC1/480	38.4	18.1	15.2	7.1	1.19	18.48
	28.0	18.0	10.3	6.0	1.74	21.42
MG2-5	72.3	38.4	25.0	8.5	1.53	11.75
	52.3	27.5	18.2	7.7	1.51	14.72
MG8-2	52.5	28.0	17.2	7.5	1.62	14.28
	39.0	21.3	12.25	6.4	1.73	16.41
MC8-1	54.2	28.5	21.0	8.3	1.35	15.31
	43.1	22.0	16.3	7.4	1.34	17.16
A26	32.1	16.2	12.0	5.6	1.35	17.44
M7-13	31.1	15.5	10.5	6.0	1.47	19.29
	22.3	11.0	8.0	5.0	1.37	22.42
M149	18.5	9.3	6.2	3.4	1.50	18.37
B630	17.5	9.3	6.3	3.1	1.47	17.71

Genus *Cadoceras* Fischer, 1882

Subgenus *Eichwaldiceras* Buckman, 1920

Cadoceras (Eichwaldiceras) intermedium Kiselev, sp. nov.

Pl. 9: 1–5; Tab. 10

Derivatio nominis: from *intermedius* (Latin) – intermediate.

Holotype. Specimen No YPU-M7-54; Ryazan region, Mikhaylov, Mikhaylovskiy section, bed 7 (lower part); Middle Callovian, Coronatum Zone, Grossouvrei Subzone

Diagnosis. The final diameter of the shell is unknown. The whorls are semi-involute or semi-evolute. The whorl cross-section is low and never isometric. The stage of high whorl is absent. The cross-section is round wide-oval, the umbilical walls are flat, with a rounded edges; the ventral side is wide and rounded. There are no obvious trends in the shape of the shell through ontogenesis. The ribs are sharply rursiradiate, smoothly passing through the ventral side without sinusoidal bends. The rib ratio is high due to the alternation of bi- and trifurcate ribs, approximately in equal proportions. The furcation point coincides with the beginning of the rursiradiate curvature of the ribs.

Variability. In the population there is an indistinct tendency of differentiation of the species into two forms: rare-ribbed ($pR = 15–17$), with coarser and more prominent ribs, and dense-ribbed ($pR = 19–23$), with smoothed ribs. Some rarely-ribbed specimens with a small diameter of the shell have some similarities with microconchs, but the presence of intermediate forms between them and explicit macroconchiate specimens does not allow separating the microconchs from the entire sample. The absence of the last body chambers, due to the peculiarities of the preservation of shells in the Mikhaylov sections, also makes it difficult to separate

these morphological groups. The stratigraphic distribution of rare- and dense-ribbed varieties is also indistinct; nevertheless, it is noted that the dense-ribbed forms, to which the holotype belongs, are more typical for the Middle Callovian (Grossouvrei Subzone), while the rarely-ribbed ones rather occurs in the Upper Callovian (Proniae Subzone).

Comparison. The main differences between species of *C. (Eichwaldiceras)* consist in the unequal density of ribbing (Fig. 13). The increase in rib density occurs in the Middle-Upper Callovian from the rarely-ribbed *C. (E.) carinatiforme* to *C. (E.) carinatum*. In general, the new species occupies an intermediate position between these species, both stratigraphically and phylogenetically, which is reflected in its name.

The new species is distinguished from the closely related *C. (E.) carinatum* (Eichwald, 1868: pl. XXXIV: 8) and *C. (E.) grande* (Arkell) (Douville, 1912: pl. IV: 56–58) from the Lamberti Zone by the absence of sinusoidal (carinate) bending of the ribs on the venter and by the high rib ratio. The closest to *C. (E.) intermedium* is the stratigraphically (Obductum Subzone) and phylogenetically preceding species *C. (E.) carinatiforme* Kiselev (Kiselev, 1999: pl. 1: 1–5) which differs from the new species by having a lower cross-section at all whorls and rare primary ribs.

Remarks. Placing the described species in the genus *Eichwaldiceras*, as well as *C. carinatiforme*, has, to a certain extent, an artificial character. It is possible that the rursicostate cadiconic morphotype originated iteratively in different cadoceratin lineages.

Distribution. Middle Callovian, Coronatum Zone, Grossouvrei Subzone – Upper Callovian, Athleta Zone, Proniae Subzone of the Ryazan region.

Material. 7 specimens from Mikhaylovskiy sections (Ryazan Region).

Table 10
Measurements (in mm) and its ratio

No	Form parameters						Sculpture parameters	
	D	Wh	Wb	U	Wh / Wb	U%	pR	br
M754 holotype	33.10	15.2	21.31	8.03	0.71	24.27	20	2.50
M755 paratype	28.40	13.2	14.40	7.20	0.92	25.35	15	2.54
M756 paratype	20.20	8.97	11.20	5.60	0.8	28.00	20	2.56
MH155/1 paratype	14.60	6.20	6.70	4.20	0.92	28.76	17	1.87
M757 paratype	19.40	7.64	9.36	5.92	0.82	30.50	16	2.80
M155 paratype	19.20	8.00	8.45	6.20	0.94	32.29	16	2.37
MG2-13 paratype	19.15	7.00	8.80	5.60	0.79	29.20	17	2.54
PC-1	33.06	15.42	22.45	9.86	0.69	29.82	19	2.87
PC-2	27.70	12.02	14.33	7.95	0.84	28.60	21	2.76
PC-3	22.65	8.70	9.32	8.08	0.93	35.69	23	2.05
PC-4	30.00	10.10	12.03	11.27	0.84	37.56	17	2.23

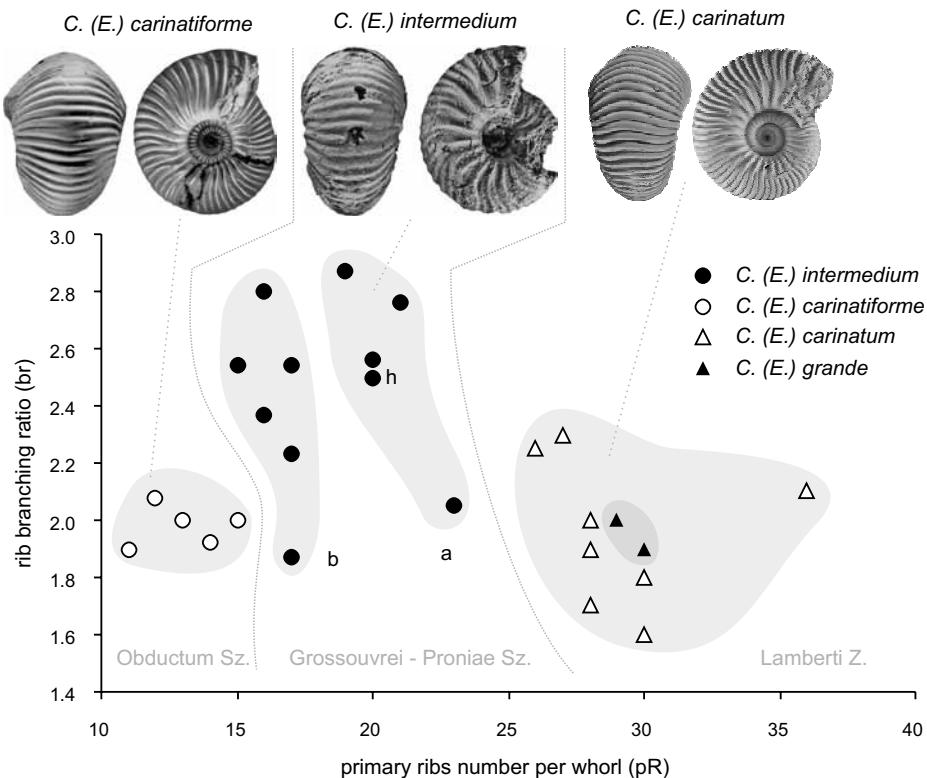


Fig. 13. Distribution of 4 species of *Cadoceras (Eichwaldiceras)* on the sculpture features

The following specimens are shown in the photo: *C. (E.) carinatiforme* Kiselev – holotype: YarGPU 3/37, Unzha River, Polovchinovo section (Kostroma region), Obductum Subzone, D = 35 mm; *C. (E.) intermedium* sp. nov. – holotype, YarGPU No. M7-54; Mikhaylovtsenement-I section, bed 7 (lower part), Grossouvrei Subzone, D = 33.1 mm; *C. (E.) carinatum* (Eichwald) – YarGPU D1-70, Dubki section (Saratov region), bed 1, *henrici* biohorizon, D = 34 mm

Suborder HALPOCERINA Besnosov et Michailova, 1983

Superfamily HAPLOCERATACEAE Zittel, 1884

Family OPPELIIDAE Bonarelli, 1894

Subfamily HECTICOCERATINAE Spath, 1923

Discussion. Although dimorphism with typical micro- and macroconchs which are distinguished by the size, coiling and apertural mature modifications is one of the typical features of Oppeliidae, recognition of micro- and macroconchiate genera within hecticoceratins is unclear in some points, mainly because the type specimens of the type species of nearly all genera and subgenera are represented by juvenile specimens lacking the mature aperture. On the other hand key features used for recognition of genera and subgenera (presence/absence of lateral groove, lateral or ventrolateral tubercles, etc.) in many cases were common for the both micro- and macroconchs. Elmi (1967) was the first who tried to provide a system of Hecticoceratinæ which includes micro- and macroconchiate genera. He recognized (Elmi 1967: p. 563–565) the following genera:

1. taxa with ventral nodes. Microconchs: *Paroecotraustes*, Macroconchs: *Eohecticoceras* (E.), *Eoh.* (*Zeissoceras*);
2. taxa with ventrolateral tubercles. Microconchs: *Jeannetioceras*. Macroconchs: *Hecticoceras*, *Chania*, *Bonarellites*, *Kheraites*, and new genus corresponding to “*Bonarellia*” from Madagascar figured by M. Collignon (1958: pl. XXVIII: 124–126);
3. taxa with external ribs prolonged into ventral side. Microconchs: *Lemoineiceras*, *Brightia*. Macroconchs: *Lunuloceras* (*Lunuloceras*), *Lun.* (*Sublunuloceras*), *Putealiceras*, *Pseudobrightia*.

However, such a subdivision of hecticoceratins on micro- and macroconchiate genera rarely became accepted by other scientists. Usually morphogenera including both micro- and macroconchs are used (*cf.* Lominadze, 1975; Rogov, 2000), or supposed micro- and macroconchs are joined within the single species (Page, 1994; Bonnot *et al.*, 1999; Roy, 2014). The last method is based mainly on the single feature, the co-occurrence of micro- and macroconchs in the studied sections. Such taxonomical procedures were not supported by detailed comparison of ontogeny as well as the distribution of micro- and macroconchs in space and time.

In this paper we follow an approach applied for nearly all studied ammonite groups (except for Pachyceratidae) and we recognize micro- and macroconchiate genera in Middle – Upper Callovian hecticoceratins. As the proposed subdivision differs from those applied by Elmi (1967), we provide here a brief review of micro- and macroconchiate genera in Hectoceratiniae:

Microconchs:

Brightia Rollier, 1922 (type species *Amm. hecticus nodosus* Quenstedt, 1849), with subgenera *Brightia* (*Brightia*) Rollier, 1922 and *Brightia* (*Glyptia*) Rogov, 2000. When introducing *Brightia*, Rollier (1922) listed its characteristics only briefly, indicating that this genus is for *Hecticoceras nodosum* Bonarelli and *Am. Brightii* auctor. (non Pratt), and that it is characterized by the presence of a lateral furrow with nodules. Although records of *B. nodosa* (Bonarelli) with terminal aperture are unknown, by its small size and evolute coiling this species (and thus the genus *Brightia*) should be considered as a microconch. The same is true for *B. (Glyptia)* with *Ammonites hecticus canaliculatus* as a type (Rogov, 2000). The lateral furrow, a key feature of this genus, in fact is very variable among different species, being well-recognized and wide in some species, but only slightly visible near the lappets or even missing in other taxa. Other key features such as lateral nodes or node-like ribs as well as fine dense falcate secondaries also should be taken into account as important for the recognition of *Brightia*. Previously some macroconchs were also commonly ascribed to *Brightia*. These are for example *B. (B.) annae* Rogov (Rogov, 2000: pl. V: 15), which should be moved to *Orbignyiceras*, and *B. (B.) nodosa* (Rogov, 2000: pl. V: 14) which belongs to *Rossiensiceras*. Alternatively both micro- and macroconchs were recognized within the single (bio)species *B. canaliculata* (Quenst.) (Bonnot *et al.*, 1999), although the differences between suggested micro- and macroconchs remains unclear.

Eulunulites Elmi, 1967 (type species *Hecticoceras pompekyi* Parona et Bonarelli, 1895). Elmi (1967: p. 551) indicated that this genus is characterized by evolute to semievolute coiling, with ribbing represented by short secondaries while primaries are usually missing; septal suture is simple. He suggested that it should be considered as the microconchiate counterpart of *Oxycerites* (Oppeliinae), but without any evidence. Here *Eulunulites* is used for Early to Middle Callovian hecticoceratin (?) microconchs, which follow the characteristics provided by Elmi. These ammonites closely resemble *Jeanneticeras*, but lack ventrolateral tubercles.

Lemoineiceras Elmi, 1967 (type species *Hecticoceras margaritae* Lemoine, 1932). This genus was introduced by S. Elmi (1967) with very brief diagnosis (ventral side is rounded or oval, without ventrolateral tubercles and spiral groove) and without indication of any other species ascribed

to this genus. The absence of a spiral groove distinguishes *Lemoineiceras* from *Brightia*, although as has been mentioned above, the degree of expressiveness of the spiral groove or furrow in fact is very variable in *Brightia*. Here *Lemoineiceras* is considered as a synonym of *Brightia*.

Lunuloceras Bonarelli, 1893 (type species *Ammonites fonticola* Menke in von Buch 1831 = *Ammonites lunula* sensu Zieten 1830 non Reinecke 1818). The micro- or macroconchiate status of the type species of the genus *Lunuloceras* is unclear, because an ammonite figured by von Zieten (1830) as *A. lunula* and subsequently referred to as *A. fonticola* by von Buch (1831) is represented by a very small nucleus without body chamber. Other specimens referred to *A. fonticola* by von Buch (1831: pl. II: 4–6) although also represented by the inner whorls without the body chamber seem to be microconchs. As microconchs sharing the features of *A. fonticola* (discoidal shells with relatively fine primaries and numerous thin secondaries) are known, here the genus *Lunuloceras* is accepted for such microconch species.

Putealiceras Buckman, 1922 in Buckman 1909–1930 (type species *Amm. putealis* Leckenby, 1859). As well as in the case of *Lunuloceras*, status of the type species of *Putealiceras* remains uncertain. The type specimen of *Putealiceras putealis* (Leckenby 1859) (Buckman 1922 in Buckman 1909–1930: pl. CCXCVII) is represented by a small-sized rather evolute ammonite with partially preserved body chamber but without aperture.

Macroconchs:

Chanasia Rollier, 1922 (type species *Hecticoceras Chanasiae* Parona et Bonarelli, 1895). This genus is mainly restricted to the Lower Callovian, where it is associated with *Hecticoceras* Bonarelli and *Jeanneticeras* Elmi, but last *Chanasia* are known from the lowermost part of the Middle Callovian (Cariou, 1985). This genus is characterized by strongly developed ventrolateral tubercles (typical for Lower Callovian hecticoceratins) and lateral groove.

Orbignyiceras Gerard et Contaut, 1936 (type species *Harpoceras pseudopunctatum* Lahusen, 1883). This genus, which is usually considered as a synonym of either *Lunuloceras* or *Sublunuloceras*, after Gerard et Contaut (1936) includes ammonites with discoidal shells of average thickness with narrow to moderate umbilicus. Here *Orbignyiceras* is considered as valid macroconchiate genus, characterized by falcate to falcoid secondaries which projected forwards at ventral side. Although it closely resembles *Sublunuloceras* (see below), the latter genus is distinguished by secondaries which disappear at the ventrolateral margin.

Rossiensiceras Gerard et Contaut, 1936 (type species *Harpoceras rossiene* Teissreyre, 1883). While establishing this genus, Gerard and Contaut emphasized the following features: thick whorls, moderate to deep umbilicus, ribs splitting on midflanks, with tubercles at the furcation point.

The type series of the *H. rossense* species consists of two specimens, one of which (Teisseire, 1883: pl. I: 6) has been chosen as a lectotype by Zeiss (1956). Now this specimen although seriously damaged due to pyrite decay is safely preserved in the collection of the Institut für Paläontologie, Universität Wien (specimen No. IPUW 1884-1-6, Pl. 20: 5). Along with coarsely ribbed macroconchs closely resembling the type species, one other group of hecticoceratins (which possibly should be further ascribed to as new genus) is also referred here to *Rossiensiceras*. These are taxa of the *R. metomphalum* group, ranging from uppermost Lower Callovian to Middle Callovian, which are characterized by a relatively narrow cross-section, usually with acute keel, and remarkable taeniola in the lower part of the flanks, *i.e.* a flattened part of the shell near to umbilical seam (*R. metomphalum* (Bonarelli), *R. daghestanicum* (Neumayr et Uhlig), *R. tae niolatum* (Bonarelli), *R. acuticosta* (Tsytovitch), *R. uhligi* (Neumayr)).

Sublunuloceras Spath, 1928a (type species *Harpoceras lairense* Waagen, 1875). Spath (1928a: p. 102) indicated that this genus is characterized by straighter ribbing, and the discoidal shells have slight tubercles *i.e.* ventrolateral tubercles. Although very few records of *Sublunuloceras* with aperture preserved are known, its involute coiling and big size strongly supports its macroconchiate affinities.

Zieteniceras Zeiss, 1956 (type species *Hecticoceras zieteni* Tsytovitch, 1911). This genus is characterized by the persistence of ventrolateral tubercles (this also occurs in the ancestral *Hecticoceras*, to which this genus in fact is very close), a feature uncommon in European post-Early Callovian hecticoceratins. It is mainly restricted to the Middle Callovian, and differs from *Sublunuloceras* by its more evolute coiling.

Genus ***Brightia*** Rollier, 1922 [m]

Subgenus ***Brightia*** Rollier, 1922

Brightia (Brightia) eccentrica Rogov, sp. nov.

Pl. 15: 14–16; Tab. 11

1932. *Hecticoceras salvadori*; Lemoine: p. 247, pl. XIV: 1, 2 (only)

1973. *Oecotraustes (Paroecotraustes) maubergei*; Paichadze: p. 58, pl. XVII: 6, 7 (only; non fig. 2–5 = *Paroecotraustes* sp.);

1988. *Oecotraustes (Paroecotraustes) maubergei*; Abdulka sumzadeh: p. 74, pl. VII: 8, 9

2005. *Brightia (Brightia) salvadori ellyptica*; Kiselev, Rogov: fig. 3, 9

Derivatio nominis: after remarkable eccentric coiling of the last whorl, from *eccentros* (Latin)

Holotype: no YPU-MIV312; Ryazan Region, Mikhaylovskiy quarry, Middle Callovian, Coronatum Zone, Obduktum Subzone, *crassum* horizon.

Description. Discoidal shells with oval cross-section in the body chamber and keeled than septated. Coiling of the last whorl is remarkably eccentric. The whorl breadth to height ratio on the last half of whorl increased from 0.6 to 0.8, respectively. Terminal body chamber occupied about the 3/5–4/5 of the whorl. The umbilicus comprises *ca.* 30–40% of the diameter. The umbilical seam is steep and became vertical on the body chamber. The greatest breadth is around the lower third of the flanks. Aperture has a strongly pronounced, but shallow constriction and lappets. Innermost whorls as far as diameter *ca.* 1–2 cm are entirely smooth. Ornamentation appears starting with thick rectiradial primary ribs or small nodules in the lower third of the flanks (total of 5–8 per half of whorl). The next stage of the sculpture development became apparent with thick but weak retroverse secondaries, detached from the primary ribs with lateral furrow, typical for the genus under description. Shortly before the end of the body chamber ornamentation became weaker or fully disappears except the lateral groove. Septal suture is poorly divided and has 3 umbilical lobes (in terms of the Russian authors) on the flanks.

Discussion. Among the species of the genus *Brightia* there are only a few ones (*e.g.*, *B. (B.) gzhelliensis* (Rogov, 2000: pl. 5: 10, 11) and *B. (B.) salvadori* (Pl. 16: 3, 4) showing eccentric coiling of the last whorl. *B. salvadori* is characterized by the more expressed and more falcoid ribbing, while *B. (B.) gzhelliensis* differs from the species under description by the smallest size, more evolute coiling and falcoid ribbing. The type of secondary ribbing allows the easy distinction of *B. (B.) eccentrica* from the Upper Callovian *B. (B.) boikoi* (Pl. 17: 2) with its more dense and falcate ribbing. The sculptural pattern in *B. (B.) noizeti* from the Athleta Zone also slightly resembles that of the *B. (B.) salvadori* but the former species has more falcate secondaries which become rursiradiate only in the terminal part of the body chamber, and a more expressed keel. Eccentric coiling is also typical of the microconchiate oppeliins, such as *Paroecotraustes* and *Thraxites*. As the *Alcidia* M occurs in the same beds as *B. (B.) eccentrica*, there are some doubts even for the allocation of the studied species within the Hecticoceratinae. At the same time the type of ribbing and simple septal suture of *B. (B.) eccentrica* resemble these characters in other genus *Brightia*.

Variability in the species under description is expressed by the rib density and their displaying as well differences in the wideness of the umbilicus and shell size. Primaries may change from rectiradial ribs to slightly inclined forward nodules.

Table 11

Measurements (in mm) and ratios (in %)

No.	Wb	Wh	D	U	Wb:Wh	Wb:D	Wh:D	U:D	Rr/2 (R/2)
Holotype MIV312*	—	19.9	50.5	15.8	—	—	39	31.2	~2.22 (7)
MIV277*	—	16.2	42.1	16.8	—	—	38	4	(7)
MIV288	10	13.1	35.5	12.5	76	28	37	35	~2.4 (6)
MIV311*	—	17.8	46.0	15.8	—	—	49	34	~3.42 (8)
MIV336*	—	12.7	30.6	9.7	—	—	41	32	(7)
MIV350	7	13.5	31.0	9.9	52	22	43	32	(6)
MIV377*	—	11.2	32.7	12.5	—	—	34	38	~3.5 (5)

* – crushed specimens

Distribution and material. Middle Callovian, Coronatum Zone, Obductum Subzone. In the Central Russia restricted to *crassum* and *obductum* biohorizons. Central Russia, Moscow Region (Alpatyev section, MIV277, MIV336, MIV337); Ryazan Region (Elatma section, MIV288; Mikhaylovtsenement section, MIV312, MIV311, MIV368, MIV475, MIV350); Northern Caucasus (Osetia); Azerbaijan (Kedabeck Region); France.

Brightia (Brightia) progzhellensis Rogov, sp. nov.

Pl. 15: 6, 7, 9, 10; Tab. 12

1961. *Hecticoceras subnodosum*; Rangheard: p. 156, pl. III: 8

1987. *Lunuloceras (Lunuloceras) cf. submathei*; Rotkyte: p. 69, pl. XV: 6.

2005. *Brightia (Brightia) progzhellensis*; Rogov in Kiselev, Rogov, 3, 8 [MS]

Derivatio nominis: after *pro-* = before, prior to (Latin) and species *B. (B.) gzhellensis* Rogov, 2000.

Holotype. No YPU-MIV 105; Ryazan Region, Mikhaylovtsenement quarry, Upper Callovian, not *in situ*.

Description. Discoidal small shells with acute to oval cross-section. The umbilicus comprises ca. 31–45% of the diameter. The umbilical seam is gentle but unusual steep. The greatest breadth is around the lower third of the flanks. Sometimes in the beginning of the body chamber (ca. 22–30 mm in diameter) whorls gradually uncoils. Innermost whorls as far as diameter ca. 1–2 cm are entirely smooth. Ornamentation appears starting with thick prorsiradial to rectiradial primaries on the diameter around 10–15 mm in the lower third of the flanks (total of 5–8 (usually 6) per half of whorl). At the diameter 15–25 mm fine and numerous (3–5 per each primaries) falcoid but slightly rursiradiate secondaries appears. These ribs as a usual are poorly expressed

Table 12

Measurements (in mm) and it ratios (in %)

No.	Wb	Wh	D	U	Wb:Wh	Wb:D	Wh:D	U:D	Rr/2 (R/2)
Holotype MIV105	6.9	10.2	26.9	10.7	77	27	35	45	(6)
MIV14	6.9	9.0	25.7	11.5	66	22	34	4	(6)
MIV15	5.6	8.5	25.1	10.0	68	25	36	37	(6)
MIV156	7.5	11.0	30.0	11.2	7	26	37	39	(7)
MIV264	6.9	9.8	26.6	10.5	72	25	35	39	(8)
MIV3	6.5	9.0	26.0	10.1	66	24	36	39	(7)
MIV305	7.9	12.0	33.0	12.8	64	22	35	37	(6)
MIV316	6.1	9.5	27.1	10.2	—	—	44	32	(7)
MIV322*	—	14.6	33.2	10.5	75	27	36	45	(6)
MIV38	6.0	8.0	22.2	9.9	62	22	36	4	(5)
MIV67	5.1	8.2	22.7	9.2	88	27	35	42	(6)
MIV711	9.9	13.1	37.1	15.6	77	26	34	45	(6)
MIV712	5.0	6.5	19.2	8.6	76	26	35	42	(6)
MIV714	6.0	7.9	22.7	9.6	61	24	39	37	(5)
MIV716	4.9	8.0	20.5	7.5	74	27	37	41	
MIV738	4.8	6.5	17.7	7.2	56	24	43	42	(6)
MIV74	5.2	9.2	21.6	9.1	93	34	36	39	~3.5 (7)
MIV851	9.3	10.0	27.5	10.8	66	26	39	43	4.3 (6)
MIV856	5.2	7.9	20.2	8.6	64	23	36	37	(6)
MIV9	5.5	8.6	24.1	9.0	74	25	34	40	(6)
MIV95	5.8	7.8	23.0	9.8	68	25	38	4	(5)

* – crushed specimens

in the inner whorls and attain their full development in the end of the phragmocone or in the body chamber. Between primaries and secondaries weak lateral furrow is situated, in some cases visible only in the body chamber.

This new species resembles the species *B. (B.) gzhellen-sis* (Rogov, 2000: pl. 5: 10, 11) in the type of sculpture, size and coiling but differs in the small inclination of the primaries and absence of the remarkable changes in the cross-section on the phragmocone – body chamber transition. This species under description differs from *B. (B.) lominadzei* sp. nov. (Pl. 20: 7–10) by the latter's very small size, coarser primaries and wider umbilicus. *B. (B.) davitashvili* Lomina-dze (Rogov, 2000: pl. 5: 3) resembles *B. (B.) progzhellen-sis* Rogov but has stronger ribbing and a wider cross-section. The close and probable contemporaneous species *B. (B.) ka-veckii* (Pakuckas) (Pakuckas, 1932: pl. II: 2; Rotkyte, 1987: pl. XXIV: 4, 5) has scarce rectiradiate primaries and a narrow umbilicus. It is also characterized by a poorly developed keel and nearly smooth inner whorls, while perumbilical umbilicus appeared in the latter species at the terminal body chamber only.

Variability of *B. (B.) progzhellensis* Rogov, sp. nov., is expressed in its rib density and is displayed as well as in the wideness of the umbilicus and shell size. All characters have a unimodal distribution. The primaries may change from recirradiial ribs to slightly inclined forward nodules. As a rule, specimens with a rounded cross-section and wide umbilicus have more expressed secondaries.

Distribution and material. Upper Callovian, Athleta Zone, Proniae Subzone. In Central Russia restricted to *proniae* and partly *rowlstonense* horizons. Central Russia, Ryazan' Region (Mikhaylovtsen' section, MIV3, MIV9, MIV15, MIV67, MIV74, MIV76, MIV95, MIV105, MIV218, MIV264, MIV316, MIV851, MIV711; MIV714, MIV712; Zmeinka section, MIV156; Spartak section, MIV14, MIV38; Dyadkovo section, MIV322, MIV856); France, Lithuania, England.

Brightia (Brightia) lominadzei Rogov, sp. nov.

Pl. 20: 7–10; Tab. 13

1877. cf. *Ammonites punctatus*; Trautschold: p. 91, pl. VII: 16, 17

Derivato nominis in honour of Dr. Tamaz A. Lominadze, the famous Georgian palaeontologist, who wrote a monograph concerning the Callovian hecticoceratins.

Holotype. No YPU-MIV 303; Moscow Region, Alpatyevо section; Upper Callovian, Athleta Zone, Proniae Subzone.

Description. Small to middle-sized discoidal shells. Cross-section acute if septated and rounded on the body chamber. The umbilicus comprises *ca.* 28–37% of the diameter. The umbilical seam is steep. The greatest breadth is around the lower quarter of the flanks. Aperture with lappets and deep constriction. Ornamentation appears on the diameter *ca.* 15–27 mm with coarse prorsiradial primaries in the lower third of the flanks. Secondaries are very fine and dense and visible only on the best preserved specimens. Sometimes secondary ribs show up only in the body chamber. Very fine longitudinal striae can be observed in the upper half of flanks on the body chamber of holotype. Between primaries and secondaries weak lateral furrow, invisible on the septated whorls, is situated.

Discussion. The species under description differs from the close *B. (B.) salvadorensis* (Pl. 16: 3, 4), and especially from weak-ribbed specimens of *B. (B.) eccentrica* (Pl. 15: 14–16) by the late appearance of the ornamentation, nearly almost absent in the upper part of whorl, and having the narrowest umbilicus. The last feature together with the narrow and high cross-section differs *B. (B.) lominadzei* from the contemporaneous *B. (B.) progzhellensis*. Earlier I thought that the described species also occurs in the Saratov area. This opinion was based on the ammonoids figured by E.A. Troizkaya under the name *Hecticoceras brightii* (in Kamysheva-Elpatievskaya et al., 1956: pl. 23: 71; Kamysheva-Elpatievskaya et al., 1958: 111).

Measurements (in mm) and its ratios (in %)

No.	Wb	Wh	D	U	Wb:Wh	Wb:D	Wh:D	U:D	Rr/2 (R/2)
Holotype MIV303	8.8	16.8	42.2	12.3	52.0	21	40	29	(7)
MIV127	10.9	21.1	45.5	13.8	52.0	24	46	32	(5)
MIV232	—	11.0	29.5	9.5	—	—	37	32	(7)
MIV301	—	14.5	34.1	9.7	—	—	42	28	
MIV304	—	11.9	26.4	7.5	—	—	45	28	
MIV362	7.5	11.5	28.5	9.7	65.0	26	4	34	
MIV730	9.8	19.0	41.0	11.6	52.0	24	46	28	(7)
MIV857	6.7	10.8	—	—	62.0	—	—	—	(6)
CH115	10.8	21.7	46.1	12.5	50.0	23	47	27	
CH95	7.6	13.7	32.2	9.9	55.5	24	41	31	
345	5.9	10.5	26.2	9.9	56.2	22	40	38	(7)

Table 13

kaya *et al.*, 1959: pl. XIX; Troizkaya, 1969: pl. XV). Re-studying of Troizkaya's collection shows that these ammonites belong to other species, for example to the last chronosubspecies of *B. (Glyptia) canaliculata* described below. Ammonoids figured by H. Trautschold (1877: pl. VII: 16, 17) as *Ammonites punctatus* resemble *B. (B.) lominadzei* but differ by their more developed ornamentation. Among the specimens of the *B. (B.) lominadzei* Rogov, sp. nov. there are two morphotypes, easily differentiated by the shell size and development of the ribbing: 1) shell size up to 25–30 mm, ornamentation appears at a diameter of *ca.* 15 mm; 2) shell size nearly 50 mm, distinct ribbing occurs mostly on the body chamber or last septated whorls. There is no any evidence concerning relations between the two morphs – are these two distinct species or do they display dimorphism (polymorphism)? Indirect confirmation of the latter opinion is the combined records of both morphs in the single thin bed in Alpatyevo. Inside morphogroups there is variability in the shell involution, breadth and ornamentation.

Distribution and material. Upper Callovian, Athleta Zone, Proniae Subzone. Central Russia, Ryazan Region (Mikhaylovtsenement section, MIV730, MIV127; Zmeinka section, MIV362, 345; Spartak section, CH95, CH105; Dyadkovo section, MIV857), Moscow Region (Alpatyevo section, MIV 304, MIV301, MIV232, MIV303).

Subgenus *Glyptia* Rogov, 2000 [m]

Brightia (Glyptia) canaliculata stankevitchae Rogov, subsp. nov.

Pl. 16: 20, 21; Tab. 14

- 1932. *Hecticoceras karpinskyi*; Corroy: p. 81, pl. II: 2
- 1936. *Lunuloceras solinophorum*; Gerard, Contaut: p. 43, pl. V: 2
- 1964. *Hecticoceras canaliculatum*; Stankevitch: p. 65, pl. XX: 1
- 2000. *Brightia (Glyptia) canaliculata*; Rogov: pl. V: 4
- 2005. *Brightia (Glyptia) canaliculata stankevitchae*; Kiselev, Rogov: fig. 3.4

Derivato nominis: in honour of Dr. E.S. Stankevitch, who figured Caucasian member of this subspecies.

Holotype. PIN 4771/21; Moscow region, Peski quarry, Upper Callovian, Lamberti Zone.

Description. Middle-sized discoidal flattened shells, with keeled ventral side. Keel is acute and well-separated from lateral sides. The umbilicus from relatively narrow to relatively wide, the umbilical seam is steep. Ribbing con-

sists from thin numerous falcate secondaries (45–50 per half of whorl), starting from wide lateral furrow. Lower part of the whorl is usually covered by the thin growth lines. Septal suture consists from well-dissected elements, with up to 3 umbilical lobes in the lateral sides.

Discussion. From the nominal subspecies *B. (G.) canaliculata canaliculata* the described subspecies is differentiated by its higher whorl section (with Wb:Wh ~45% in new species but ~62% in *B. (G.) canaliculata canaliculata*) and narrower umbilicus. The described subspecies, perhaps, immigrated to the Russian Sea from the Northern Caucasus.

Distribution and material. Upper Callovian of France, Northern Caucasus and the Central Russia. 3 specimens from Peski quarry (Moscow region): PIN 4771/12, PIN 4771/20 and PIN 4771/21.

Genus *Zieteniceras* Zeiss, 1956 [M]

Zieteniceras rarecostatum Rogov, sp. nov.

Pl. 17: 10, 11, 14.

1907. *Harpoceras pseudopunctatum*; Benecke: S. 420, Taf. XI, Abb. 1 (only)

Derivato nominis: after *rarus* = rare, and *costa* – rib (Latin).

Holotype. No YPU-MIV374; Ryazan Region, Mikhaylovtsenement quarry; Middle Callovian, Coronatum Zone, Grossouvrei Subzone.

Description. Big-sized discoidal shells with semi-involute coiling and moderately wide umbilicus. Keel is observed in the inner whorls but disappears in the terminal body chamber (at the diameter *ca.* 150 mm). Slightly inclined forwards coarse primaries are visible until the ~50 mm diameter. Secondaries are relatively numerous (rib ratio 2.5–3.0), nearly radial and wide. There are nearly 15–16 secondaries per half of the whorl at the 100 mm shell diameter. All specimens belonging to this species are crushed and partially preserved.

Discussion. The described species differs from nearly all the other known species of the genus *Zieteniceras* by its big size. From the comparably big *Z. giganteum* (Spath, 1928b: p. 194, pl. XVI: 5) it differs by the earliest disappearance of primaries. The closely allied species *Z. pseudolunula* (Elmi, 1967: p. 611, pl. 6: 1–3), which is also characterized by early disappearance of the primaries, shows much more dense secondaries. Below the stratigraphic interval containing

Measurements (in mm) and its ratios (in %)

No	Wb	Wh	D	U	Wb:Wh	Wb:D	Wh:D	U:D
Holotype 4771/21	7,8	18,6	36	9,8	42	22	52	27

Table 14

Z. rarecostatum sp. nov. in the Mikhaylov section quarry one more *Zieteniceras* has been recorded; the latter, ascribed to *Z. aff. rarecostatum* (Pl. 17: 13), characterized by a narrower umbilicus and dense secondaries. This ammonite could be ancestral to *Z. rarecostatum* but also possible that it could be included in the range of variability of the discussed species.

Distribution and material. Upper Callovian, Coronatum Zone, Grossouvre Subzone, *posterior* horizon. Central Russia, Ryazan Region (Mikhaylov section, MIV373, 374, two crushed moulds).

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Supplement 1

LIST OF KEY CALLOVIAN SECTIONS OF THE EUROPEAN RUSSIA, MENTIONED IN TEXT:

Alpatyevo – 54° 53' 06.47" N, 39°19' 41.36" E
Berdyanka River, Belyaevka village, Khanskaya Gora – 51°25' 04.28" N, 55°24' 12.41" E
Burdovo – 58°53' 25.10" N, 44°10' 53.16" E
Chermenino – 59°04' 08.88" N, 43°57' 08.61" E
Dubki – 51°40' 22.14" N, 46°01' 18.12" E
Elatma – 54°56' 42.38" N, 41°45' 46.49" E
Guryevo – 54°23' 17.23" N, 38°10' 42.83" E
Gzhel – 55°37' 44.37" N, 38°26' 44.86" E
Koltsovo – 56°47' 46.01" N, 35°59' 34.47" E
Makaryev – 57°53' 54.65" N, 43°48' 57.59" E
Mikhaylovtsenement – 54°12' 35.20" N, 38°56' 10.76" E
Mikhaylov-Gorenka – 54°13' 56.94" N, 38°52' 07.57" E
Malinoviy Ovrag – 51°48' 49.10" N, 45°54' 24.93" E
Moscow City (foundation pit for the Moscow City) – 55°44' 52.14" N, 37°31' 59.55" E
Nikitino – 54°21' 15.29" N, 40°24' 27.64" E
Peski – 55°11' 41.24" N, 38°47' 54.11" E
Polovchinovo – 57°56' 42.17" N, 43°55' 49.17" E
Rybinsk (Konyushino) – 57°59' 02.75" N, 38°52' 48.00" E
Rybinsk (Mikhaylovskoye) – 57°58' 40.41" N, 38°53' 16.25" E
Rybinsk (Perebory) – 58°05' 28.17" N, 38°43' 23.53" E
Spartak – 54°14' 13.68" N, 38°50' 56.94" E
Sukhaya Peschanka River – 51°13' 12.64" N, 54°05' 30.79" E
Uzhovka – 54°48' 04.25" N, 44°54' 08.98" E
Vasilkovo – 57°58' 09.12" N, 43°58' 07.36" E
Votcha – 61°05' 55.98" N, 50°19' 25.75" E
Yoda River – 57°58' 48.16" N, 38°53' 15.19" E
Zmeinka – 54°13' 47.77" N, 38°57' 27.84" E

All specimens are figured in natural size except for large ones, scale bar = 1 cm. All specimens were coated with ammonium chloride prior to photographing with the exception of specimens photographed in the field and specimens from the Teissyre collection. Abbreviations: YPU – Geological Museum of the Yaroslavl State Pedagogical University, PIN – Paleontological Museum (Moscow), BM – Natural History Museum, London, IPUW – Institut für Paläontologie, Universität Wien.

PLATE 1

- Fig. 1–3. *Kosmoceras (Zugokosmoceras) grossouvrei* Douv. Fig. 1a–c: YPU-M/7b-12, Fig. 2a, b: YPU-M/7b-1, Fig. 3a, b: YPU-MK-23. Mikhaylovtsement I, bed 7 – Coronatum Zone, Grossouvrei Subzone, *grossouvrei* biohorizon
- Fig. 4a, b. *Kosmoceras (Zugokosmoceras) posterior* Brinkmann. YPU-M7a-9. Mikhaylovtsement I – Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon
- Fig. 5. *Kosmoceras (Kosmoceras) pollucinum* Teiss. YPU-MK-312. Mikhaylovtsement I, bed 6 – Coronatum Zone, Obductum Subzone, *crassum* biohorizon
- Fig. 6, 7. *Kosmoceras (Kosmoceras) gemmatum* (Phillips). Fig. 6: YPU-MK166, Fig. 7a, b: *Kosmoceras (Kosmoceras) gemmatum* (Phillips). YPU-M7-53. Mikhaylovtsement I – Coronatum Zone, Grossouvrei Subzone

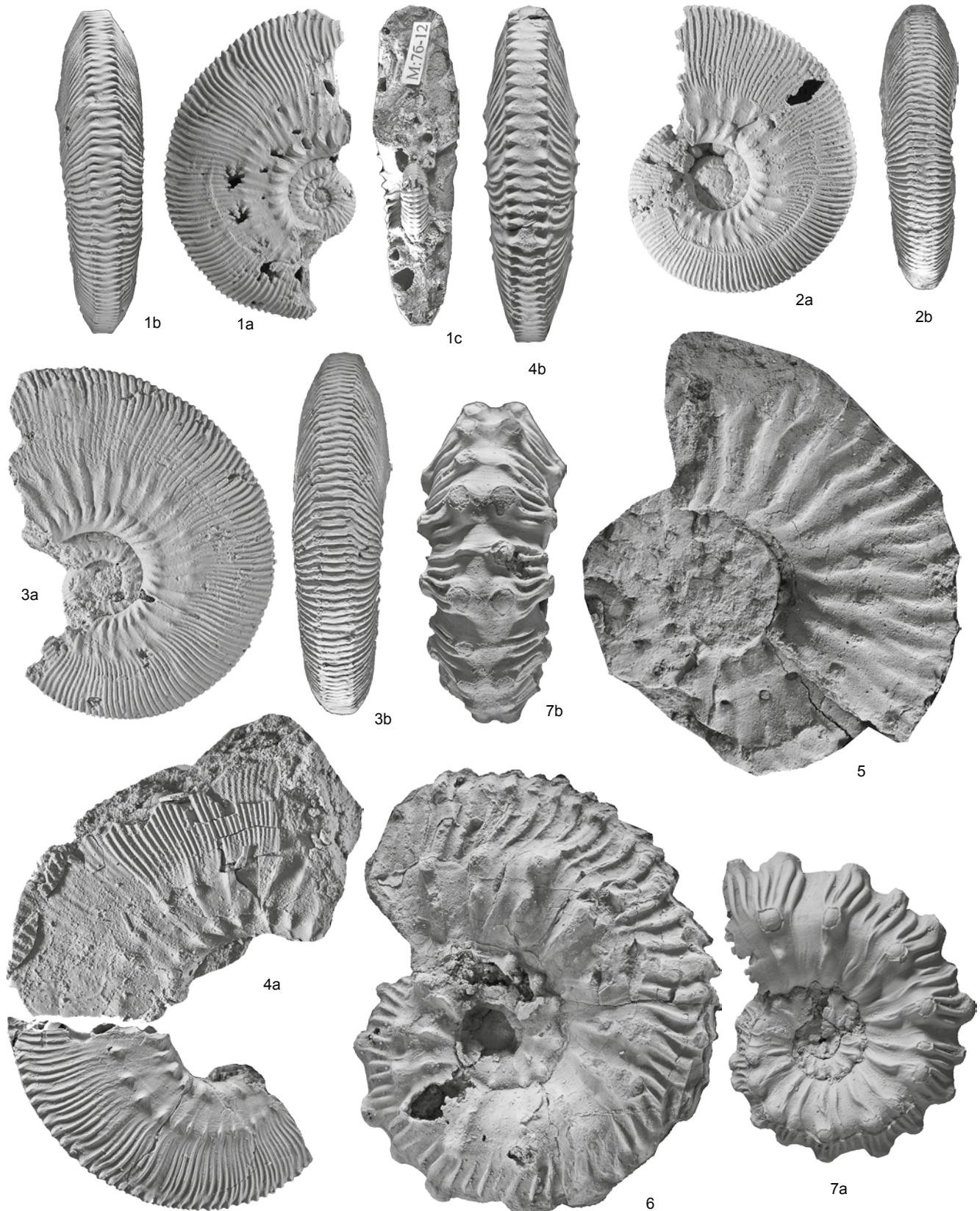
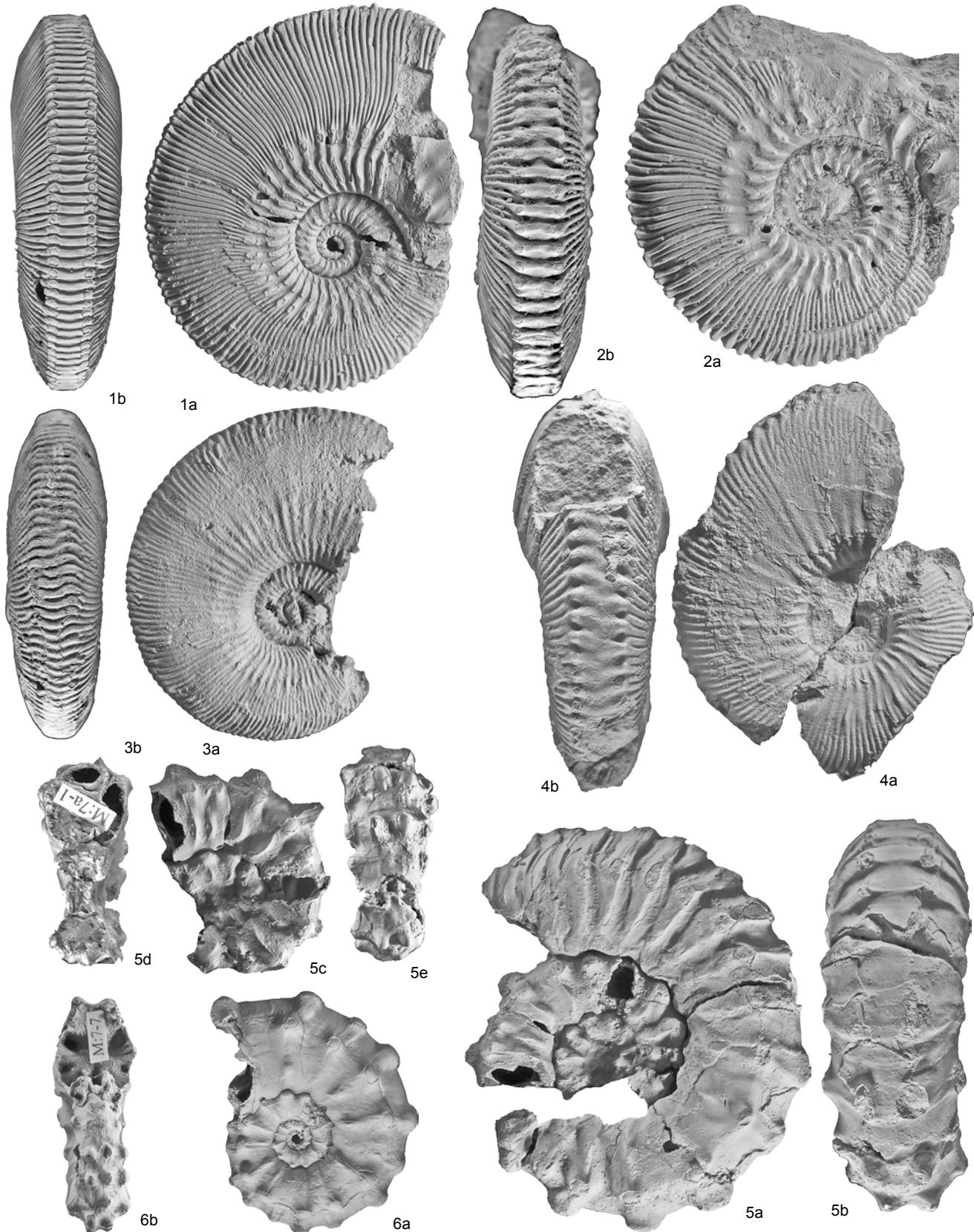


PLATE 2

- Fig. 1a, b. *Kosmoceras (Lobokosmoceras) proniae* Teiss. YPU-M / 7d-1. Mikhaylovtsenement I, bed 8 (0.7 m above the base) – Athleta Zone, Proniae Subzone, *proniae* biohorizon
- Fig. 2a, b. *Kosmoceras (Zugokosmoceras) phaeinum* (Buckman). YPU-AM-52. Mikhaylovtsenement I, bed 7 – Athleta Zone, Phaeinum Subzone
- Fig. 3a, b. *Komoceras (Lobokosmoceras) rowlstonense* (Young et Bird). YPU-M7d-6. Mikhaylovtsenement I, bed 8.1 m below top – Athleta Zone, Proniae Subzone, *rowlstonense* biohorizon
- Fig. 4a, b. *Kosmoceras (Lobokosmoceras) kuklikum* (Buckman). YPU-M8-6. Mikhaylovtsenement I, bed 9 – Athleta Zone, the Kuklikum Subzone, *kuklikum* biohorizon
- Fig. 5, 6. *Gulielmiceras (Spinikosmoceras) pollux* (Rein.). Fig. 5a–e: YPU-M7a-1. Mikhaylovtsenement I, bed 7 (0.45 m above top) – Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon; Fig. 6a, b: YPU-M7-7. Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone



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PLATE 3

- Fig. 1a, b. *Kosmoceras (Kosmoceras) spinosum* (Sow.). YPU-M10-2. Mikhaylovtsement I, bed 10 – Lamberti Zone, Henrici Subzone
- Fig. 2a, b. *Kosmoceras (Kosmoceras) rotundum* var. *subspinosum* Nikolaeva et Rozhdestvenskaya. YPU-G-1. The quarry near Gzhel (Moscow region) – Athleta Zone, Kuklikum Subzone, *kuklikum* biohorizon
- Fig. 3, 4. *Kosmoceras (Kosmoceras) rotundum* var. *rotundum* (Quenstedt). Fig. 3a–d: YPU-K-4. The right bank of the Oka River near the Kostino village; Fig. 4a, b: YPU-MG/3-3. Mikhaylov-Gorenka, bed 11s. All: Athleta Zone, Kuklikum Subzone, *kuklikum* biohorizon
- Fig. 5a, b. *Kosmoceras (Lobokosmoceras) kuklikum* (Buckman). YPU-K-5. The right bank of the Oka River near the Kostino village – Athleta Zone, Kuklikum Subzone, *kuklikum* biohorizon
- Fig. 6a, b. *Kosmoceras (Lobokosmoceras) rowlstonense* (Young et Bird). YPU-MK-27. Quarry near the Peski village (Moscow region), bed 1 – Athleta Zone, Proniae Subzone, *rowlstonense* biohorizon
- Fig. 7a, b. *Kepplerites (Gowericeras) gowerianus* (Sowerby). Private coll. of A.A. Mironenko. Mikhaylovtsement II, bed 2, in redeposited nodules

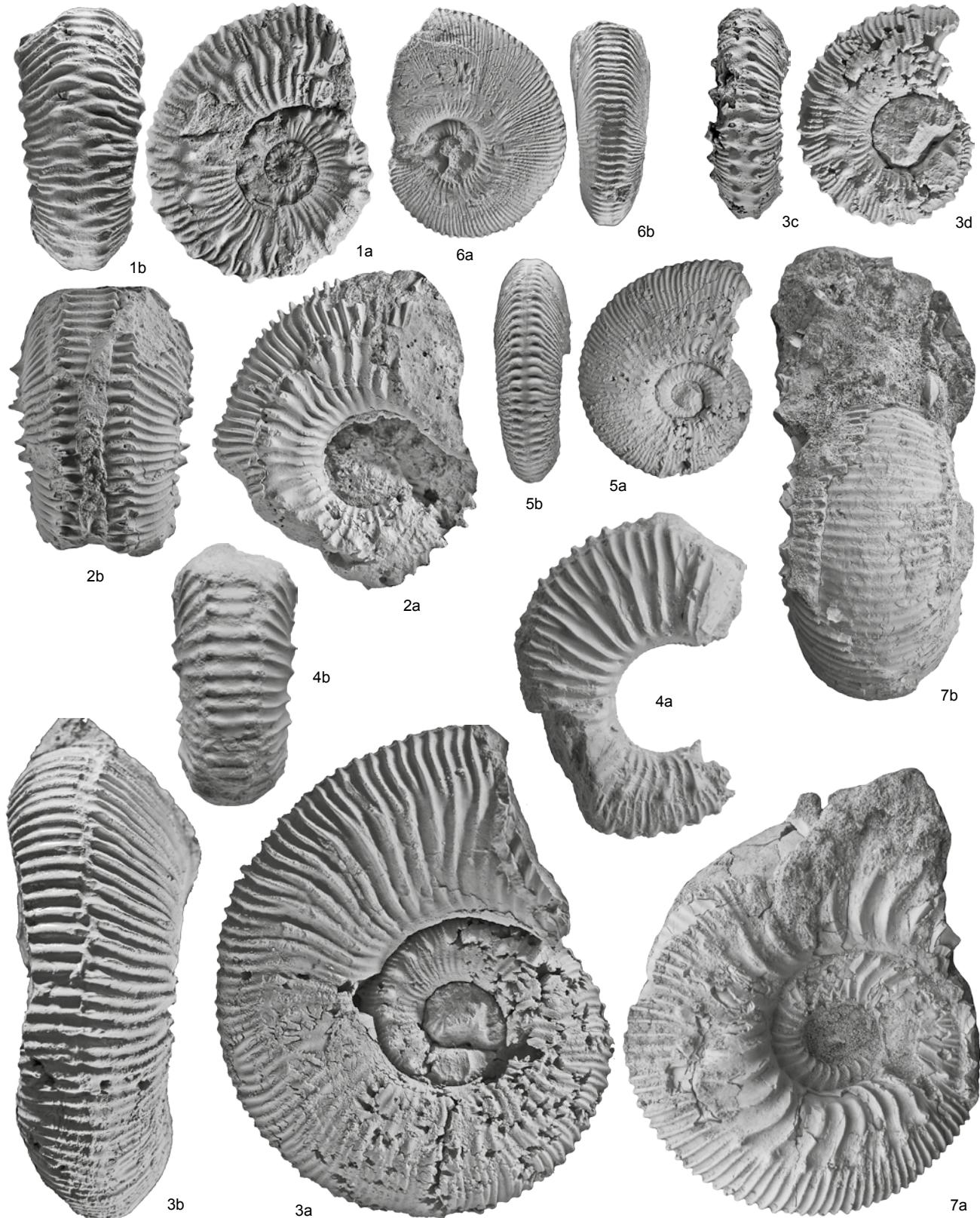
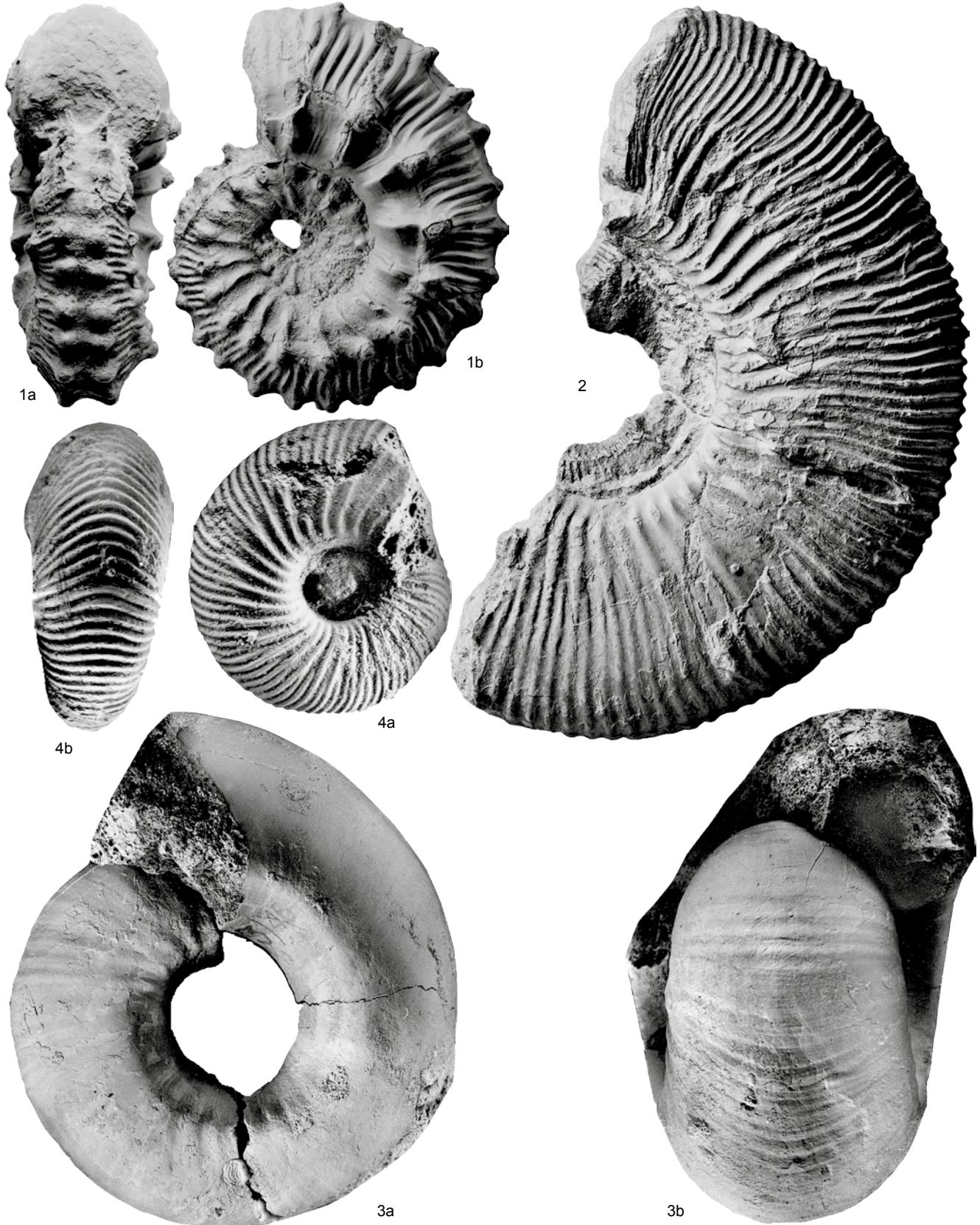


PLATE 4

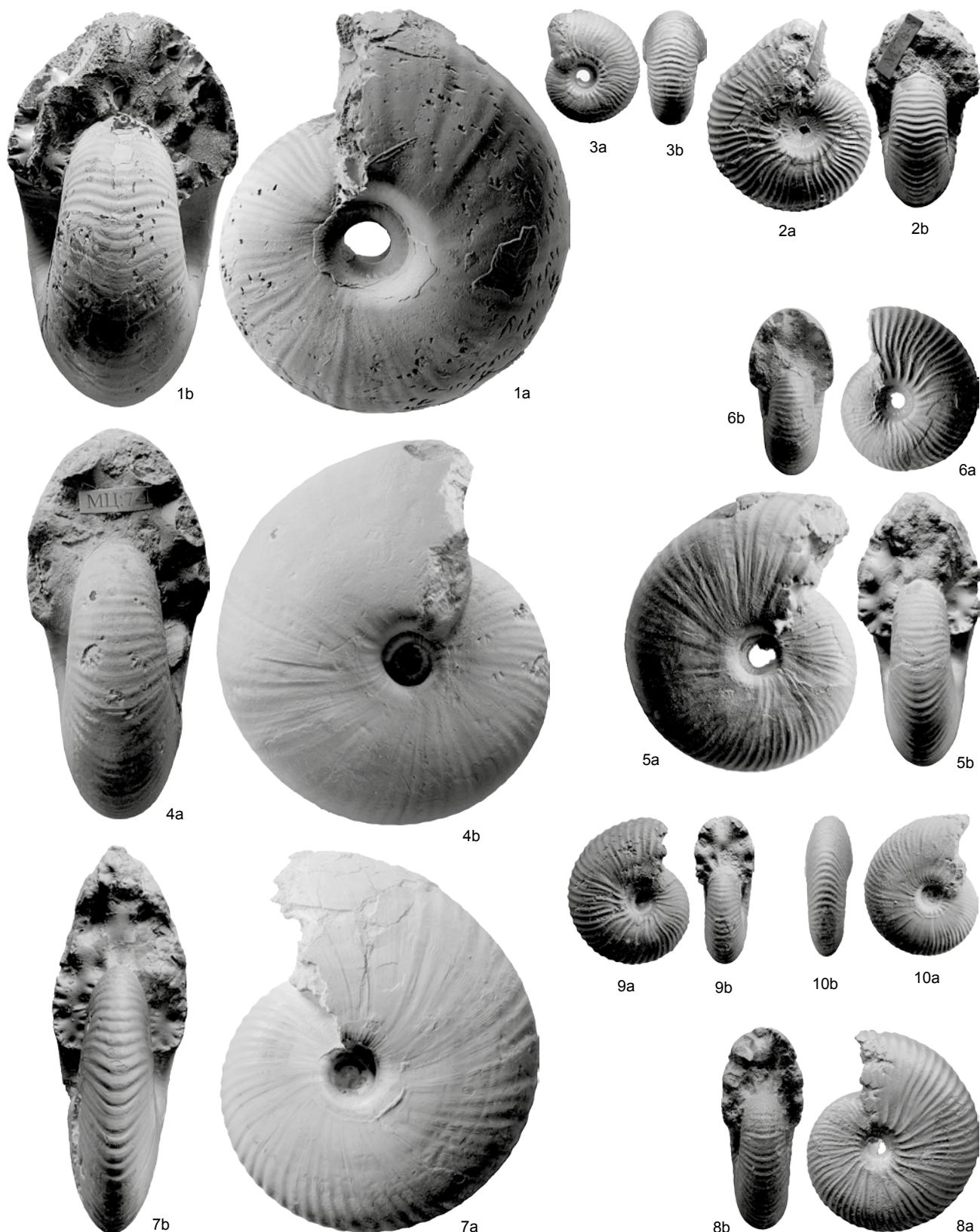
- Fig. 1a, b. *Kosmoceras (Kosmoceras) gemmatum* (Phillips). YPU-M7-58. Mikhaylovtsement I – Athleta Zone, Phaeinum Subzone
- Fig. 2. *Kosmoceras (Lobokosmoceras) geminatum* (Buckman). YPU-MG / 2-29. Mikhaylov-Gorenka, bed 11 (concretion horizon D) – Lamberti Zone, Henrici Subzone
- Fig. 3, 4. *Cadoceras arcticoides* Kiselev et Meledina. Fig. 3a, b: PIN 4839/25; Fig. 4a, b: YPU 3/47; Mikhaylov-Gorenka – Middle Callovian, Jason Zone, Medea Subzone, *medea medea* biohorizon



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PLATE 5

- Fig. 1–3. *Funiferites allae allae* (Kiselev). Fig. 1a, b: YPU-MC:7-6, Mikhaylovtsenement I, bed 7c – Athleta Zone, Phaeinum Subzone; Fig. 2a, b: YPU-M7B-8 – Phaeinum Subzone. Fig. 3a, b: YPU-MK319, bed 7 (0.75 m above the base) – *grossouvrei* biohorizon
- Fig. 4–6. *Funiferites allae compressum* subsp. nov. Fig. 4a, b: Holotype, YPU-M7-1. Mikhaylovtsenement I, bed 7g; Fig. 5a, b: YPU-MC: 7-3. Mikhaylovtsenement II, bed 4; Fig. 6a, b: YPU-MC: 7-8. Mikhaylovtsenement I, bed 7g. All: Athleta Zone, Proniae Subzone, *allae compressum* biohorizon
- Fig. 7–10. *Funiferites patruus* (Eichwald). Fig. 7a, b: YPU-MG/2-5. Mikhaylov-Gorenka, bed 10c (80 cm below top); Fig. 8a, b: YPU-B295. Mikhaylovtsenement I, bed 8; Fig. 9a, b: YPU-MC: 8-5. Mikhaylovtsenement II, bed 4; Fig. 10a, b: YPU-M165. Mikhaylovtsenement I, bed 8. All: Athleta Zone, Proniae Subzone, *patruus* biohorizon



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PLATE 6

- Fig. 1, 2. *Funiferites allae allae* (Kiselev). Fig. 1a–c: Holotype, PIN 4839/19. Mikhaylovtsenement I, bed 7b – Coronatum Zone, Grossouvrei Subzone, *grossouvrei* biohorizon; Fig. 2a, b: YPU-MC:7-5, bed 7b – Athleta Zone, Phaeinum Subzone
- Fig. 3, 4. *Funiferites funiferus* (Phillips). Fig. 3: YPU-MK321; Fig. 4a, b: YPU-MK223. Mikhaylovtsenement I, bed 8 (top) – Athleta Zone, Proniae Subzone
- Fig. 5–7. *Cadoceras proniense* Sasonov. Fig. 5a, b: YPU-3/40. Rybinsk, Perebory section; Fig. 6a, b: YPU-H-13. Ryazan Region, Nikitino Village; Fig. 7a, b: YPU-H-8. Ryazan Region, Nikitino Village. All: Middle Callovian, Jason Zone



PLATE 7

- Fig. 1, 2. *Longaeviceras placenta* (Leckenby). Fig. 1a, b: YArGPU MC:10-1; Fig. 2a, b: YPU-MC:10-2. Mikhaylovtsenement I, bed 10 (top) – Athleta Zone, Kuklikum Subzone
- Fig. 3. *Cadoceras (Rondiceras) milaschevici milaschevici* (Nikitin). YPU-MG/1-18. Mikhaylov-Gorenka, section 1, bed 8 – Jason Zone, Medea Subzone, *media medea* biohorizon



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PLATE 8

- Fig. 1a, b. *Eboraciceras longilobatum* (Buckman). YPU-M11-1. Mikhaylovtsement I, bed 10 (horizon of basal nodules) – Lamberti Zone, Henrici Subzone
- Fig. 2a, b, 3a, b. *Lamberticeras pseudolamberti* (Sintzow). YPU-MC(5)-31. Mikhaylovtsement II, bed 5 (0.45 m below the top) – Lamberti Zone, Lamberti Subzone, *paucicostatum* biohorizon
- Fig. 4a, b. *Cadoceras (Eichwaldiceras) carinatum* (Eichwald). YPU-MC(5)-33. Mikhaylovtsement II, bed 5 (concretion horizon “d”) – Lamberti Zone, Lamberti Subzone, *praelamberti* biohorizon
- Fig. 5. *Quenstedtoceras paucicostatum* (Lange). YPU-MC(5)-21. Mikhaylovtsement II, bed 5 (top) – Lamberti Zone, Lamberti Subzone, *paucicostatum* biohorizon
- Fig. 6–8. *Cardioceras (Scarburgiceras) cf. scarburgense* (Young et Bird). Fig. 6: YPU-M12-5; Fig. 7: YPU-M12-4. Mikhaylovtsement I, bed 12 (lower third); Fig. 8: YPU-MK168. Mikhaylov-Zmeinka. All: Mariae Zone, Scarburgense Subzone, *scarburgense* biohorizon



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PLATE 9

- Fig. 1–5. *Cadoceras (Eichwaldiceras) intermedium* sp. nov. Fig. 1a–c: YPU-M7-54 – holotype; Fig. 2a, b: YPU-M7-55; Fig. 3a–c: YPU-M7-56; Fig. 4a, b: YPU-M7-57; Fig. 5a, b: YPU-M7-58. Mikhaylovtsenement I, bed 7 – Figs. 1, 3 – Coronatum Zone, Grossouvrei Subzone; Figs. 2, 4, 5 – Athleta Zone, Proniae Subzone
- Fig. 6a, b. *Longaeviceras placenta* (Leckenby). YPU-M8-12. Mikhaylovtsenement I, bed 9 – Athleta Zone, Kuklikum Subzone, *kuklikum* biohorizon
- Fig. 7a, b. *Lamberticeras henrici* Douville. YPU-M11-2. bed 10 (horizon of basal nodules) – Lamberti Zone, Henrici Subzone
- Fig. 8, 9. *Lamberticeras praelamberti* Douville. Fig. 8a, b: YPU-M/z5-1; Fig. 9a, b: YPU-M11-7. bed 11 – Lamberti Zone, Lamberti Subzone, *praelamberti* biohorizon
- Fig. 10a, b. *Quenstedtoceras macer* (Quenstedt). YPU-M11-18. Mikhaylovtsenement I, bed 11 (the horizon of basal nodules) – Lamberti Zone, Henrici Subzone
- Fig. 11a, b. *Quenstedtoceras damoni* (Nikitin). YPU-M11-14. Mikhaylovtsenement I, bed 11 (the horizon of basal nodules) – Lamberti Zone, Henrici Subzone
- Fig. 12a, b. *Quenstedtoceras leachi* (Sowerby). YPU-A-1. Mikhaylovtsenement I, bed 10 – Lamberti Zone, Henrici Subzone
- Fig. 13a–c. *Cardioceras gallicum* Maire. YPU-M13-2. Mikhaylovtsenement I, bed 12c – Mariae Zone, Praecordatum Subzone, *alphacordatum* biohorizon
- Fig. 14, 15. *Protocardioceras cf. praemartini* (Spath). Fig. 14a, b: YPU-M12-1. Mikhaylovtsenement I, bed 12b; Fig. 15: YPU-MG/3-17. Mikhaylov-Gorenka, bed 13 (2 m above the base) – Mariae Zone, Praecordatum Subzone
- Fig. 16a, b. *Cardioceras (Scarburgiceras) transitorium* Spath. YPU-M12-2. Mikhaylovtsenement I, bed 12b – Mariae Zone, Praecordatum Subzone
- Fig. 17a, b. *Cardioceras (Cardioceras) percaelatum* Pavlow. YPU-M282. Mikhaylovtsenement I, bed 13 – Cordatum Zone, Costicardia Subzone

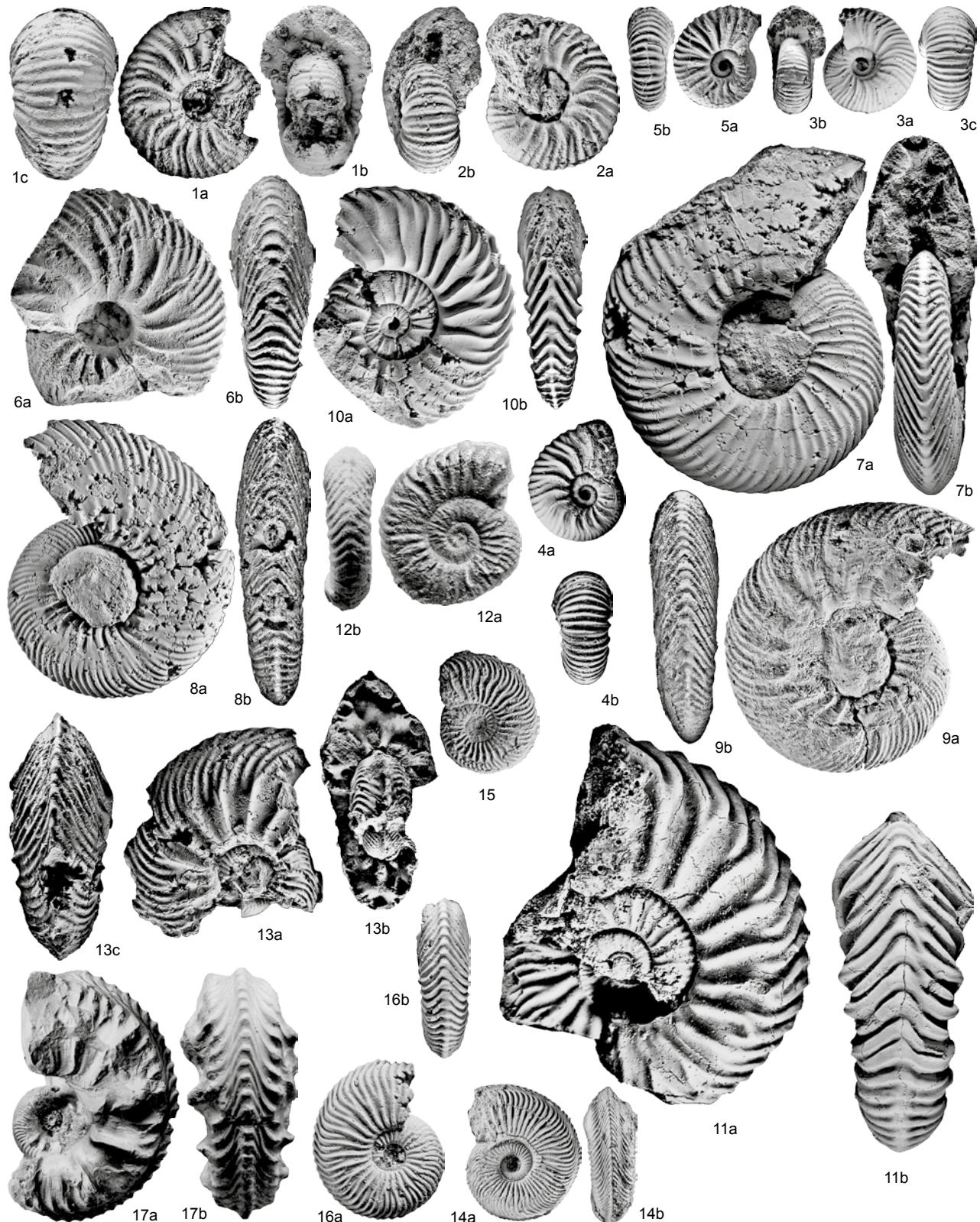


PLATE 10

- Fig. 1a, b. *Goliathiceras goliathum* (d'Orb.). YPU-M14-15. Mikhaylovtsenement I, bed 13
- Fig. 2a, b. *Goliathiceras (Pachycardioceras) elatum* (Maire). YPU-M14-5. Mikhaylovtsenement I, bed 13
- Fig. 3a, b. *Cardioceras cf. bukowskii* Maire YPU-M14-16; Mikhaylovtsenement I, bed 13
- Fig. 4a, b. *Vertebriceras quadrarium* var. *biplicatum* Arkell. YPU-M14-1. Mikhaylovtsenement I, bed 13
- Fig. 5, 7, 9. *Vertebriceras gracile* Arkell. Fig. 5a, b: YPU-M14-13; Fig. 7a, b: YPU-MC12-2; Fig. 9a, b: YArGPU MC12-1. Mikhaylovtsenement I, bed 13
- Fig. 6a, b. *Cardioceras (Scoticardioceras) lahuseni* Maire. YPU-MCs12-5. Mikhaylovtsenement I, bed 13
- Fig. 8, 10. *Vertebriceras quadrarium* var. *quadrarium* (Buckman). Fig. 8a, b: YPU-M14-14; Fig. 10a, b: YPU-M14-12. All: Mikhaylovtsenement I, bed 13
- Fig. 11, 12. *Cardioceras (Cardioceras) costicardia* var. *vulgare* Arkell. Fig. 11a, b: YPU-MK306. Mikhaylovtsenement I, bed 13; Fig. 12a, b: YPU-MC(9)-2. Mikhaylovtsenement II, bed 9
- Fig. 13a–c. *Vertebriceras quadrarium* var. *anglogallicum* Arkell. YPU-MG / 3-21. Mikhaylov-Gorenka, bed 13

All specimens came from the Lower Oxfordian, Cordatum Zone, Costicardia Subzone

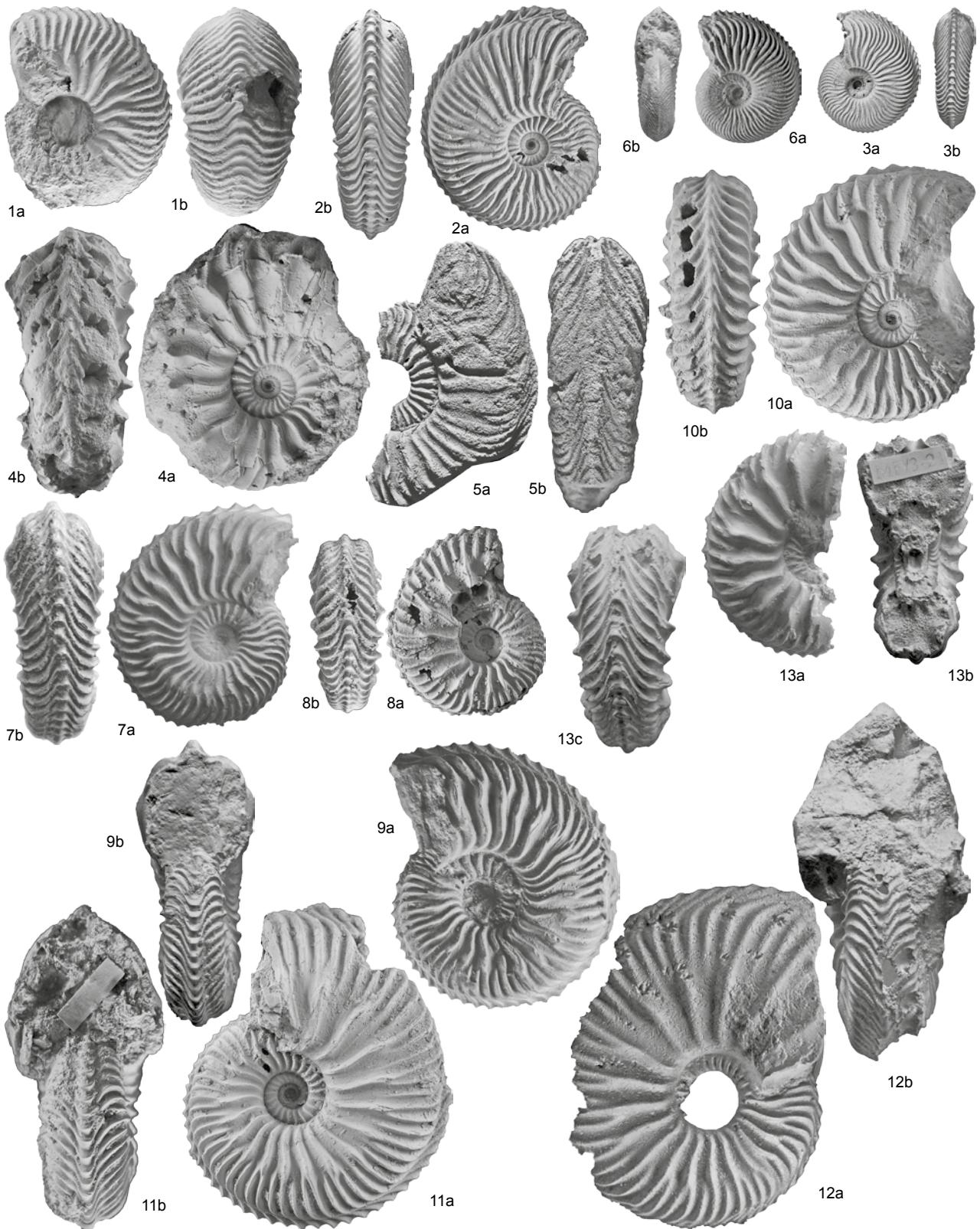


PLATE 11

- Fig. 1a-d. *Cardioceras (Scarburgiceras) alphacordatum* Spath. YPU-M13-1. Mikhaylovtsenement I, bed 12c – Mariae Zone, Praecordatum Subzone, *alphacordatum* biohorizon
- Fig. 2, 3. *Protocardioceras praecordatum* (Douville). Fig. 2: YPU-MC12-7; Fig. 3: YPU-MC12-8. Mikhaylovtsenement I, bed 12g – Mariae Zone, Praecordatum Subzone, *praecordatum* biohorizon
- Fig. 4a, b. *Rursiceras reversum* Buckman. YPU-M/3:6-1. Mikhaylov-Zmeinka – Lamberti Zone, Henrici Subzone
- Fig. 5a, b. *Alligaticeras* aff. *rotifer* (Brown) sensu Cox. YPU-MK270. Mikhaylov-Zmeinka – Athleta Zone, Kuklikum Subzone



PLATE 12

- Fig. 1a, b. *Peltoceras retrospinatum* Gerard et Contaut sensu Courville et Bonnot. YPU-MC (5)-32. Mikhaylovtsen II, bed 5 (concretion horizon «c») – Lamberti Zone, Henrici Subzone
- Fig. 2a, b. *Okaites mosquensis* (Fischer). YPU-M7b-5. Mikhaylovtsen I, bed 7 – Coronatum Zone, Grossouvrei Subzone
- Fig. 3a, b. *Okaites comptoni rossicus* (Siem.). YPU-M7b-6. Mikhaylovtsen I, bed 7 – Coronatum Zone, Grossouvrei Subzone
- Fig. 4a, b. *Pseudopeltoceras chauvinianum* (d'Orb.). YPU-M7-19. Mikhaylovtsen I, bed 7c – Athleta Zone, Phaeinum Subzone
- Fig. 5, 6. *Binatisphinctes fluctuosus* (Pratt). Fig. 5a, b: YPU-M7a-4; Fig. 6a, b: YPU-M7b-3. Mikhaylovtsen I, bed 7 – Coronatum Zone, Grossouvrei Subzone



PLATE 13

- Fig. 1, 2. *Peltoceras retrospinatum* Gerard et Contaut sensu Courville et Bonnot. Fig. 1: YPU-M9-1. Mikhaylovtsenement I, bed 10 (middle part) – Athleta Zone, Kuklikum Subzone, *kuklikum* biohorizon; Fig. 2: YPU-MC (5)-12. Mikhaylovtsenement II, bed 5 (concretion horizon «c») – Lamberti Zone, Henrici Subzone
- Fig. 3a, b. *Peltoceras athleta* (Phillips). YPU-G-2. The quarry near Gzhel (Moscow area) – Athleta Zone, Kuklikum Subzone, *kuklikum* biohorizon
- Fig. 4, 5. *Perisphinctes orbignyi* Tarkowski, Mikhaylovtsenement I, bed 13 – Cordatum Zone, Costicardia Subzone. Fig. 4: specimen without number; Fig. 5a, b: YPU-MK1503

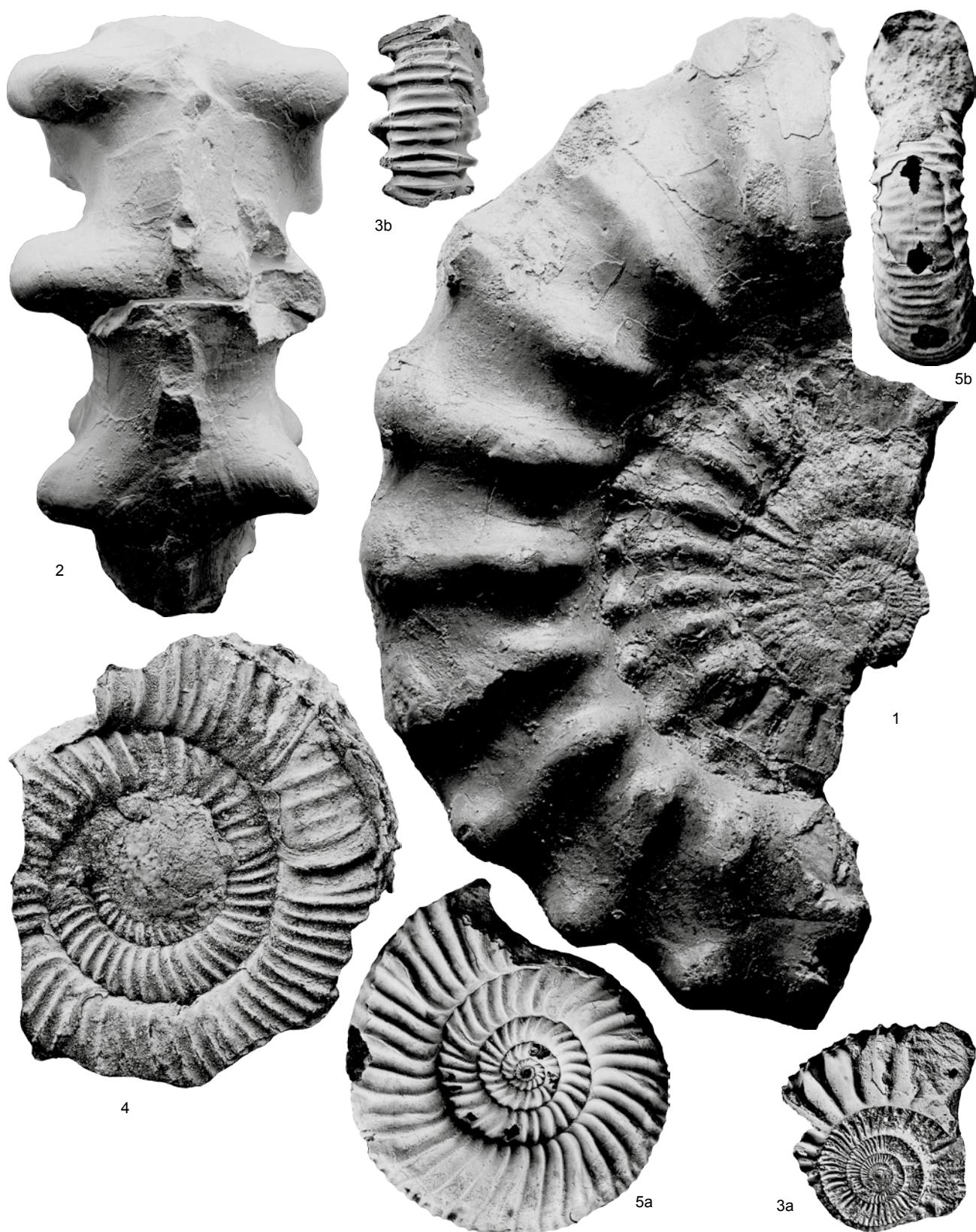


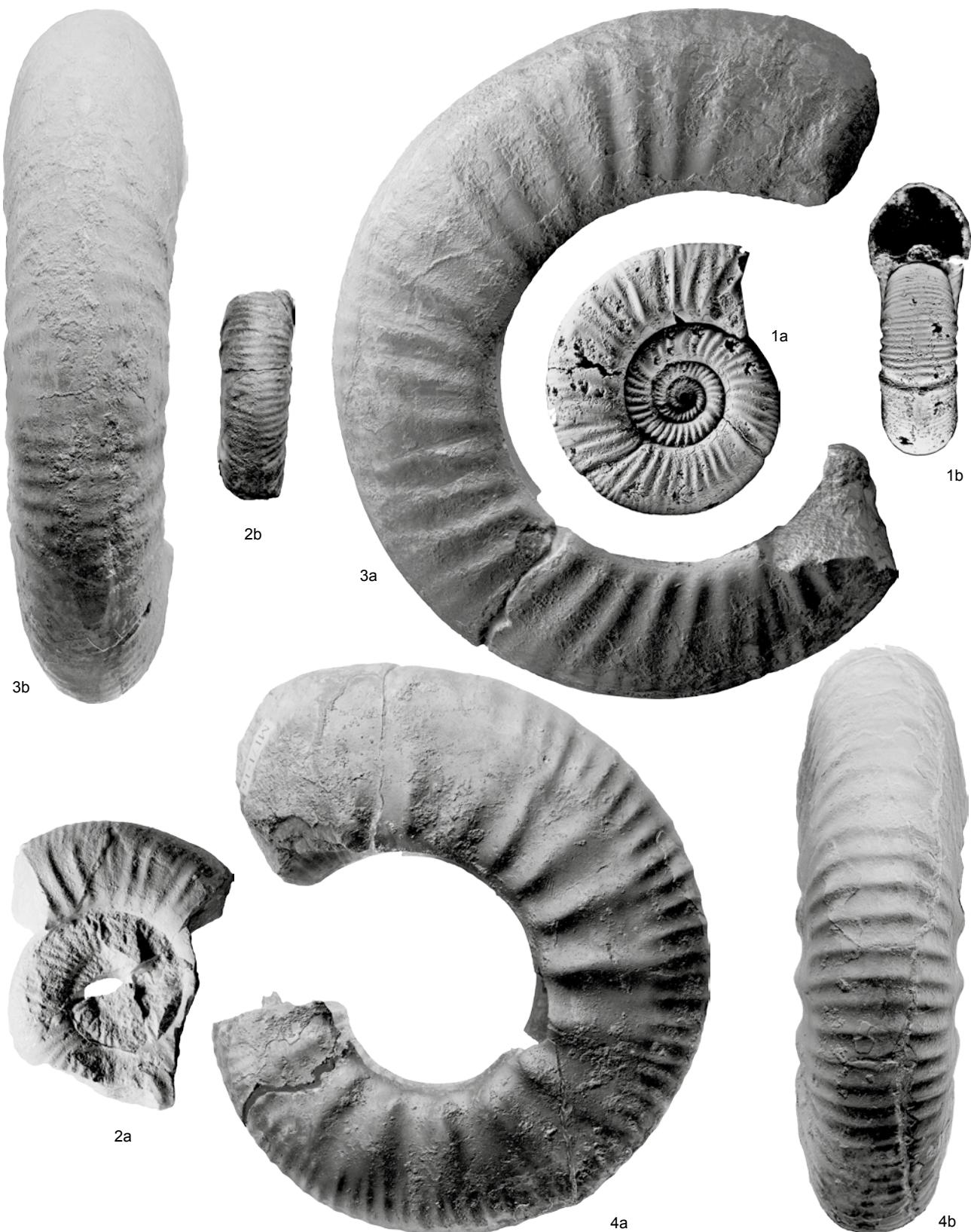
PLATE 14

Fig. 1a, b. *Alligaticeras* aff. *rotifer* (Brown) sensu Cox. YPU-MK257. Venev (Tula region) – Athleta Zone, Kuklikum Subzone

Fig. 2a, b. *Binatisphinctes binatus* (Leckenby). YPU-M8-8. Mikhaylovtsement I, bed 8 (basal horizon of concretions) – Athleta Zone, Kuklikum Subzone

Fig. 3a, b. *Orionoides termieri* Gerard et Contaut. YPU-MG4-8. Mikhaylov-Gorenka, bed 11 (concretion horizon C) – Athleta Zone, Kuklikum Subzone

Fig. 4a, b. *Choffatia* cf. *poculum* (Leckenby). YPU-MG1-16. Mikhaylov-Gorenka, bed 11 (80 cm above the concretion horizon D) – Lamberti Zone, Lamberti Subzone



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PLATE 15

- Fig. 1–3. *Brightia (Brightia) brightii* (Pratt). Fig. 1: PIN 4771/9; Fig. 2: PIN No. 4771/10. Mikhaylovtsenement I, talus. Fig. 3: YPU-MIV848. Mikhaylovtsenement I, bed 7 (140 cm above the base) – Coronatum Zone, Grossouvrei Subzone, *grossouvrei* biohorizon
- Fig. 4. *Brightia (Brightia) aff. brightii* (Pratt). YPU-MIV854. Mikhaylovtsenement I, bed 7 (50 cm above the base) – Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon
- Fig. 5. *Brightia (Brightia) aff. progzhellensis* Rogov, sp. nov. YPU-MIV277. Mikhaylovtsenement I, bed 7 (130 cm above the base) – Coronatum Zone, Grossouvrei Subzone, *grossouvrei* biohorizon
- Fig. 6, 7, 9, 10. *Brightia (Brightia) progzhellensis* Rogov, sp. nov. Fig. 6. Holotype YPU-MIV 156; Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone. Fig. 7a, b: YPU-MIV105. Mikhaylovtsenement I, talus. Fig. 9a, b: YPU-MIV264. Mikhaylovtsenement I, talus. Fig. 10: YPU-MIV911, Mikhaylovtsenement I (1.45 m below the top of the bed 8) – Athleta Zone, Proniae Subzone
- Fig. 8, 11. *Brightia (Brightia) cf. progzhellensis* Rogov, sp. nov. Fig. 8: YPU-MIV730. Mikhaylovtsenement I, bed 7, talus of Proniae Subzone. Fig. 11: YPU-MIV926. Mikhaylovtsenement I, bed 8 (90 cm below the top) – Athleta Zone, Proniae Subzone
- Fig. 12. *Brightia (Brightia) davitashvili* Lominadze. PIN No. 4771/11. Mikhaylovtsenement I – ?Middle Callovian, talus
- Fig. 13. *Brightia (Brightia) cf. submathei* (Lee). YPU-MIV 15. Mikhaylovtsenement I – Middle Callovian, talus
- Fig. 14–16. *Brightia (Brightia) eccentrica* Rogov, sp. nov. Fig. 14a, b: YPU-MIV288. Elatma section – Coronatum Zone, Obductum Subzone, *crassum* biohorizon. Fig. 15: YPU-MIV311. Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone. Fig. 16: holotype – YPU-MIV312. Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone
- Fig. 17–19. *Brightia (Brightia) mangoldi* (Lominadze). Fig. 17: YPU-MIV 71. Mikhaylovtsenement I, talus. Fig. 18: YPU-MIV360. Mikhaylovtsenement I, bed 7 (30 cm above the base) – Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon. Fig. 19: YPU-MIV377 – Coronatum Zone, Grossouvrei Subzone
- Fig. 20, 21. *Brightia (Brightia) nodosa* (Quenstedt). Fig. 20: YPU-MIV271. Mikhaylovtsenement I, bed 8 (45 cm below the top). Fig. 21: YPU-CH45. Mikhaylov-Gorenka, bed 10c (45 cm below the top). All: Athleta Zone, Proniae Subzone, *funiferus* biohorizon
- Fig. 22, 23. *Brightia (Brightia) nodosiformis* Rogov. Fig. 22: holotype, PIN 4771/14 Mikhaylovtsenement I, bed 8. Fig. 23: PIN 4771/15. Mikhaylov-Gorenka, bed 10c. All: Athleta Zone, Proniae Subzone
- Fig. 24, 25. *Brightia (Brightia) schalchi* (Zeiss). Fig. 24: YPU-MIV214. Mikhaylovtsenement I, talus. Fig. 25: YPU-MIV 131. Mikhaylov-Zmeinka – Middle Callovian, talus
- Fig. 26–28. *Rossiensiceras rossiense* (Teisseyre). Fig. 26a, b: YPU-MIV256. Mikhaylovtsenement I, talus. Fig. 27: YPU-MIV281. Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon. Fig. 28: YPU-MIV57. Mikhaylov-Zmeinka – Coronatum Zone



PLATE 16

- Fig. 1, 2. *Brightia (Brightia) rursicostata* (Buckman). Fig. 1: BM32348, Chippenham, Wiltshire, (?)Upper Callovian, Proniae Zone, Phaeinum Subzone. Fig. 2: YPU-702. Mikhaylovtsenement II – Coronatum Zone, talus
- Fig. 3, 4. *Brightia (Brightia) salvadori* (Parona et Bonarelli). Fig. 3: PIN 4771/18. The right bank of the Raka River near Boloshnevo village (Ryazan region) – Athleta Zone. Fig. 4: YPU-MIV372. Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone
- Fig. 5–7. *Brightia (Brightia) aff. salvadori* (Parona et Bonarelli). Fig. 5: YPU-B460. Mikhaylovtsenement I, bed 7 (460 cm above the soles) – Athleta Zone, Proniae Subzone. Fig. 6: YPU-MIV315. Mikhaylovtsenement I, talus. Fig. 7: YPU-MIV480. Mikhaylovtsenement I, bed 8 (45 cm below the top) – Athleta Zone, Proniae Subzone, *funiferus* biohorizon
- Fig. 8–11. *Brightia (Brightia) subinvoluta* (Bonarelli). Fig. 8: YPU-MIV154. Mikhaylovtsenement I, talus. Fig. 9: YPU-MIV904. Mikhaylovtsenement I, talus. Fig. 10: YPU-B116. Mikhaylovtsenement I, bed 7 (116 cm above the base) – Coronatum Zone, Grossouvrei Subzone. Fig. 11: YPU-MIV253. Mikhaylovtsenement I, talus
- Fig. 12. *Brightia (Brightia) aff. subinvoluta* (Bonarelli). YPU-MIV926. Mikhaylovtsenement I, talus
- Fig. 13. *Brightia (Brightia) cf. pseudocracoviense* (Tsytovitch). YPU-MIV109. Mikhaylovtsenement I, talus
- Fig. 14–16. *Brightia (Brightia) pseudocracoviense* (Tsytovitch). Fig. 14a, b: YPU-MIV153. Mikhaylovtsenement I, bed 7 – Coronatum Zone. Fig. 15a, b: YPU-MIV260. Mikhaylovtsenement I, talus. Fig. 16: YPU-MIV260. Mikhaylovtsenement I, talus
- Fig. 17, 26. *Brightia (Brightia) difformis* (Tsytovitch). Fig. 17: YPU-MIV141. Mikhaylovtsenement I, talus – ?Middle Callovian. Fig. 26a, b: YPU-MIV257. Mikhaylovtsenement II, talus
- Fig. 18. *Brightia (Glyptia) cf. canaliculata* (Quenstedt). PIN 4771/3. Quarry near Peski village (Moscow region), talus – ?Athleta Zone
- Fig. 19. *Brightia (Glyptia) canaliculata canaliculata* (Quenstedt). YPU-MIV212. The right bank of the Oka River near the Novoselki village (Ryazan region) – Athleta Zone, Kuklikum Subzone
- Fig. 20, 21. *Brightia (Glyptia) canaliculata stankevitchae* Rogov, subsp. nov. Fig. 20: PIN 4771/12. Fig. 21: Holotype – PIN 4771/21. All: quarry near Peski village (Moscow region) – Lamberti Zone
- Fig. 22. *Alcidia cf. nurraensis* (Spath). YPU-MIV489. Mikhaylovtsenement I – Coronatum Zone, Obductum Subzone, *crassum* biohorizon
- Fig. 23a, b. *Lunuloceras fonticola* (Menke). YPU-MIV80. Mikhaylovtsenement I, talus
- Fig. 24. *Lunuloceras fallax* (Zeiss). YPU-MIV367. Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon
- Fig. 25. *Orbignyiceras orbignyi* (Tsytovitch). YPU-MIV 296. Elatma section (Ryazan region) – Coronatum Zone, Obductum Subzone

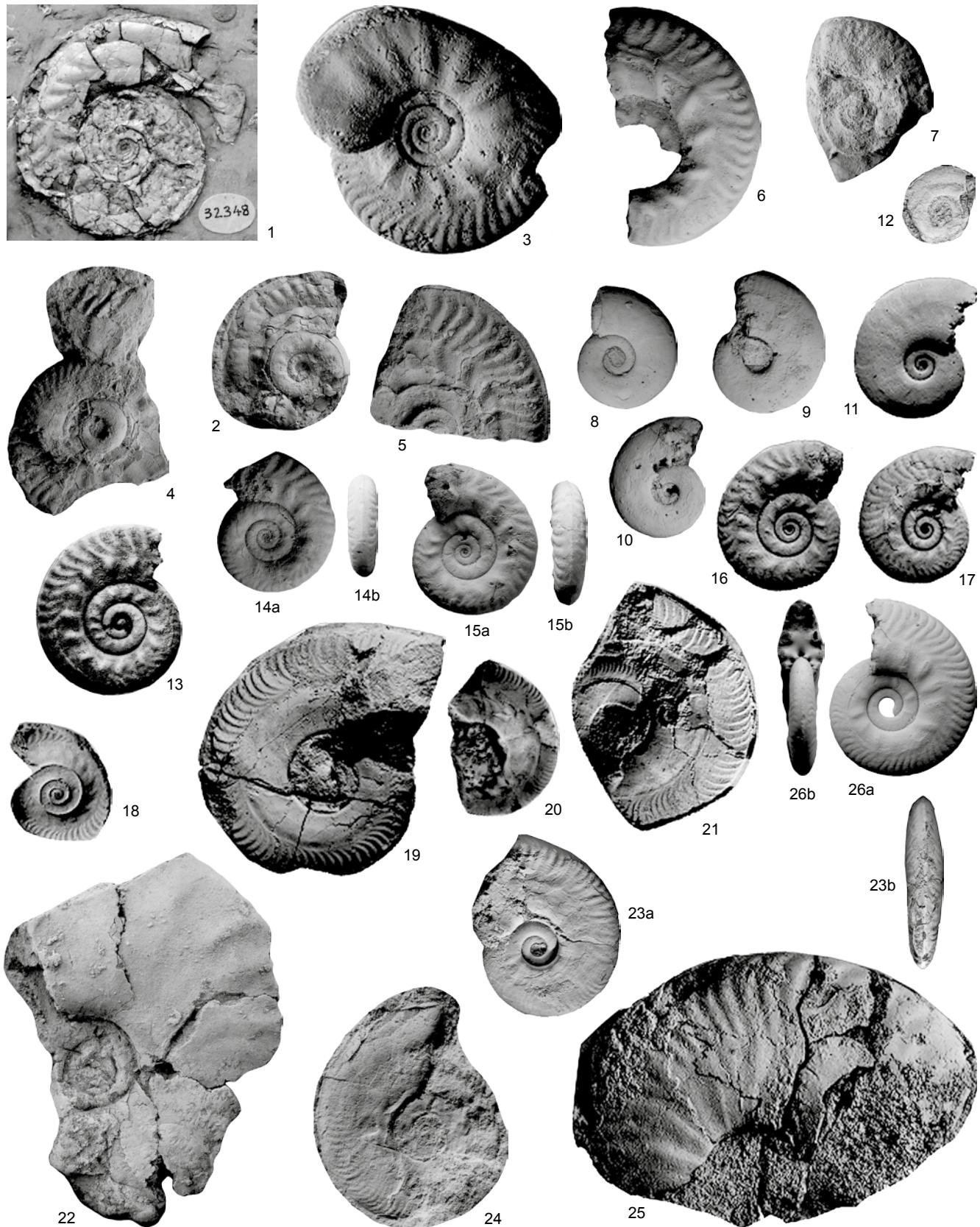


PLATE 17

- Fig. 1. *Brightia (Brightia) retrocostata* (Buckman). YPU-MIV 21. Mikhaylov-Zmeinka, talus
- Fig. 2. *Brightia (Brightia) boikoi* Rogov. Holotype – PIN 4771/4. Mikhaylovtsenement I, talus
- Fig. 3a, b. *Brightia (Brightia) difforme* (Tsytovitch). YPU-MIV257. Mikhaylovtsenement II, talus
- Fig. 4. *Brightia* sp. YPU-MIV710. Mikhaylovtsenement I, bed 8 (100 cm below the top) – Athleta Zone, the Proniae Subzone
- Fig. 5, 6. *Brightia (Brightia) pseudonodosa* (Tsytovitch). Fig. 5: YPU-MIV924. Mikhaylovtsenement I, bed 8 (160 cm below the top) – Athleta Zone, Proniae Subzone. Fig. 6: PIN 4771/17. Mikhaylov-Gorenka – Athleta Zone, Kuklikum Subzone
- Fig. 7a, b. *Brightia (Brightia) cf. kaveckii* (Pakuckas). YPU-MIV127. Mikhaylovtsenement I, talus
- Fig. 8. *Brightia* cf. *lominadzei* Rogov, sp. nov. YPU-MIV711. Mikhaylovtsenement I, bed 7 (600 cm above the base) – Athleta Zone, Proniae Subzone
- Fig. 9. *Brightia (Glyptia) tenuicostata* Rogov. Holotype – PIN 4771/8. Mikhaylovtsenement I – Upper Callovian, talus
- Fig. 10, 11, 14. *Zieteniceras rarecostatum* Rogov sp. nov. Fig. 10 – holotype – YPU-MIV374. Fig. 11 – YPU-MIV486, talus of Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon; Fig. 14 – YPU-MIV 374, Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone
- Fig. 12. *Zieteniceras cf. demolyi* (Lemoine). YPU-B 690. Mikhaylovtsenement I – Athleta Zone, Proniae Subzone.
- Fig. 13. *Zieteniceras aff. rarecostatum* Rogov sp. nov. YPU-MIV155, Mikhaylovtsenement I, bed 7 – Coronatum Zone, Grossouvrei Subzone, *posterior* biohorizon
- Fig. 15, 16. *Orbignyiceras diversicostatum* (Gerard et Contaut). Fig. 15a, b: YPU-ZN 160. Mikhaylov-Zmeinka (1.6 m below the top of the analogues bed 8 of the Mikhaylovtsenement I). Fig. 16: YPU-CH 115. Mikhaylov-Spartak (1.6 m below the top of the analogs bed 8 of the Mikhaylovtsenement I). All: Athleta Zone, Proniae Subzone
- Fig. 17a, b. *Orbignyiceras cf. diversicostatum* (Gerard et Contaut). YPU-MIV729. Mikhaylovtsenement I, bed 7 (top) – Athleta Zone, Proniae Subzone
- Fig. 18a, b. *Orbignyiceras kaspiense* Repin et Rashvan. YPU-CH105. Mikhaylov-Spartak, analogues of bed 10c of the Gorenka section (105 cm below the top) – Athleta Zone, Proniae Subzone

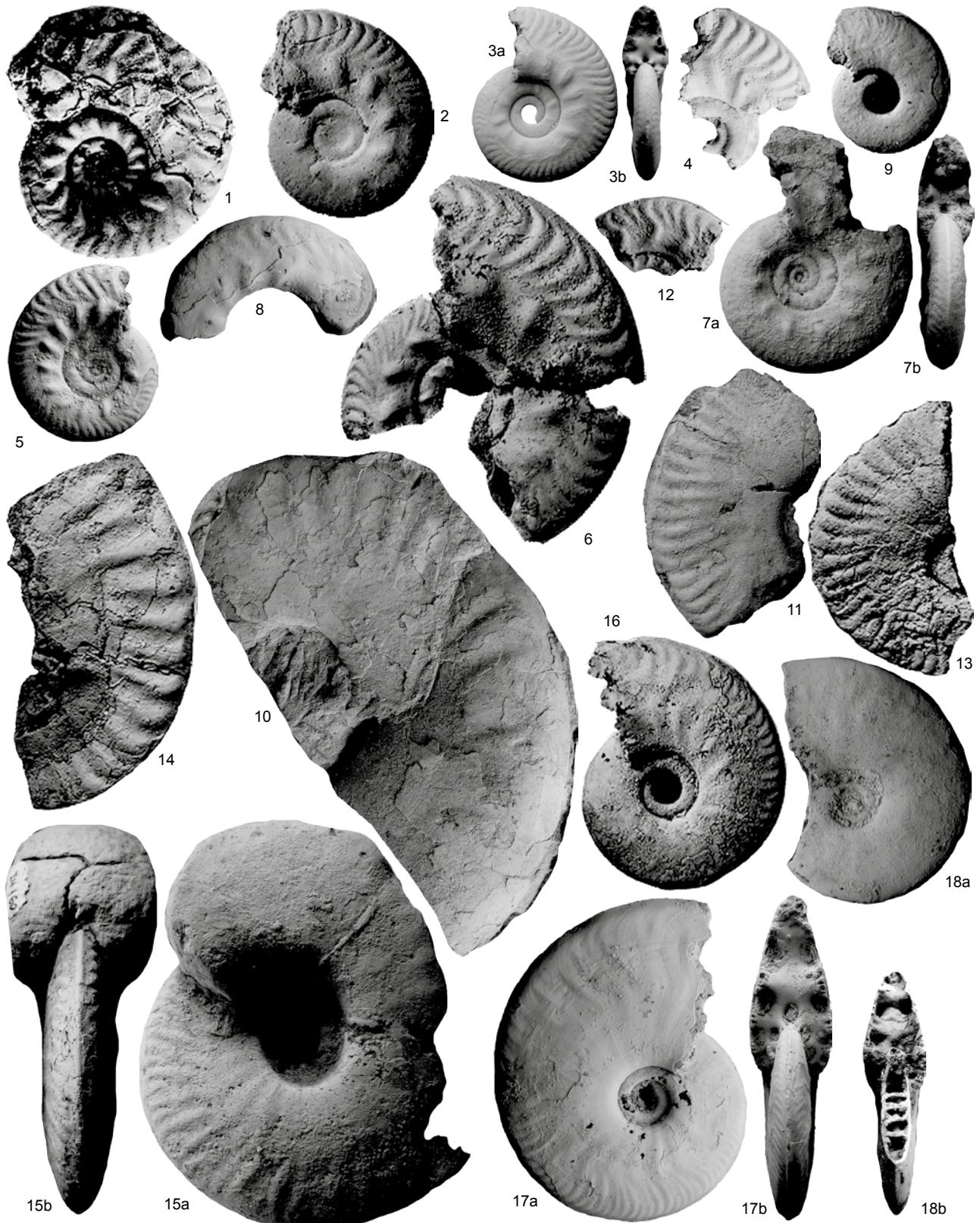


PLATE 18

- Fig. 1, 2, 6. *Orbignyiceras cf. lonsdalii* (Pratt). Fig. 1a, b: YPU MIV261. Fig. 2a, b: YPU-MIV149. Fig. 6: YPU-MIV20. All: Mikhaylovtsenement I, talus
- Fig. 3–5. *Orbignyiceras lonsdalii* (Pratt). Fig. 3a, b. YPU MIV272. Mikhaylovtsenement I, talus. Fig. 4. YPU-MIV484. Mikhaylovtsenement I, talus. Fig. 5. YPU-MIV280. Mikhaylovtsenement I – Coronatum Zone, Obductum Subzone, *crassum* biohorizon
- Fig. 7, 8. *Orbignyiceras mikhailowense* (Zeiss). Fig. 7a, b. YPU-372, Zmeinka, the lower part of the Upper Callovian (3.72 m above the „0“ mark); Fig. 8a, b. YPU-MIV140. Mikhaylovtsenement I, talus
- Fig. 9. *Sublunuloceras cf. virguloides* (Gerard et Contaut), YPU-MIV479. Mikhaylovtsenement I, talus
- Fig. 10. *Orbignyiceras lahuseni* (Tsytovitch). YPU-MIV 149. Mikhaylovtsenement I, talus
- Fig. 11a, b. *Orbignyiceras pseudopunctatum* (Lahusen). YPU-MIV949. Mikhaylovtsenement I, Upper Callovian, talus
- Fig. 12. *Orbignyiceras cf. beineui* (Amannijasov). YPU-MIV 139. Mikhaylovtsenement I, talus

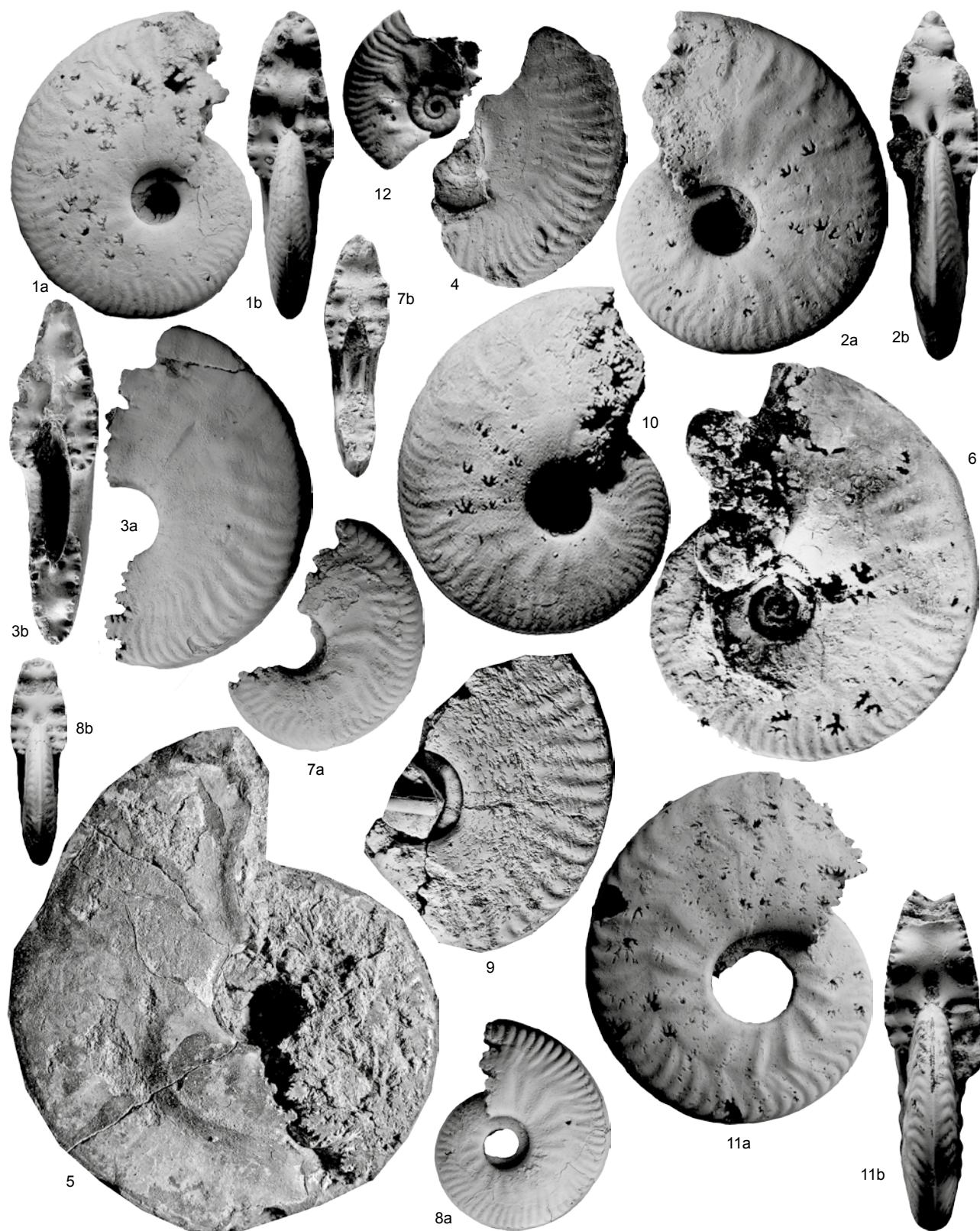
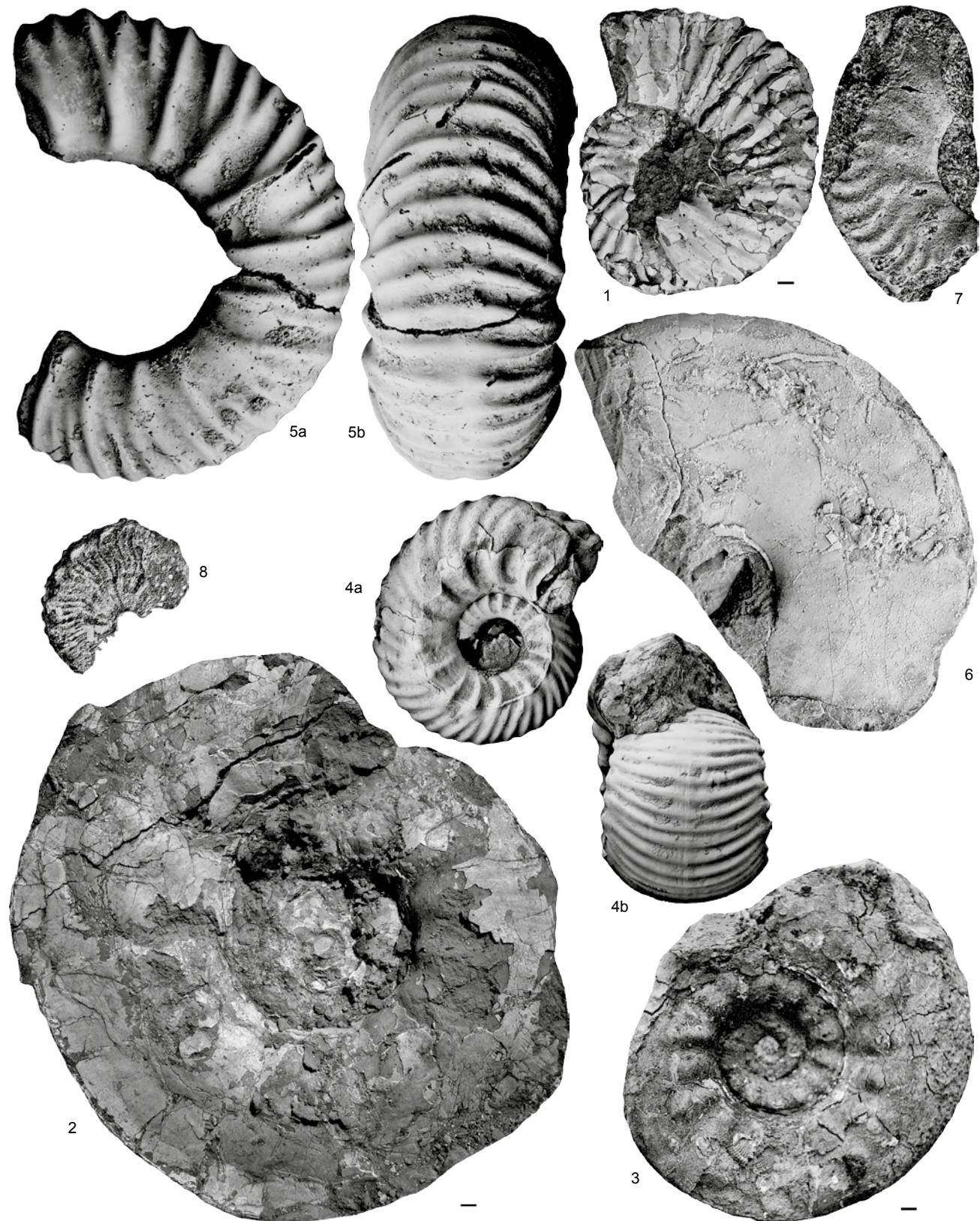


PLATE 19

- Fig. 1–3. *Erymnoceras ex gr. coronatum* (Bruguiere). Field photos, Coronatum Zone, Obductum Subzone. 1, 2: Mikhaylovtsenement II, bed 3 (in Fig. 1 – 0.5 m above the base). Fig. 3: Mikhaylovtsenement I, bed 6
- Fig. 4a, b. *Erymnoceras doliforme* Roman. YPU-Number. Mikhaylovtsenement II, bed 4 – Coronatum Zone, Grossouvrei Subzone
- Fig. 5a, b. *Erymnoceras baylei* Jeannet. YPU-MV2. Mikhaylovtsenement I, bed 6 – Coronatum Zone, Obductum Subzone, *obductum* biohorizon
- Fig. 6. *Alcidia mazetieri* (Petitclerc). YPU-MIV909. Mikhaylovtsenement I, bed 8, base (2.5 m below the top) – Athleta Zone, Proniae Subzone
- Fig. 7. *Rossiensiceras uhligi* (Till). YPU-MK7991, Mikhaylovtsenement II, bed 3 (0.1 m above the base) – Jason Zone, Medea Subzone
- Fig. 8. *Taramelliceras cf. flexispinatum* (Oppel). Private collection of A. Bryatov. Mikhaylovtsenement I, probably layer 11 – Lamberti Zone



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PLATE 20

- Fig. 1. *Kosmoceras subnodatum* Teisseyre. Lectotype: IPUW 1884-2-9 (*Cosmoceras subnodatum*: Teisseyre, 1883: Taf. 2: 9a–d). Ryazan Region, Pronya River
- Fig. 2. *Kosmoceras proniae* Teisseyre. Lectotype: IPUW 1884-3-15 (*Cosmoceras proniae*: Teisseyre, 1883: Taf. 3: 15a–d). Ryazan Region, Pronya River
- Fig. 3a–c. *Kosmoceras jenzeni* Teisseyre. Lectotype: IPUW 1884-3-23 (*Cosmoceras jenzeni*: Teisseyre, 1883: Taf. 3: 23a–c). Ryazan Region, Pronsk
- Fig. 4. *Kosmoceras pollucinum* Teisseyre. Lectotype: IPUW 1884-5-30 (*Cosmoceras pollucinum*: Teisseyre, 1883: Taf. 5: 30a, b). Ryazan Region, Pronsk
- Fig. 5a, b. *Rossiensiceras rossiense* (Teisseyre). Lectotype: IPUW 1884-1-6 (*Harpoceras rossiense*: Teisseyre, 1883: Taf. 1: 6a–d). Ryazan Region, Pronsk
- Fig. 6a, b. *Binatisphinctes subaurigerus* (Teisseyre). Lectotype: IPUW 1884-5-39 (*Perisphinctes subaurigerus*: Teisseyre, 1883: Taf. 5: 39a–d). Ryazan Region, Pronsk – Ornamententon
- Fig. 7–10. *Brightia lominadzei* Rogov. Fig. 7: YPU-MIV 232. Fig. 8: YPU-MIV305. Figs. 9, 10 – holotype: YPU-MIV303. Moscow region, Alpatyovo village – Upper Callovian
- Fig. 11a–c. *Sublunuloceras* cf. *dynastes* (Waagen). YPU-MIV1, Mikhaylovtsenement I, bed 8 – Athleta Zone, Kuklikum Subzone

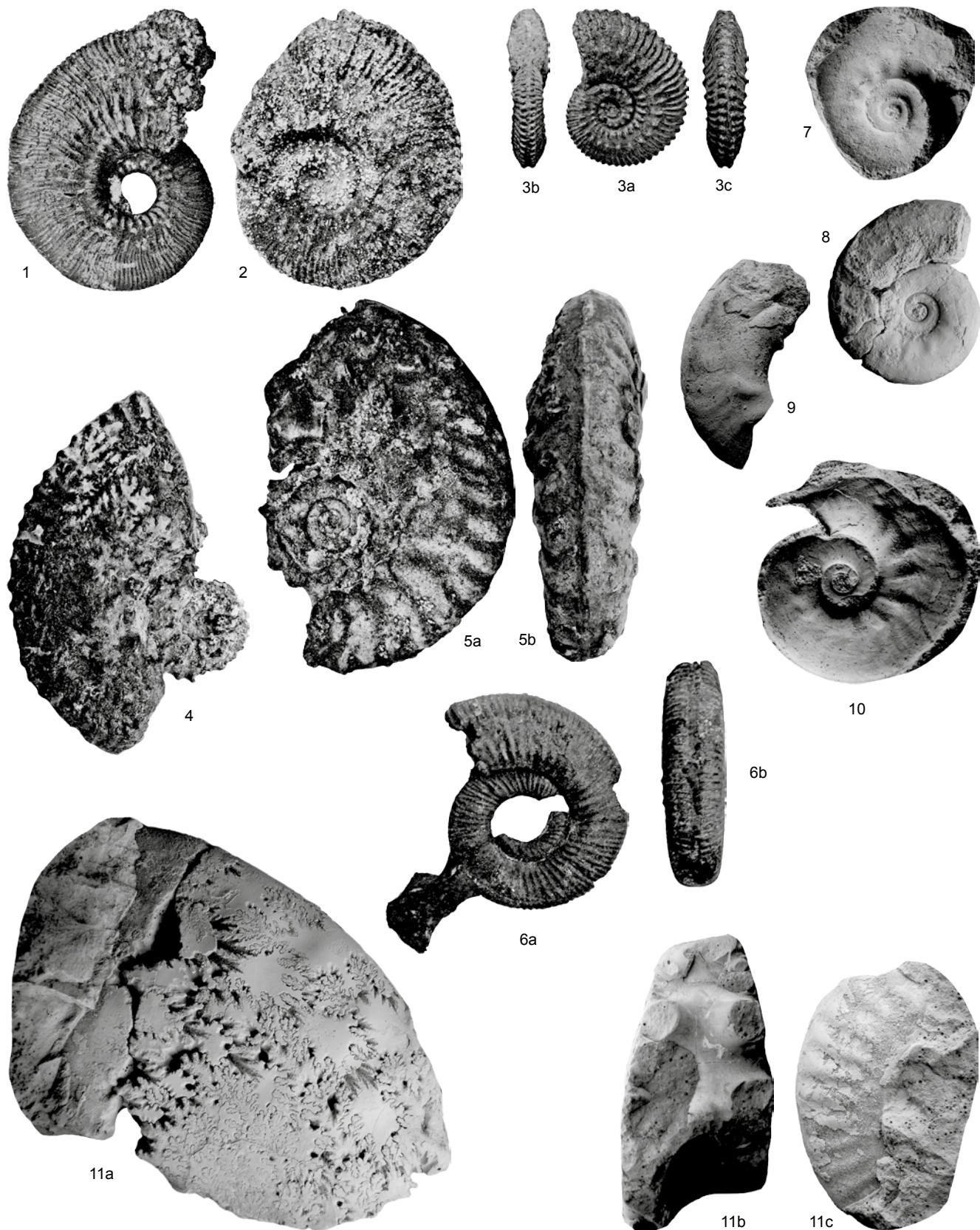
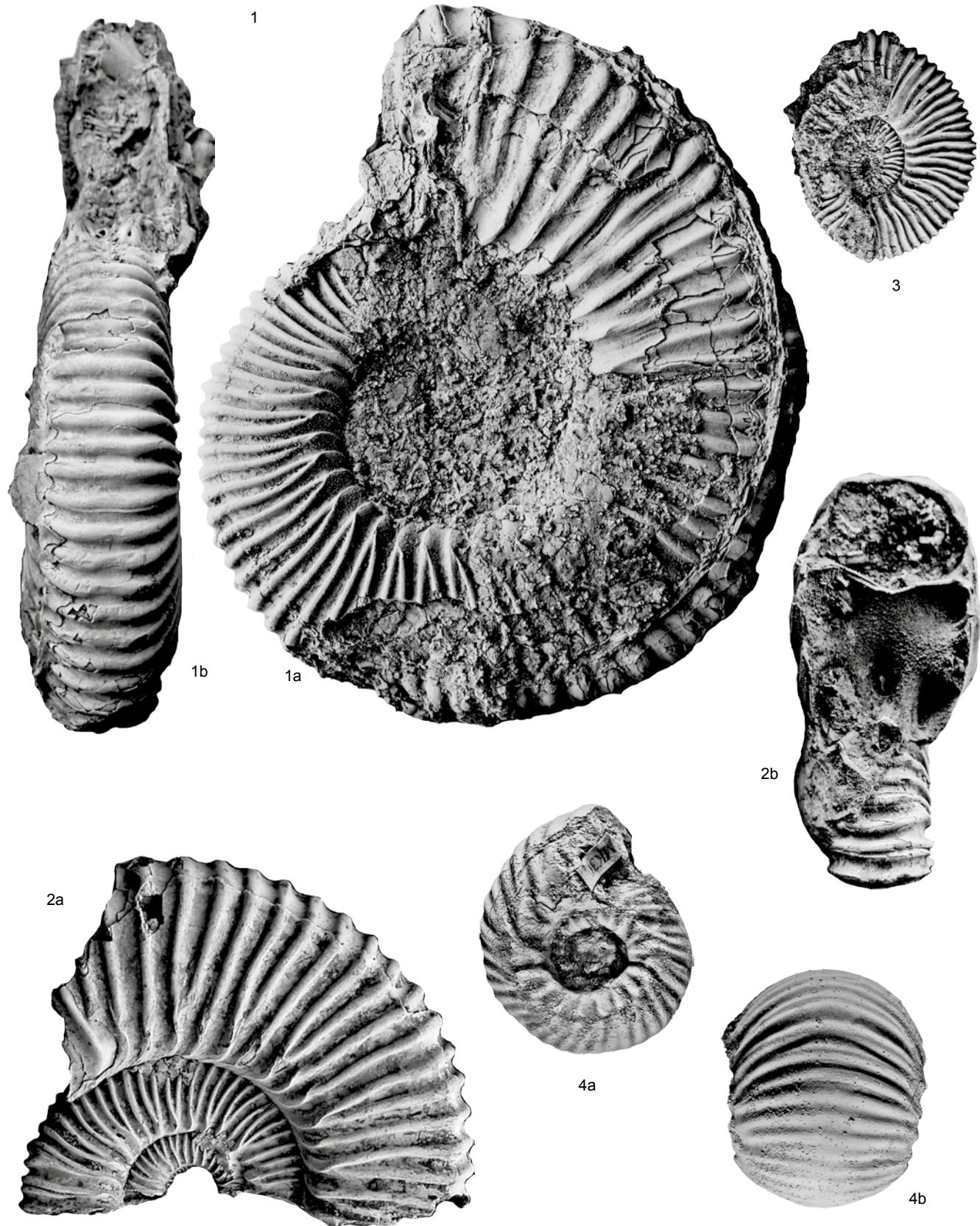


PLATE 21

Fig. 1, 2. *Peltoceras (Peltoceratoides) williamsoni* (Phillips). Fig. 1a, b: YPU-MK1499. Fig. 2a, b: YPU-MK1502.
Mikhaylovtsenement I, bed 13 – Cordatum Zone, Costicardia Subzone

Fig. 3. *Parawedekindia arduennensis* (d'Orb.). YPU-number. Mikhaylovtsenement I, bed 13 – Cordatum Zone, Costicardia Subzone

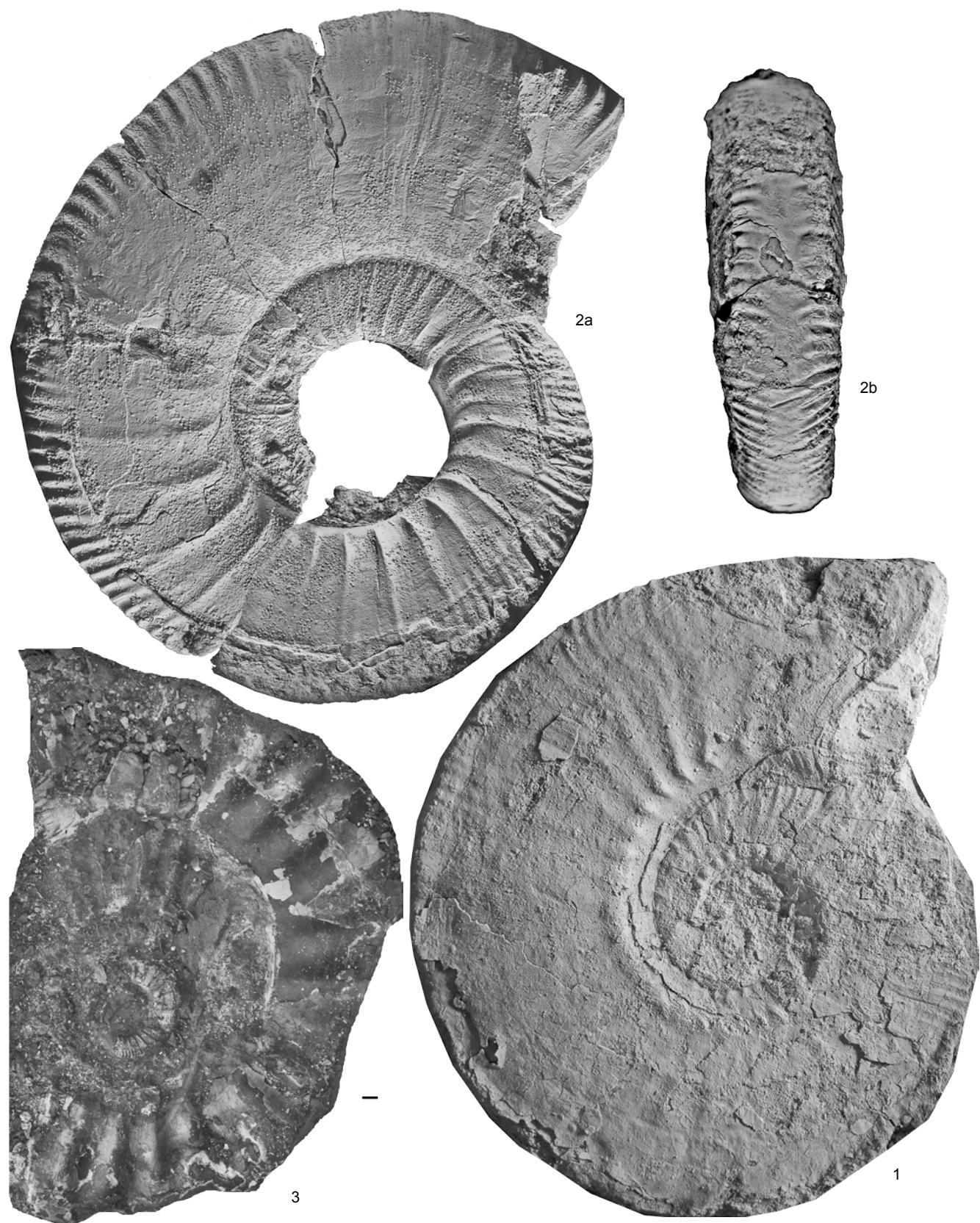
Fig. 4a, b. *Erymnoceras doliforme* Roman. YPU-MK301. Mikhaylovtsenement I, bed 7 (58 cm above the base) – Coronatum Zone, Grossouvrei Subzone



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PLATE 22

- Fig. 1. *Kosmoceras (Zugokosmoceras) crassum* Tintant. YPU-MK-180. Mikhaylovtsement I, bed 6 – Coronatum Zone, Obductum Subzone, *crassum* biohorizon
- Fig. 2a, b. *Binatisphinctes fluctuosus* Buckman. YPU-M7b-13. Mikhaylovtsement I, bed 7 – Coronatum Zone, Grossouvrei Subzone
- Fig. 3. *Binatisphinctes welschi* Gerard et Contaut. Field photos. Mikhaylov-Gorenka, bed 10c (in Fig. 4 – 6.1 m above the base) – Athleta Zone, Proniae Subzone, *patruus* biohorizon



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PLATE 23

- Fig. 1. Basal Jurassic beds in the Mikhaylovtsement II section. The red star labelled the pebble horizon of redeposited Carboniferous rocks (see Fig. 4). Photo made in the year 2017
- Fig. 2. Basal Jurassic beds in the Mikhaylov-Gorenka-2 section (see Fig. 4). Photo made in the year 2014
- Fig. 3. Callovian – Oxfordian boundary beds in the Mikhaylov-Gorenka section. The concretion horizons are indicated in red letters (see Fig. 5). Photo made in the year 2014

