

Stratigraphy of the Bathonian–Callovian Boundary Deposits in the Prosek Section (Middle Volga Region). Article 1. Ammonites and Infrazonal Biostratigraphy

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Received January 21, 2007; in final form, March 28, 2007

Abstract—In European Russia, the most complete succession of Boreal sediments of the terminal Bathonian and lower Callovian is exposed near the Prosek Settlement. After its revision, the infrazonal division of the upper Bathonian and lower Callovian and position of the Bathonian–Callovian boundary are defined more carefully. The *Calyx* Zone and *bodylevskyi* Biohorizon are established in the upper Bathonian. The base of the lower Callovian is defined at the first occurrence level of *Macrocephalites jacquoti*. Based on four successive ammonite assemblages occurring in lower part of the *Elatmae* Zone, the *breve*, *frearsi*, *quenstedti*, and *elatmae* biohorizons are identified. The joint occurrence of Boreal, Subboreal, and Tethyan ammonites in the section facilitate its correlation with the other sections of the Panboreal paleobiogeographic superrealm.

DOI: 10.1134/S0869593807050036

Key words: Bathonian–Callovian boundary, European Russia, East Greenland, ammonites.

INTRODUCTION

The study of the Bathonian–Callovian boundary in European Russia is important now for several reasons. When Boreal marine sediments of the upper Bathonian, which contain ammonite assemblage of the East Greenland affinity in general, have been discovered in the Middle Volga region, first in the Novgorod oblast (Mitta and Starodubtseva, 1998; Gulyaev and Kiselev, 1999a, 1999b) and then in Mordovia (Mitta, 2004a, 2004b), it was a good opportunity to solve several stratigraphic problems. Objectives of prime significance were to get a deeper insight into the Bathonian–Callovian boundary stratigraphy in European Russia, to correlate directly the ammonite successions of East Greenland and Subboreal regions, to substantiate better the Boreal–Tethyan correlation, and to detail the standard scale accepted for the Panboreal Superrealm (Zakharov et al., 1997) or the Boreal secondary standard (Callomon, 1993, 2003). Researchers who studied the upper Bathonian sediments in the Middle Volga region suggested different ammonite zonations and correlation schemes for the upper Bathonian–lower Callovian boundary sediments. The schemes were controversial, requiring additional examination of most complete, relatively continuous sections containing the diverse paleontological remains.

The Bathonian–Callovian boundary in Boreal sediments attracts attention in connection with intend to select the GSSP for the lower boundary of the Callovian Stage. According to recommendations of the Inter-

national Stratigraphic Commission (Remane et al., 1996), the candidate type section should be (1) of appropriate thickness and sedimentation rates, (2) continuous, (3) lacking synsedimentary and tectonic distortions, (4) free of metamorphic and significant diagenetic alterations, (5) containing abundant and diverse fossils throughout the entire succession, (6) without facies changes near the boundary, (7) composed of marine sediments, (8) appropriate for magnetostratigraphic, chemostratigraphic, and isotopic studies and (9) accessible.

Callomon and Dietl (2000) stated in addition that the GSSP candidate should correspond above and below the boundary to succession of standard biostratigraphic units (in rank of chronosubzone) possessing global or nearly global correlation potential and meet requirements of the priority principle and existing conventions.

The Albstadt–Pfeffingen section in Germany is at present the only candidate for the GSSP of the Callovian Stage lower boundary (Callomon and Dietl, 1990; 2000). Having the historical priority, this section in the Swabian Alb, the type site of the *Kepplerites keppleri* Subzone, is included into the standard scale as a basal zone of the Callovian Stage (Callomon et al, 1988; Callomon and Dietl, 1990). The high correlation potential of the section is determined by a wide geographic distribution of the *Keppleri* Subzone index species, and the ammonite assemblage of the *Keppleri* faunal horizon consists of species belonging to different bio-

chores, the representatives of four Tethyan to Sub-Tethyan and two Boreal families (Callomon and Dietl, 1990).

The section in question includes four faunal horizons, the lower one (*hochstetteri*) of the Bathonian and three others of the lower Callovian *Keppleri* Subzone. It is lacking internal breaks in sedimentation significant in terms of biostratigraphy, being bracketed although by hiatuses below the base of the *hochstetteri* faunal horizon and at the top of the *suevicum* faunal horizon (Dietl, 1994; Callomon and Dietl, 1990, 2000).

Besides the advantages mentioned above, the Albstadt–Pfeffingen section has serious disadvantages (R. Jordan in Callomon and Dietl, 2000; Mitta, 2004b) diminishing its status of candidate for the GSSP. First, these are signs of sediment condensation observable throughout the section, which mean potential gaps in the biostratigraphic record. Callomon and Dietl are however of opinion that there is no unconformity of biostratigraphic significance in the boundary interval proper, since ...“where, ‘elsewhere,’ have additional distinguishable faunal horizons been found that are identifiably of ages intermediate between those of the *hochstetteri* and *keppleri* horizons? The answer is, that after 140 years of intensive work, nowhere. And the close similarity of the faunas of these horizons suggests that the future chances are small” (Callomon and Dietl, 2000, p. 49).

The existing doubts in appropriateness of the Albstadt–Pfeffingen section for the GSSP forced members of the International Working Group on the Callovian Stratigraphy to propose alternative variants of the Bathonian–Callovian boundary stratotype section. During the 7th International Congress on the Jurassic System (Krakow, 2006), a group of specialists paid attention to advantages of the section in the Prosek–Isady area (Nizhni Novgorod oblast). Owing to abundant and diverse fossils, obvious continuity, and other features, this section can certainly be a GSSP candidate for the Bathonian–Callovian boundary. In October of 2006, a multidisciplinary study of the section was carried out by a team of researchers from different regions and organizations of Russia. The team consisted of D.N. Kiselev (Yaroslavl State Pedagogical University), M.A. Rogov, S.Yu. Malenkina (Geological Institute of the RAS, Moscow), L.A. Glinskikh (Institute of Geology and Geophysics, Siberian Division of the RAS, Novosibirsk), M.V. Pimenov, and A.V. Manikin (Saratov State University, Saratov). In this work, a detailed infrazonal scale based on distribution of ammonites is suggested.

INVESTIGATION HISTORY

The Prosek–Isady section of Middle–Upper Jurassic deposits (Lyskovo area, Nizhni Novgorod oblast) is exposed on the Volga River right bank between eponymous settlements southwest of the former (Fig. 1a).

History of its investigation lasted 120 years since its discovery by A.R. Ferkhmin in 1886. The first period of investigation was dedicated to description of its Callovian part largely (Sibirtsev, 1886; Gerasimov and Kazakov, 1939; Kulinich and Fridman, 1990; Gulyaev, 1997). The lower, sandy portion of the Middle Jurassic was attributed to the Bathonian conditionally, because macrofauna has not been found there.

The diverse assemblage of Boreal marine fossils discovered in the sandy member motivated its correlation with the upper Bathonian (Gulyaev and Kiselev, 1999a, 1999b). Found ammonites similar or identical to species from the *Cadoceras calyx* Zone of East Greenland substantiated the late Bathonian age of sand beds. The ammonite assemblage is dominated by *Keplerites svalbardensis* Sokolov et Bodylevski. Rare Cadoceratinae specimens have been determined as new species *Cadoceras infimum* Gulyaev et Kiselev and *Costacadoceras pisciculus* Gulyaev. The peculiar composition of the ammonite assemblage was inappropriate for confident identification of biostratigraphic units established in East Greenland, and Bed 1 of the section was attributed to the new *Infimum* Zone and synonymous biohorizon.¹

Ammonites were found in concretions (well preserved) and matrix of the bed (deformed). The ammonite assemblage consists mainly of forms from large sandstone concretions, which have not been found first in situ. Their occurrence was thought to be in the interval of 0.5–2.5 m below the top of the sand bed. It was assumed that concretions occur at several levels. When concretions were discovered in situ, it became clear that they occur substantially lower, in a single horizon within the interval of 2.5–3.5 m (Gulyaev, 2001).

In matrix of the sand bed upper part, Gulyaev (2001) found Cadoceratinae specimens close to *C. infimum* from concretions, although differing from the latter in morphology. Because of a poor preservation, this form was first described in open nomenclature as *C. cf. aff. infimum* and attributed subsequently to new subspecies *C. infimum* subsp. nov. (Gulyaev, 2005). According to its peculiar morphology and occurrence in the section separately from *C. infimum infimum*. Gulyaev defined two biohorizons in the *Infimum* Zone (Table 1).

Mitta (2000) attributed the sand member (Bed 1) to the Callovian but not the Bathonian. He failed to find concretions with fossils under consideration. Mitta revised determinations by Gulyaev and Kiselev and attributed *Keplerites svalbardensis* Sokolov et Bodylevski to *K. aff. keppleri* (Oppel). After revision of Cadoceratinae forms, he regarded specimens of *Cadoceras infimum* Gulyaev et Kiselev as different species: the holotype and all other species from concretions as *Cadoceras frearsi* (d’Orbigny), and specimen from Bed 1 (Gulyaev and Kiselev, 1999a, Plate 2,

¹ The term “biohorizon” is used in this paper as a synonym of the term “faunal horizon” (see discussion in works by Page, 1995, and Gulyaev, 2002).

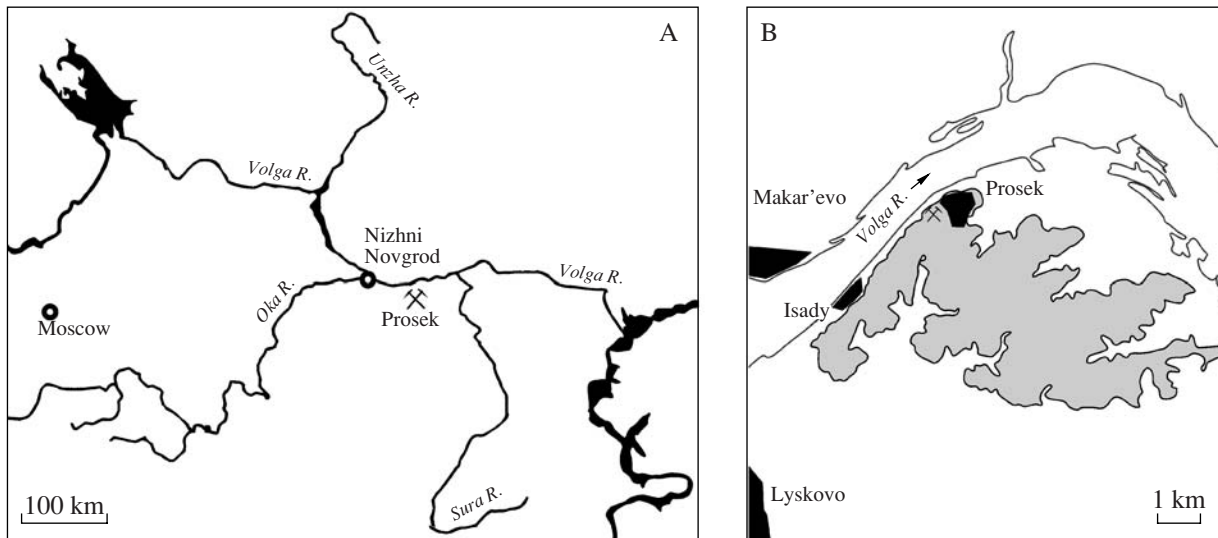


Fig. 1. Schematic location of sections near the Prosek and Isady settlements. (A) Large-scale scheme; (B) location of the main section and erosion outlier of Jurassic sediments in the Lyskovo area. Outlier boundaries are given along the isohyps of 160 m.

fig. 6) as *C. bodylevskyi* Frebold. As number of horizons with concretions was unknown at that time, Mitta assumed that they occur at two levels with different ammonite assemblages: at the lower one with *C. bodylevskyi* (the index of synonymous faunal horizon in his opinion,) and at the upper level with *Cadoceras frearsi* (a species from the *kepleri* faunal horizon, as Mitta assumed). As is shown below, the specimen determined by Mitta as *C. bodylevskyi* is from a bed located above but not below concretions with ammonite identified as *C. frearsi*.

All the researchers attribute the overlying clay member (Bed 2) to the *Cadoceras elatmae* Zone of the

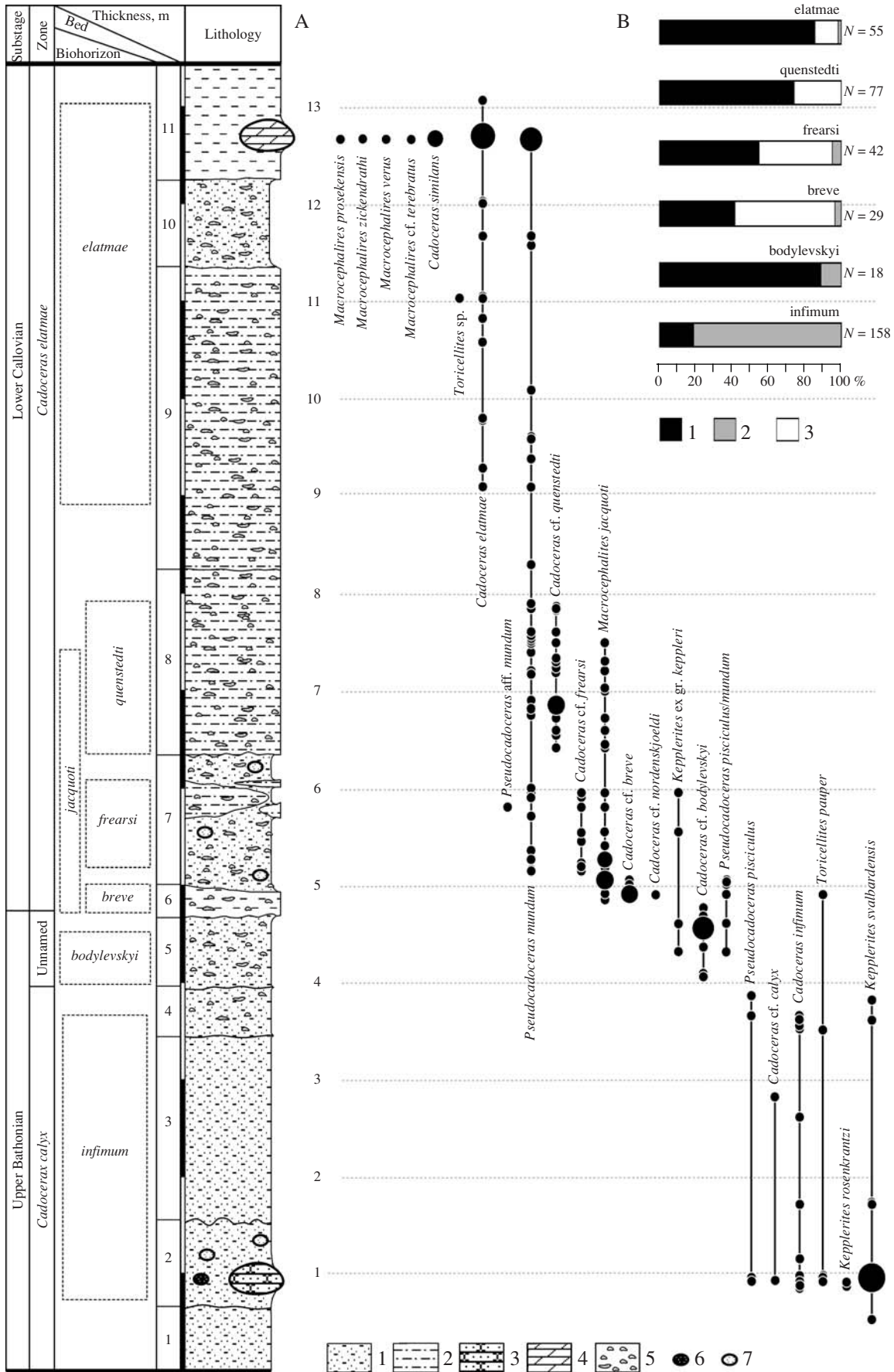
lower Callovian. Gulyaev and Mitta suggested substantially different internal subdivision of the last zone (Table 1). The controversial interpretation concerns primarily the zone lower part approximately 5 m thick. According to Mitta, this part of the section presumably corresponds to the *kepleri-falsum* horizons that is argued for only by its position in the section, since no data on ammonites from the respective sediments have been presented.

In the same interval, Gulyaev (2001) discovered an ammonite assemblage consisting of both the Boreal (cadoceratins and *Keplerites*) and Tethyan (*Macrocephalites*) species. He established that this assemblage

Table 1. Stratigraphy of the Prosek–Isady section, according to different authors

Member	Gulyaev and Kiselev, 1999a		Gulyaev, 2001		Gulyaev, 2005		Mitta, 2000		This work		
Clayey	Lower Callovian	<i>Elatmae</i>	<i>elatmae</i>	Lower Callovian	<i>Elatmae</i>	<i>subpatruus</i>	<i>subpatruus</i>	<i>elatmae</i>	<i>subpatruus</i>	<i>Elatmae</i>	
						<i>surensis</i>	<i>surensis</i>		<i>surensis</i>		<i>surensis</i>
						<i>elatmae</i>	<i>elatmae elatmae</i>		<i>elatmae</i>		<i>elatmae</i>
						<i>elatmae anabarense</i>	<i>elatmae</i>		<i>elatmae</i>		
Sandy	Upper Bathonian	<i>Infimum</i>	<i>infimum</i>	Upper Bathonian	<i>Infimum</i>	<i>cf./aff. infimum</i>	<i>infimum</i>	<i>infimum</i>	<i>infimum</i>	<i>Infimum</i>	
						<i>infimum</i>	<i>infimum subsp. nov.</i>		<i>infimum</i>		<i>infimum</i>
						<i>infimum</i>	<i>infimum infimum</i>		<i>infimum</i>		<i>infimum</i>
						<i>infimum</i>	<i>infimum</i>		<i>infimum</i>		<i>infimum</i>

Note: Double lines indicate boundaries of biohorizons, simple lines designate boundaries of zones and substages.



includes *Macrocephalites jacquoti* H. Douvillé, an index species of the basal Callovian biohorizon that is analogue of the *Keppleri* biohorizon. Being first found in Russia, this very important species indicated presence of the *jacquoti* Biohorizon defined originally in West Europe (Westermann and Callomon, 1988; Thierry et al., 1997), and accordingly the base of the Callovian Stage can be established in the section. Since *M. jacquoti* is also known from two upper faunal horizons (*hollandi* and *hochstetteri*, see in Callomon et al., 1989; Dietl, 1994) of the Bathonian Stage, Gulyaev (2002, p. 82) supposed possibility to correlate the lower part of the *Elatmae* Zone containing *M. jacquoti* with the upper part of the Bathonian Stage.

Gulyaev mentioned also the *Kepplerites* species close to *K. keppleri* in the assemblage from this biohorizon. Because of their poor preservation, these species were identified only in open nomenclature, but despite this their occurrence was an additional argument for defining the Callovian lower boundary at the base of Bed 2.

Later on, Gulyaev (2005) attempted to establish more detailed subdivision of the *Elatmae* Zone lower half based on distribution of cardioceratids. He defined here three the *poultoni*, *primaevum*, and *elatmae anabarensis* biohorizons like in the Pizhma River basin and proposed the same subdivision of the *Elatmae* Zone in the Prosek–Isady section.

The Prosek–Isady section is of key importance by constructing and detailing the upper Bathonian and lower Callovian biostratigraphic scales of European Russia. As is shown above however, there is no uniform viewpoint on the section structure and age of its beds. All the units of the stratigraphic hierarchy (stages, zones, infrazones) are controversially interpreted, and this stimulated reconsideration of previous concepts based on a more comprehensive study.

DESCRIPTION OF STUDIED SECTION

Jurassic sediments of the Lyskovo area are exposed along the right bended bank of the Volga River between the Prosek and Isady settlements in the erosion remnant approximately 7 km long and up to 1.5 km wide (Fig. 1b). The base of the Jurassic section is at the altitude of approximately 160 m, being underlain by the Upper Permian strata. Outcrops of the Jurassic rocks are observable in several ravines crossing the bank slope and in the quarry near the Prosek site. The main section with visible contact between the Bathonian and Callovian sediments is located immediately below the quarry.

Additional sections are exposed in two ravines crossing the riverbank at a distance of 1.5 km to the north of the main section. Their visible parts are composed of the Bathonian sediments overlying the Upper Permian deposits. Between these sections and the Isady site, Jurassic sediments are unexposed and their last outcrop within the erosion remnant is observable right near this site. Since only the lower Callovian and Upper Jurassic strata are exposed in this section, it is not considered here.

The lower part of the Middle Jurassic succession in the main section is concealed under talus, and described below (from the base upward) is only the upper part of the observable composite section. The upper Bathonian interval studied above the talus spans approximately a half of the stage total thickness.

Upper Bathonian

1. Sand, fine-grained, silty, yellowish gray, obscurely bedded, compact, bioturbated; at the top there is a 2- to 5-mm-thick lamina of ferruginate sand. The apparent thickness is 0.6–0.8 m.

2. Sand, fine-grained, clayey to silty, brownish gray, obscurely bedded, compact, with rounded inclusions of incoherent light gray sand. The bed encloses a horizon of large (up to 0.7 m) concretions of carbonate sandstone (compact in their central part and loose around) and small potato-shaped nodules of phosphatic sandstone. Sandstone concretions frequently contain abundant shells of ammonites *Kepplerites* (*Kepplerites*) *svalbardensis* Sokolov et Bodylevsky (Plate I, figs. 1–3), *K. (K.) rosenkrantzi* Spath (Plate I, fig. 4; Plate II, fig. 1), *Toricellites pauper* (Spath), *Cadoceras* (*Catacadoceras*) *infimum* Gulyaev et Kiselev (Plate III, figs. 3–7), *C. (Bryocadoceras)* *calyx* Spath (Plate III, fig. 1), and *Pseudocadoceras* (*Costacadoceras*) *pisciculus* (Gulyaev) (Plate III, figs. 8–9). The bed upper surface is uneven, undulating. The apparent thickness is 0.8–0.9 m.

3. Sand, fine-grained, clayey to silty, slightly micaceous, ocherous, grayish brown, compact. Closer to the top, the bed contains pocket-shaped inclusions of incoherent sand. Among fossils occurring as slightly ferruginous sand casts, ammonites are rare, represented by taxa of the previous assemblage. Upper boundary of the bed is slightly undulating, marked by a thin lamina of ferruginate sand. The thickness is 1.9 m.

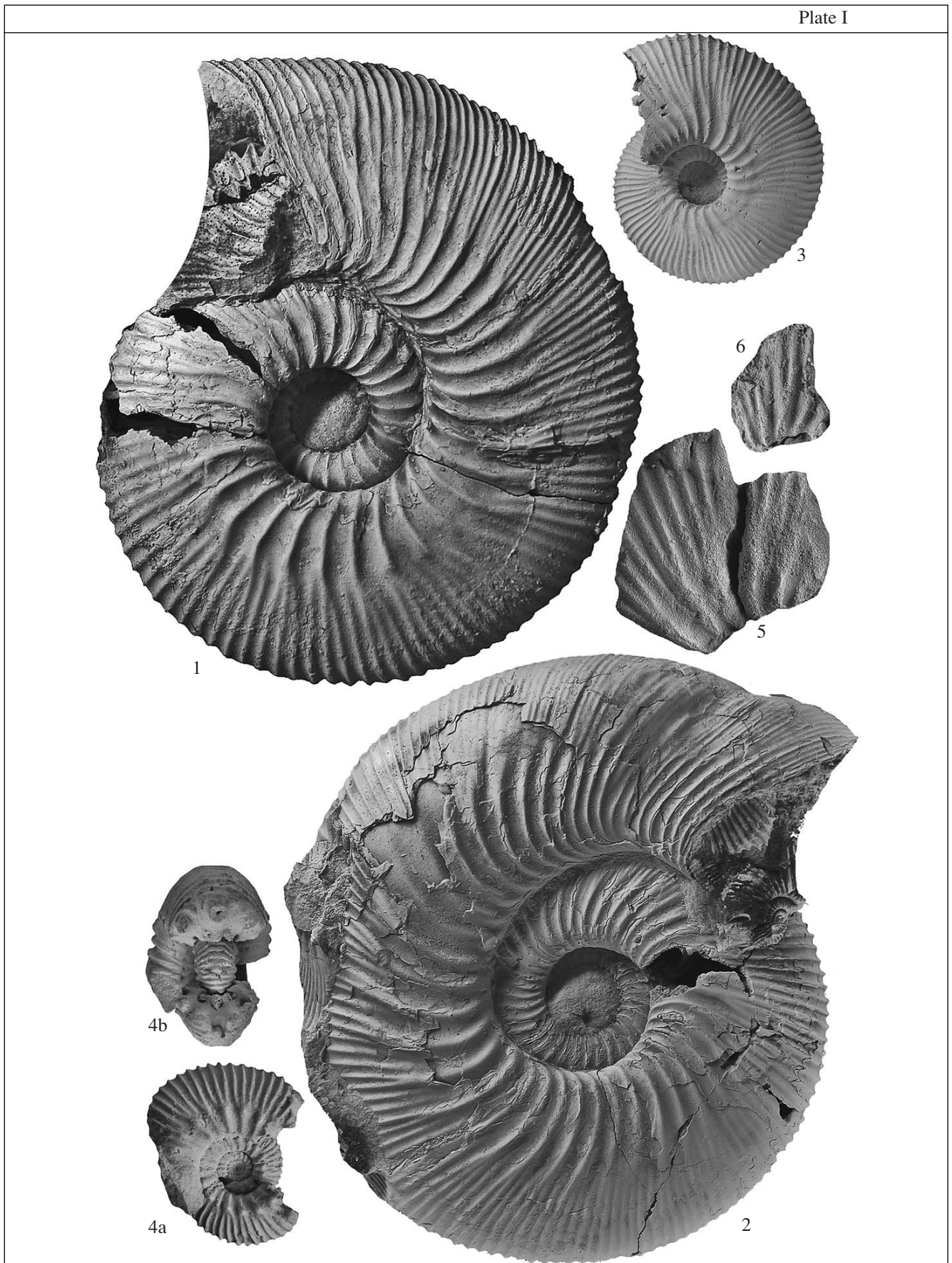
4. Bed similar to the previous one. Its top is marked by a thin lamina of ferruginous sand. The thickness is 0.5 m.

5. Bed similar to the previous one. The ammonite assemblage includes *K. (K.)* ex gr. *keppleri* (Oppel) (cf. *plenus* McLearn) (Plate I, fig. 5), *T. pauper* (Spath), *C. (Paracadoceras)* cf. *bodylevskyi* Frebold (Plate IV, figs. 1, 2), *Ps. (Cos.)* cf. *pisciculus* (Gulyaev) (Plate IV, fig. 7). The thickness is 0.75–0.8 m.

Fig. 2. (A) Upper Bathonian–lower Callovian section near the Prosek Settlement.

(1) Clayey–silty sand; (2) sandy–silty clay; (3) sandstone; (4) marlstone; (5) ichnofossil casts; (6) phosphorite concretions; (7) nest-like sandy “concretions.”

(B) Changes in the taxonomic composition of ammonites in the upper Bathonian (*Elatmae* Zone)–lower Callovian Prosek section (sampling of 2006). (1) Cadoceratinae; (2) Kosmocerotidae; (3) Macrocephalitinae. (N) number of specimens in the selection.



Lower Callovian

6. Clay, sandy to silty, slightly micaceous, dark gray, massive, intensely bioturbated. Ammonites are represented by strongly deformed casts. Their assemblage consists of *C. (P.) cf. breve* Blake (Plate IV, fig. 6), *C. (Cat.) cf. nordenskjoldi* Callomon et Birkelund (Plate IV, fig. 5), *Ps. (Cos.) cf. pisciculus* (Gulyaev), *K. (K.) ex gr. keppleri* (Oppel), *Macrocephalites jacquoti* (Douvillé) (Plate II, figs. 4–6). The thickness is 0.3–0.4 m.

7. Sand, fine-grained, clayey to silty, slightly micaceous, compact, brownish gray to yellowish gray with ocherous limonite patches. The bed with abundant depressed clayey casts of ichnofossils contains rare potato-shaped inclusions of incoherent fine-grained sand. In the upper half, it encloses lenses of sandy clay with abundant sandy casts of ichnofossils. Deformed casts of ammonites belong to *K. (K.) ex gr. keppleri* (Oppel) (Plate I, 6), *C. (P.) cf. frearsi* (Orbigny), *Ps. (Cos.) mundum* (Sasonov), *Ps. (Cos.) aff. mundum* (Sasonov) (Plate IV, fig. 4), *M. jacquoti* (Douvillé) (Plate II, fig. 3). The thickness is 1.2–1.3 m.

8. Clay sandy to silty, slightly micaceous, dark gray, intensely bioturbated, with abundant creamy-gray spots and limonite patches. The ammonite assemblage includes *C. (P.) cf. quenstedti* Spath (Plate IV, figs. 8–10), *Ps. (Cos.) mundum* (Sasonov), *M. jacquoti* (Douvillé) (Plate II, fig. 7). The thickness is 1.9 m.

9. Clay, sandy to silty, creamy-gray, with dark gray spots and limonite patches, massive, containing abundant sand casts of depressed ichnofossils. Ammonites are represented by deformed casts of *Ps. (Cos.) mundum* (Sasonov) and rare *C. (P.) elatmae* (Nikitin) (Plate IV, fig. 11). The thickness is 3.1 m.

10. Sand as in Bed 7, although lacking inclusions. The ammonite assemblage is similar to that from Bed 9. The thickness is 0.9 m.

11. Clay, dark gray, calcareous, homogeneous, massive. The basal part (0.3–0.5 m) encloses a horizon of large oval septate marl concretions (gray in central parts and dark around). Ammonites occurring as deformed casts in clays (Plate IV, fig. 1) are better preserved in concretions. Concretions yielded the most diverse ammonites of the *Elatmae* Zone: *C. (P.) elatmae* (Nikitin) (Plate VI, fig. 2), *C. (Bryocadoceras) simulans* Spath, *Ps. (Cos.) mundum* (Sasonov), *M. verus* Buckman (Plate V, fig. 3), *M. prosekensis* Gulyaev (Plate V, fig. 2), *M. cf. terebratus* (Phillips) (Plate V, fig. 1), *M. zickendrathi* Mitta. The apparent thickness is 1.1 m.

SUBSTANTIATION OF BIOSTRATIGRAPHIC SUBDIVISION

A thorough study showed that the section is of a more complex structure than was previously thought (Gulyaev and Kiselev, 1999a, 1999b; Gulyaev, 2001). It is indivisible clearly into sandy and clayey sequences. All the beds consisting largely of sandy fraction contain

admixture of clayey particles, while clayey beds are enriched in sand grains. The more clayey member (beds 6–11) is composed of alternating clayey and sandy beds, the former becoming thicker upward. There is only a general trend of growing abundance of clay material upward in the section. The examined sedimentary succession corresponds to a transgressive series of sediments deposited most likely during a continuous sedimentation.

Ammonites found throughout the succession (Fig. 2A) facilitate a detailed biostratigraphic subdivision. They represent six successive assemblages of species from the subfamilies Cadoceratinae, Keppleritinae, and Macrocephalitinae. Proportions of these subfamilies in assemblages vary notably in different intervals of the section (Fig. 2B). Only the family Cadoceratinae is distributed throughout the section being represented by successive species of the common phylogenetic lineage *Cadoceras* (*Catacadoceras*)–*C. (Paracadoceras)*. The infrazonal biostratigraphic units are defined based on this lineage. The Keppleritinae and Macrocephalitinae species occur only at separate levels, being indicators of zonal and stage units.

Upper Bathonian

Beds 1–5 that previously united into a uniform sandy bed (Bed 1) are attributed to the upper Bathonian. Their Bathonian age is confirmed by finds of *Cadoceras calyx* in beds 1–4. The *Calyx* Zone defined in East Greenland (Callomon and Birkelund, 1973, in Surlyk et al., 1973) is established in the section owing to occurrence of the index species *Cadoceras (Bryocadoceras) calyx* Spath and associated *Kepplerites (Kepplerites) svalbardensis* Sokolov et Bodylevski, *K. (K.) rosenkrantzi* Spath, and *Toricellites pauper* (Spath). All of these species are characteristic of the *Calyx* Zone in East Greenland (Callomon, 1993).

The main ammonite assemblage includes species from sandstone concretions found in situ. We defined the real position of concretions in the section interval of 3.7–3.9 m below the first occurrence of clay (Bed 6), i.e., is slightly lower than it was assumed in previous works (Gulyaev and Kiselev, 1999a, 1999b) and is close to the interval determined later (Gulyaev, 2001). Concretions are confined to a single level and have yielded the whole assemblage of the *infimum* Biohorizon.

The *Calyx* Zone correspond only to the *infimum* Biohorizon defined earlier (Gulyaev and Kiselev, 1999a, 1999b). The biohorizon corresponds to a largest

Plate I. Bathonian *Kepplerites* from the Prosek section

(1–3) *Kepplerites (Kepplerites) svalbardensis* Sokolov et Bodylevsky: (1) R-form, 33 primary ribs, YarGPU Pr2-7, concretion 2/2, (2) S-form, 43 primary ribs, YarGPU Pr2-5, concretion 2/2, (3) YarGPU Pr2-65, concretion 2/1; (4) *Kepplerites (Kepplerites) rosenkrantzi* Spath, YarGPU 6/1, concretion 2/1: (a) side view, (b) ventral view. All the specimens from upper Bathonian, *Calyx* Zone, *infimum* Biohorizon; (5, 6) *Kepplerites (Kepplerites) ex gr. keppleri* (Oppel): (5) YarGPU Pr5-3. Bed 5, 0.6 m above the base. Upper Bathonian, *bodylevskiy* Biohorizon, (6) YarGPU Pr7-3. Bed 7, 0.8 m above the base. *Elatmae* Zone, *fearsii* Biohorizon



part of the zone, beds 2 and 3 included. Most of *C. infimum* specimens are found in concretions of Bed 2. The matrix of Bed 3 yielded several deformed specimens of ammonites similar to their counterparts from Bed 2. Bed 3 yielded also the deformed cast of specimen with the terminal body chamber (Plate II, fig. 2) figured earlier (Gulyaev and Kiselev, 1999a, 1999b, Plate 2, fig. 6) and erroneously determined by Mitta as *Cadoceras bodylevskiyi* Frebold (this specimen retains primary and secondary ribs up to the terminal aperture edge that is typical of the *Catacadoceras* forms).

Bed 5 contains a peculiar ammonite assemblage represented predominantly by deformed casts of Cadoceratinae macroconchs. We class the *Cadoceras* specimens with *Cadoceras* cf. *bodylevskiyi* Frebold. The latter corresponds to morphotype transitional between *C. (Catacadoceras)*–*C. (Paracadoceras)* being similar to species *C. breve* Blake and *C. apertum* Callomon et Birkelund from the Bathonian–Callovian boundary strata of the Panboreal Superrealm. These species characterize probably the isochronous stratigraphic intervals. *C. apertum* is reliably recorded above the *Calyx* Zone in East Greenland (Callomon, 1985, 1993) and serves as an index form of the *Apertum* Zone with the Bathonian–Callovian boundary inside according to opinion of Callomon. Based on occurrence of *C. cf. bodylevskiyi* in Bed 5, we define the *bodylevskiyi* Biohorizon of the Bathonian age that is substantiated by its position below the first occurrence level of *Macrocephalites jacquoti* and *Kepplerites* ex gr. *keppleri* that marks the base of the Callovian Stage (*jacquoti* Biohorizon). The belonging of the *bodylevskiyi* Biohorizon to the previously defined zone remains unclear, although its index species similar to *C. apertum* suggests its correlation with one of the biohorizons of the *Apertum* Zone.

Lower Callovian

The lower Callovian begins in the section with Bed 6 being largely represented by clayey sediments of the *Elatmae* Zone. Its lower boundary corresponds to the first occurrence level of *Macrocephalites jacquoti* (Douville), the index species of the basal Callovian biohorizon in West Europe (Westermann and Callomon, 1988; Thierry et al., 1997). The *jacquoti* Biohorizon spans in the section three beds, including Bed 6 with most abundant index species. Subordinate ammonites from this bed are Cadoceratinae forms whose macroconchs are similar or identical to *Cadoceras breve*

Blake (= *C. poultoni* Gulyaev), the index species of the defined biohorizon, which belongs to the *C. (Catacadoceras)* – *C. (Paracadoceras)* phyletic lineage. In beds 7 and 8, this species is replaced by *C. (P.) quenstedti* Spath, the next member of this lineage and simultaneously the other index species of the biohorizon. Consequently, the *jacquoti* Biohorizon corresponds to two *Cadoceras* biohorizons.

Bed 6 yielded also an ammonite specimen similar to *C. (Catacadoceras) nordenskoeldi* Callomon et Birkelund, an index species in ammonite zonation of the East Greenland. Its occurrence in the *jacquoti* Biohorizon suggests different correlation of the *Apertum* and *Nordenskoeldi* zones with the West European zonal standard (see below).

The *Kepplerites* forms are rare in beds 6 and 7, being poorly preserved, they are identified with *K. ex gr. keppleri*. Therefore, it would be untimely to define the *keppleri* Biohorizon in the section under consideration.

Beds 9–11 are attributed to the *elatmae* Biohorizon, the most representative ammonites of which are known from concretions of Bed 11. This unit is easily recognizable in the section and corresponds to bioturbated sandy clays with concretions occurring at a single level. Ammonites of the *elatmae* Biohorizon are represented by the classical assemblage of Cadoceratinae and Macrocephalitoiinae described in publications (Gulyaev, 1999, 2001; Mitta, 2000).

DIAGNOSIS OF AMMONITES

The ambiguity of most biostratigraphic scales proposed recently for the Bathonian–Callovian boundary strata of European Russia is a consequence of many reasons. In our opinion, the main problem is taxonomic diagnosis of indicative ammonite species. The competitive schemes of biohorizons proposed by Gulyaev (1999, 2001, 2005) and Mitta (Mitta, 2000, 2005, 2006; Mitta and Starodubtseva, 1998) are based on reconstructed phyletic lineages of three ammonite subfamilies Keppleritinae, Cadoceratinae, and Macrocephalitoiinae. Evolution of these taxa progressed with insignificant quantitative changes in morphological parameters of their shells, which can be determined using statistical approach only. Therefore, identification of close species of a common phyletic lineage based on single specimens is fraught with serious errors. The objective reasons are (a) really negligible morphological distinc-

Plate II. Bathonian–Callovian ammonites from the Prosek section

(1) *Kepplerites (Kepplerites) rosenkrantzi* Spath. YarGPU Pr2-21, concretion 2/2: (a, c) side view, (b) ventral view; (2) *Cadoceras (Catacadoceras) infimum* Gulyaev et Kiselev. YarGPU 6/3, Bed 3. Upper Bathonian, *Calyx* Zone, *infimum* Biohorizon. Reproduced from (Gulyaev and Kiselev, 1999a, Plate 2, fig. 6): (a) side view, the shape is corrected to reduce deformation, (b) view from the left, with the terminal aperture, (c) ventral view; (3–7) *Macrocephalites (Macrocephalites) jacquoti* (Douville), all the specimens from lower Callovian, *Elatmae* Zone: (3) YarGPU Pr7-8. Bed 7, 0.55 m above the base. *frearsi* Biohorizon, (4) YarGPU Pr6-2. Bed 6, 0.25 m above the base. *breve* Biohorizon, (5, 6) YarGPU Pr6-6. Bed 6, 0.23 m above the base. *breve* Biohorizon, (7) YarGPU Pr8-4. Bed 8, 0.75 m above the base. *quenstedti* Biohorizon.

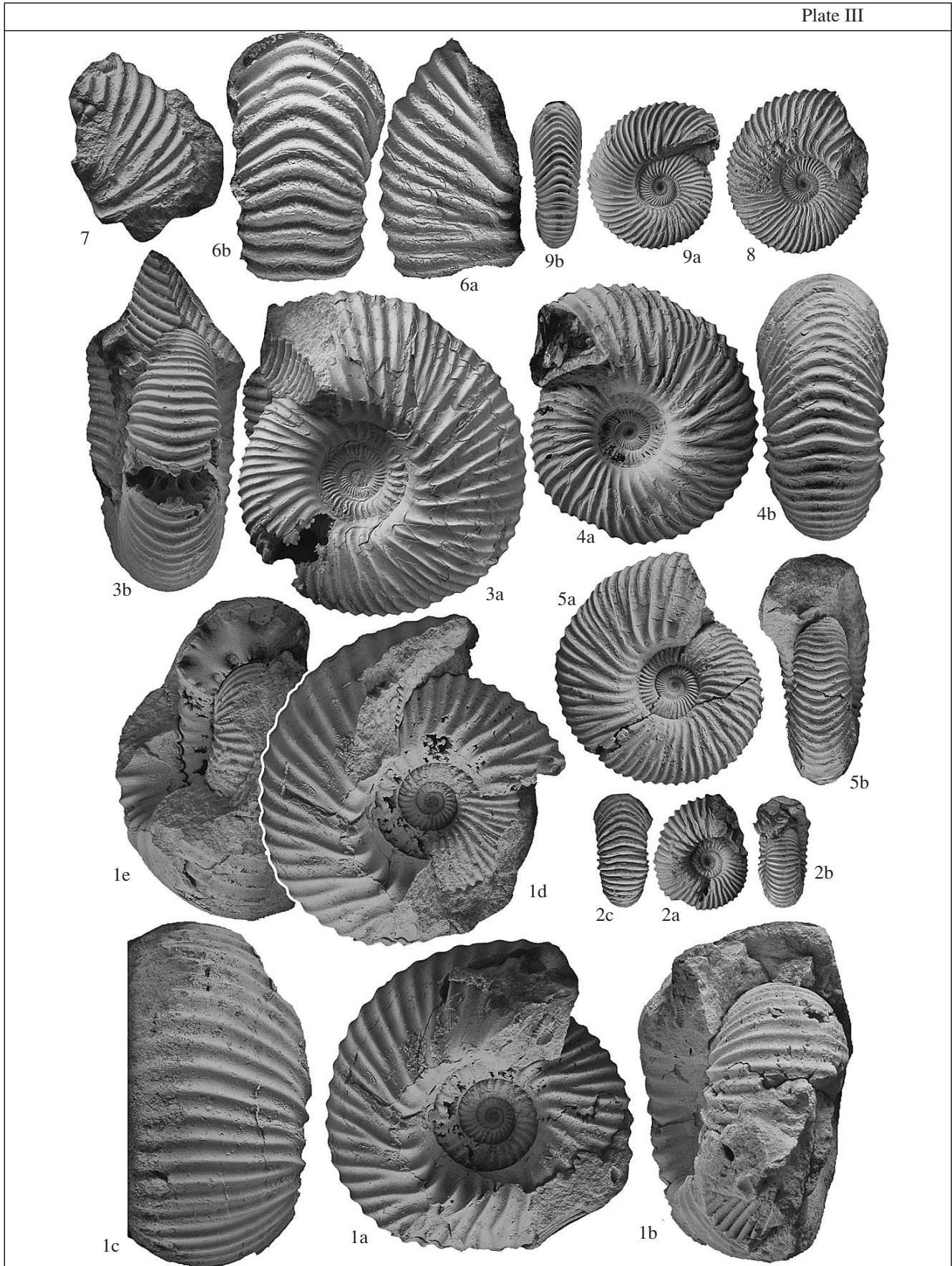


Plate III. Cardioceratidae from the Bathonian *Calyx* Zone (*imfimum* Biohorizon) of the Prosek section

(1, 2) *Cadoceras* (*Bryocadoceras*) *calyx* Spath: (1) YarGPU Pr2-49: (a) side view, (b) apertural view, (c) ventral view, (d) side view with visible internal whorls, (e) ventral view with visible internal whorls; (2) YarGPU Pr2-58: (a) side view, (b) apertural view, (c) ventral view; (3–7) *Cadoceras* (*Catacadoceras*) *imfimum* Gulyaev et Kiselev: (3) YarGPU Pr2-50: (a) side view, (b) apertural view, (4) YarGPU Pr2-52: (a) side view, (b) ventral view, (5) YarGPU Pr2-54: (a) side view, (b) apertural view, (6) YarGPU Pr2-56: (a) side view, (b) ventral view, (7) YarGPU Pr2-57; (8, 9) *Pseudocadoceras* (*Costacadoceras*) *pisciculus* (Gulyaev): (8) YarGPU Pr2-63, (9) YarGPU Pr2-64: (a) side view, (b) ventral view. All the specimens originate from concretion 2/2.

tions of close species, (b) parallelism, and (c) recurrent development of diagnostic features with time periods observable, for example, in genera *Keplerites* (Callomon, 2004) and *Cadoceras*. A objective reason consists in ignoring the phylogenetic trend, when species are identified based on highly variable features.

A confusion in current nomenclature led to an impasse, as researchers proposed sometimes two or more taxonomic names defining the same biostratigraphic unit. The validity of nomenclature can be estimated only after the morphometric analysis of phylogenetic diagnostic features in a whole phyletic lineage.

Keplerites

When determining position of the Bathonian–Callovian boundary based on the *Keplerites* genus, it is important to establish whether the specimen under consideration belongs to *Keplerites kepleri* or not. In this case, inaccuracy in taxonomic determination automatically results in stratigraphic error of a substage rank. As for the Prosek section, debatable here is diagnosis of *Keplerites* from Bed 2. According to the first determination (Gulyaev and Kiselev, 1999a, 1999b), which are accepted in this work, this genus is represented largely by *K. svalbardensis* Sok. et Bodyl. (approximately 150 specimens) and rare *K. rosenkrantzi* Spath (3 specimens). In opinion of Mitta (2000), all the figured specimens are close to *K. kepleri* (Opp.). Mitta determined *K. kepleri* (= *K. svalbardensis* in our opinion) in collection by V.A. Shchirovskii (Mitta and Starodubtseva, 2000, Plate 5, fig. 1). He considers presence of well-developed tubercles at furcation points ribs in adult whorls as a diagnostic feature of this species.

In opinion of Callomon (2004), the main morphological trend in phylogeny of *Keplerites* s. str. corresponds to changes in density of primary ribs on the terminal whorl. Even taking this trend into consideration, it is difficult to individualize close *Keplerites* species because of recurrent development of that morphological character. For example, according to Callomon, the early Callovian *K. tenuifasciculatus* Callomon is morphologically close to the upper Bathonian *Keplerites* forms from the *K. tychonis* Ravn group. Therefore, distinctions of species even having remote phylogenetic positions are “perceptible only by the trained eye” (Callomon, 2004, p. 45).

In order to solve the problems in question, we carried out the morphometric comparison of *Keplerites* specimens from Bed 2 of the Prosek section with well-

known species using such sculptural features as density of primary ribs (pr) in the terminal whorl and rib ratio (RR) or ratio between secondary and primary ribs.²

Correlating data on sculptural features, it is possible to determine the morphological space of the subgenus *Keplerites* s. str., where each species is characterized by its own field. The field size reflects the variability extent of ornamentation and, to some degree, the amount of measured specimens. The most reliable database is obtained for *K. kepleri* (18 specimens, ten of which are topotypes) and *K. svalbardensis* (19 specimens, 14 specimens from the Prosek section and 5 topotypes inclusive). Other specimens represent largely nomenclature types of different species.

The analysis of the *Keplerites* s. str. morphological space leads to the following inferences:

(1) Sculptural features are correlative in a certain manner: the rib density is reversely proportional to the rib ratio. Correlation of this type is generally characteristic of ammonites with fine ornamentation, being observable in different families, Cardioceratidae included (Kiselev, 1999a, 1999b).

(2) Morphological distinctions in sculptural features of species represent a phylogenetic trend, as is noted by Callomon (2004). The Bathonian–initial Callovian, evolution of *Keplerites* species from the *K. tychonis-fasciculatus* group to the *K. kepleri-plenus* group is accompanied by the rib density decrease (Fig. 3). Beginning from the *kepleri* chron, the reversed trend (only in the Arctic basin) resulted in appearance of species *K. ingrahami* sensu Imlay and *K. tenuifasciculatus* with denser arranged ribs (Fig. 4).

(3) The fields of *K. kepleri* and *K. svalbardensis* are located in different areas of the morphological space (Fig. 5) with overlap not exceeding 25%. Greater parts of the *K. kepleri* and *K. svalbardensis* fields are occupied respectively by topotypes from Germany and by specimens from the Prosek section. This means that identification of the latter with *K. kepleri* would be erroneous. The average rib density is 25–27 and 35–40 in *K. kepleri* and *K. svalbardensis*, respectively. Variability of the rib density in both species is relatively high, and *K. svalbardensis* with rare ribs resembles therefore *K. kepleri* or *K. traillensis* with the dense arrangement of ribs. In addition, variability of rib density in *K. svalbardensis* is accompanied by develop-

² Tables with measured data are accessible via Internet at: <http://jurassic.ru/msm.htm>.

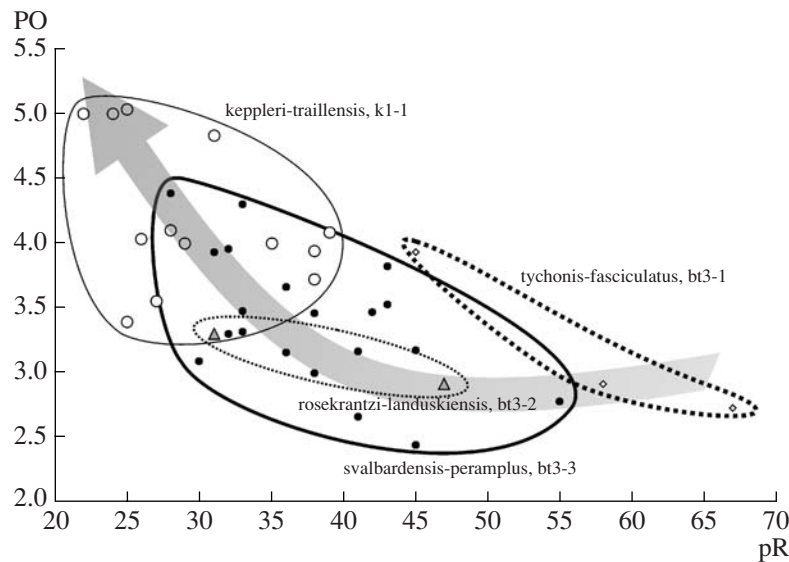


Fig. 3. The distribution of *Kepplerites* species in the morphological space of the terminal body chamber features from the late Bathonian to the initial *Keppleri* chron. The group of coeval species is contoured by line.

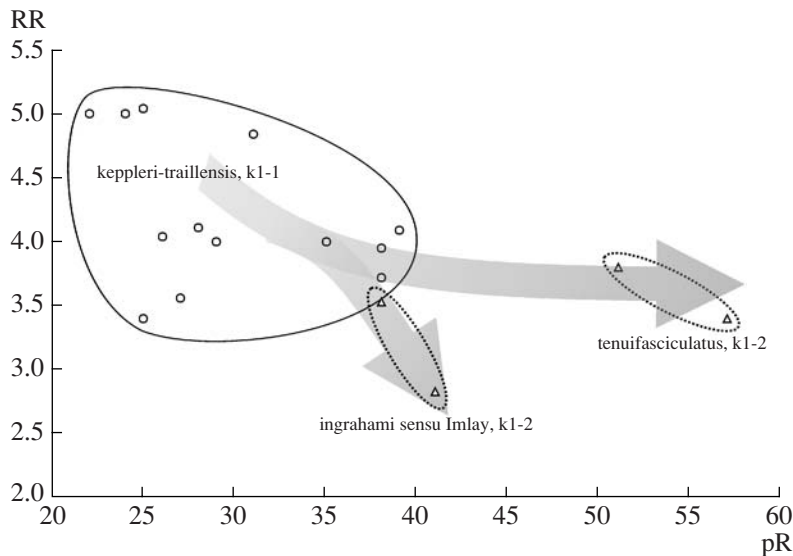


Fig. 4. The distribution of *Kepplerites* species in the morphological space of the terminal body chamber features from the initial to the terminal *Keppleri* chron. The group of coeval species is contoured by line.

ment of tubercles at the rib furcation points, and varieties with rare ribs have coarser ornamentation (Plate I, fig. 1).

An error in identification can also be connected with the development degree of ornamentation on the internal surface of a shell. *Kepplerites* species are commonly divisible in two relatively discrete varieties: S-forms with smoothed internal surface of shells well ribbed outside (their casts look smoothed, Plate I, fig. 2) and R-form with the ornamented internal surface (their casts are always ribbed, Plate I, fig. 1). These varieties have been repeatedly determined as species of different Keppleritinae groups, for example as *K. (Gowericeras)*

curtilobus (Buckman) and *K. (G.) crucifer* (Buckman). In the case of *K. svalbardensis*, smoothed forms retain primary ribs on the casts being deprived of ornamentation on the ventral side.

According to combinations of different sculptural features, 16 morphotypes of *K. svalbardensis* are determined (Table 2).

(4) Arctic *Kepplerites* forms close to *K. keppleri* (*K. plenus* McLearn 1927, *K. gitinsi* McLearn 1927, *K. mcevoyi* McLearn 1928, *K. traillensis* Donovan 1953) fall into morphological field of *K. keppleri* but correspond there to extreme varieties of this species with high-density ribs (Fig. 5). These forms should be

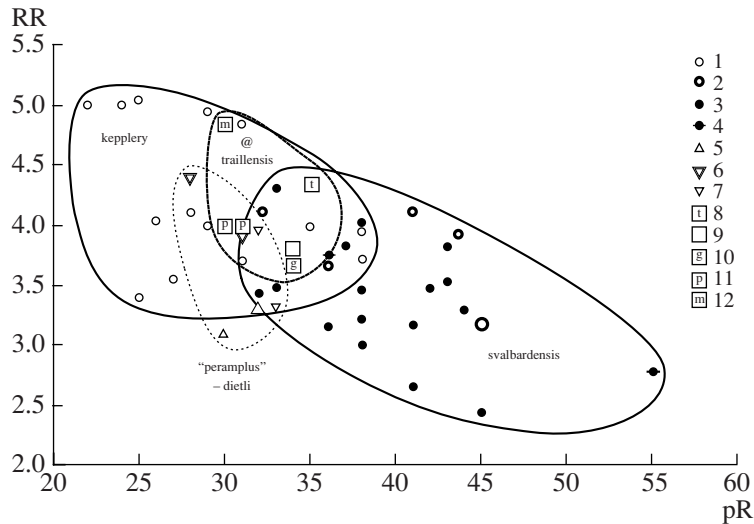


Fig. 5. Morphological areas of the *Kepplerites* species from the upper Bathonian–lower Callovian interval in the morphological space of the terminal body chamber features. The group of coeval species is contoured by a line. Nomenclature types are shown by larger symbols.

- (1) *Kepplerites keppleri*; (2) *K. svalbardensis* (topotypes); (3) *K. svalbardensis* (Prosek); (4) *K. svalbardensis* (Middle Volga region); (5) *K. dietli* (topotypes); (6) *K. peramplus* (topotypes); (7) *K. aff. paramplus* (Middle Volga region); (8) *K. traillensis* (holotype); (9) *K. ex gr. traillensis* (Middle Volga region); (10) *K. ginitzi* (holotype); (11) *K. plenus* (holotype and topotype); (12) *K. mcevoyi* (topotype).

considered as subspecies of *K. keppleri* not identified completely with this taxon as it has been done by Calomon (2001). Among them, *K. plenus* is of senior priority and the given form (species or subspecies) should be identified under this name.

Cadoceras

There is no uniform viewpoint on taxonomic affinity of macroconchiate Cadoceratinae forms occurring in the Bathonian–Callovian boundary strata below the *elatmae* Biohorizon. In competitive scales proposed by Gulyaev and Mitta for the Bathonian–lower Callovian of European Russia, this interval is subdivided based on practically identical succession of *Cadoceras* species

and the same type specimens, which are differently named in each scale (Tables, 1, 3).

Gulyaev and Mitta differently understand not only species, but also higher taxonomic groups of the genus and subgenus ranks. This concerns primarily genera *Paracadoceras* Crickmay and *Catacadoceras* Bodylevsky.

Such a difference in understanding of the *Cadoceras* taxonomy is explainable by objective reasons, not only by subjectivism that is unavoidable by identification. Difficulties in diagnosis of the Bathonian–Callovian Cadoceratinae are connected, in our opinion, with uncertain morphology of their shells by transition from *Catacadoceras* to *Paracadoceras*. Transitional species have features of both the ancestral (plesiomorphic) and

Table 2. Affiliation of figured *K. svalbardensis* specimens with different variability forms

		With rare ribs (32–34)	With relatively rare ribs (35–42)	With frequent ribs (43–50)	With very frequent ribs (>50)
Tubercles are undeveloped	S form		Mitta and Starodubtseva, 2000, Plate 3, fig. 1	Pr2-5; A/30	Mitta, 2004b, Plate 1, fig. 1
	R form	6/4	2/675	Holotype; Pr2-13	
Tubercles are slightly developed	S form	Pr2-3; Mitta, 2004b, Plate 2, fig. 1			
	R form	Pr2-7; ?Mitta, 2004b, Plate 2, fig. 2	Pr-2-10; Kopik and Wierzbowski, 1988, Plate 20, fig. 2; Plate 21, fig. 2		

Table 3. Revision of *Cadoceras* from the Bathonian–Callovian interval figured by D.B. Gulyaev and V.V. Mitta

Nomenclature type of <i>Cadoceras</i> species	Identification		
	Gulyaev, 2001, 2005	Mitta, 2000, 2005a	This work
<i>C. (Cat.) infimum</i> Gulyaev et Kiselev: Gulyaev and Kiselev, 1999a, Plate 1, fig. 1, 2 (holotype)	<i>Par. infimum</i> Gulyaev et Kiselev	<i>C. bodylevskiyi</i> Frebold	<i>C. (Cat.) infimum</i> Gulyaev et Kiselev
<i>C. bodylevskiyi</i> Frebold: Frebold, 1964, Plate 17, fig. 1 (holotype)		<i>C. bodylevskiyi</i> Frebold	
<i>C. bodylevskiyi</i> Frebold: Poulton 1987, Plate 27, figs. 4–6	<i>Par. poultoni</i> Gulyaev	<i>C. bodylevskiyi</i> Frebold	<i>C. breve</i> Blake
<i>C. variabile</i> Spath: Meledina, 1994, Plate 8, fig. 1	<i>Par. poultoni</i> Gulyaev	? <i>Par. keuppi</i> Mitta	<i>C. breve</i> Blake
<i>C. frearsi</i> (Orbigny): Sazonov, 1957, Plate 4, fig. 1 (neotype)	<i>Par. primaevum</i> (Sazonov)	<i>C. frearsi</i> (Orbigny)	
<i>C. primaevum</i> (Sazonov): Sazonov, 1957, Plate 6, fig. 1 (holotype)	<i>Par. primaevum</i> (Sazonov)	<i>C. frearsi</i> (Orbigny)	
<i>C. (Par.) anabarensis</i> Bodylevsky: Bodylevsky, 1960, Plate 4, fig. 3 (holotype)	<i>Par. elatmae</i> anabarensis (Bodyl.)		<i>C. (Par.) anabarensis</i> Bodyl.

descendant (apomorphic) taxa. Therefore, it is difficult to attribute species of such morphotype to a certain taxon. Accordingly, when identifying fossils, each author uses features most important from his standpoint,

In order to solve the problem, one should determine principal morphological features that characterize the phylogenetic trend of a taxon. Like in most ammonites, these features in *Cadoceras* representatives are localized on the terminal body chamber (TBC). Main distinctive features of *Cadoceras* forms from the Bathonian–Callovian transition are the relative size of umbilicus (U%) and number of primary ribs. The latter are preserved on the TBC as oblique tubercles (bullae) representing frequently the only sculptural elements. Correlation of both features that form the morphological space can be used to evaluate morphological distinction between *Cadoceras* species. Only specimens with the TBS have been measured.

Analysis of the morphological space of Bathonian–early Callovian *Cadoceras* species shows the following:

(1) There is a distinct morphological trend in changes of the umbilicus width and rib density on the TBS of *Cadoceras* shells from the Bathonian–Callovian transition. Both features are well correlative ($R^2 = 0.7815$), thus being of a high diagnostic potential. Based on this inference, individualism of species described in publications can be tested. For example, it is clearly seen (Fig. 6) that type specimens of *C. poultoni* (Gulyaev, 2005) correspond, in terms of morphology, to specimens of *C. tchegemicum* Lominadze 2004. Accordingly, the former species represents a junior synonym of the latter. Similarly, the results prove that *C. bodylevskiyi* Frebold 1964 differs from *C. tche-*

gemicum and *C. poultoni* (= *C. bodylevskiyi* sensu Poulton, 1987; Mitta, 2000).

(2) The *Cadoceras* morphotype evolved from involute (*bodylevskiyi* chron) to moderately evolute (*elatmae* chron) forms. The Early Callovian species *C. apertum* and *C. frearsi* are of a close morphotype. They are probably vicarious species in the Arctic basin and Central Russian sea.

(3) During the late Bathonian–early Callovian, evolution of *Cadoceras* was of a recurrent character. The evolute morphotype with high rib density (UR) and involute morphotype with rare ribs (ur) originated repeatedly (Fig. 7). The UR-morphotype characteristic of the earliest late Bathonian species *C. barnstoni*, *C. subcatostoma*, *C. keuppi*, *C. nageli*, and *C. infimum* was replaced by the ur-morphotype of *C. bodylevskiyi* and *C. breve*. The intermediate ur/UR morphotype is characteristic of *C. apertum* and *C. frearsi*. The UR-morphotype appears again in species *C. quenstedti* and *C. elatmae* during the *elatmae* chron. The *subpartus* chron is marked by next development of the ur-morphotype (*Cadochamoussetia tchernyschewi*, *Cadoch. surensis*, and other species), which gave rise to appearance of *Chamoussetia*. In the terminal early (*Koengi* chron) and middle Callovian, phylogenesis was characterized by the other morphological changes.

(4) It is logical to consider diagnosis of the *Cadoceras* from the standpoint of phylogenetic trend assuming that its reversals define morphological limits of subgenera (Fig. 7). The genus *Cadochamoussetia* Mitta 1996 was defined (Mitta, 1999) using such a principle, i.e., the appearance of ur-morphotypes in the *Subpartus* chron. Meanwhile, two preceding reversals of trend are not reflected in taxonomy. In recent works by Gulyaev (2005) and Mitta (2005a, 2005b), late

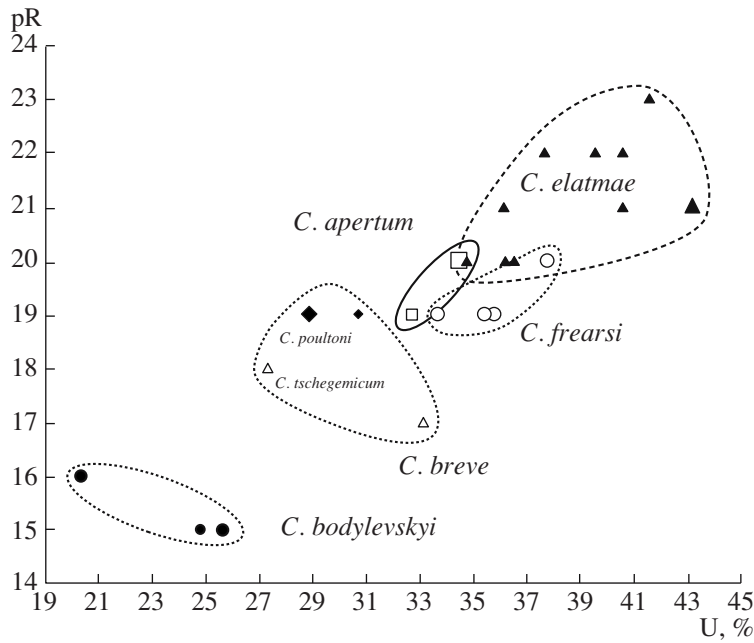


Fig. 6. Correlation between the umbilicus width (U%) and number of primary ribs (pR) in the terminal body chamber of *Cadoceras* from the Bathonian–Callovian boundary interval. Larger symbols designate nomenclature types of species.

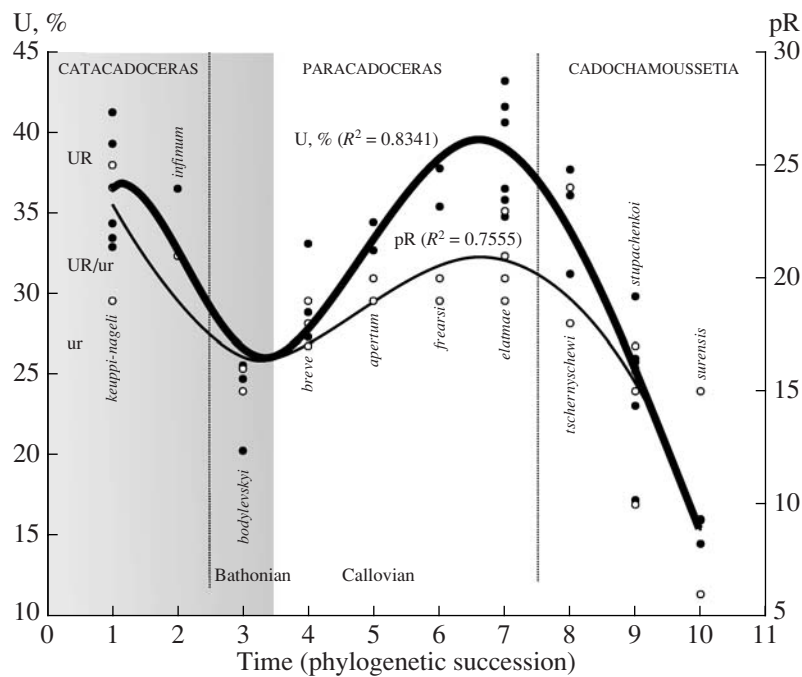


Fig. 7. Evolution of terminal body chamber features in macroconchiate Cadoceratinae during the late Bathonian–early Callovian. The thick line shows the trend in development of the umbilicus width (U%), thin line demonstrates that of the ornamentation density (pR). (UR) evolute morphotype with dense rib arrangement; (ur) involute morphotype with rare ribs; (UR/ur) transitional morphotype.

Bathonian species of the UR-morphotype, having ribs covering the TBC are referred to the genus *Paracadoceras* Crickmay 1930 emend Imlay 1953. This seems unsubstantiated properly the more so that the name *Catacadoceras* Bodylevsky 1960 emend

Meledina 1977 was already proposed for these forms. The genus *Paracadoceras* includes younger species, development of which begins with the ur-morphotype (*C. bodylevskyi*) and terminates with the UR-morphotype (*C. elatmae*).

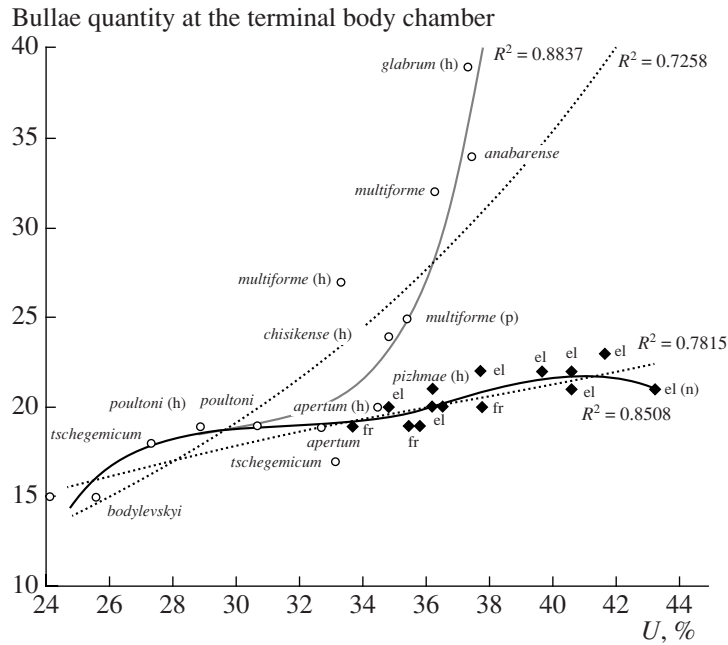


Fig. 8. Correlation trends showing changes in terminal body chamber features of Cadoceratinae from Central Russia (solid line) and the Arctic region (gray line). Dashed line demonstrates corresponding lines of the exponential dependence. (fr.) *Cadoceras fearsi*; (el) *C. elatmae*; (h) holotype; (n) neotype.

(5) Younger *C. (Paracadoceras)* species from Arctic regions and Central Russia characterize own (*Paracadoceras*) morphotype (TBC of the UR-type with smooth ventral and lateral sides). Phylogeny of North Siberian and South Alaskan species *C. anabarense* Bodylevsky 1960, *C. glabrum* Imlay 1953, and *C. multiforme* Imlay 1953 evolve in line with the phylogenetic trend of Central Russian forms, i.e., from the ur- to UR-morphotypes. At the same time, they deviate near the *C. apertum* field toward the involute morphotype with higher quantity of bullae on the TBC, as compared with the *C. elatmae*. This happened likely after the *apertum* chron (Fig. 8).

C. anabarense and *C. elatmae* are stratigraphic and morphological analogues of *C. elatmae*. Both of them represent index species of equivalent zonal units in North Siberia and European Russia. Gulayev (2005) suggests that *C. anabarense* is an older subspecies of

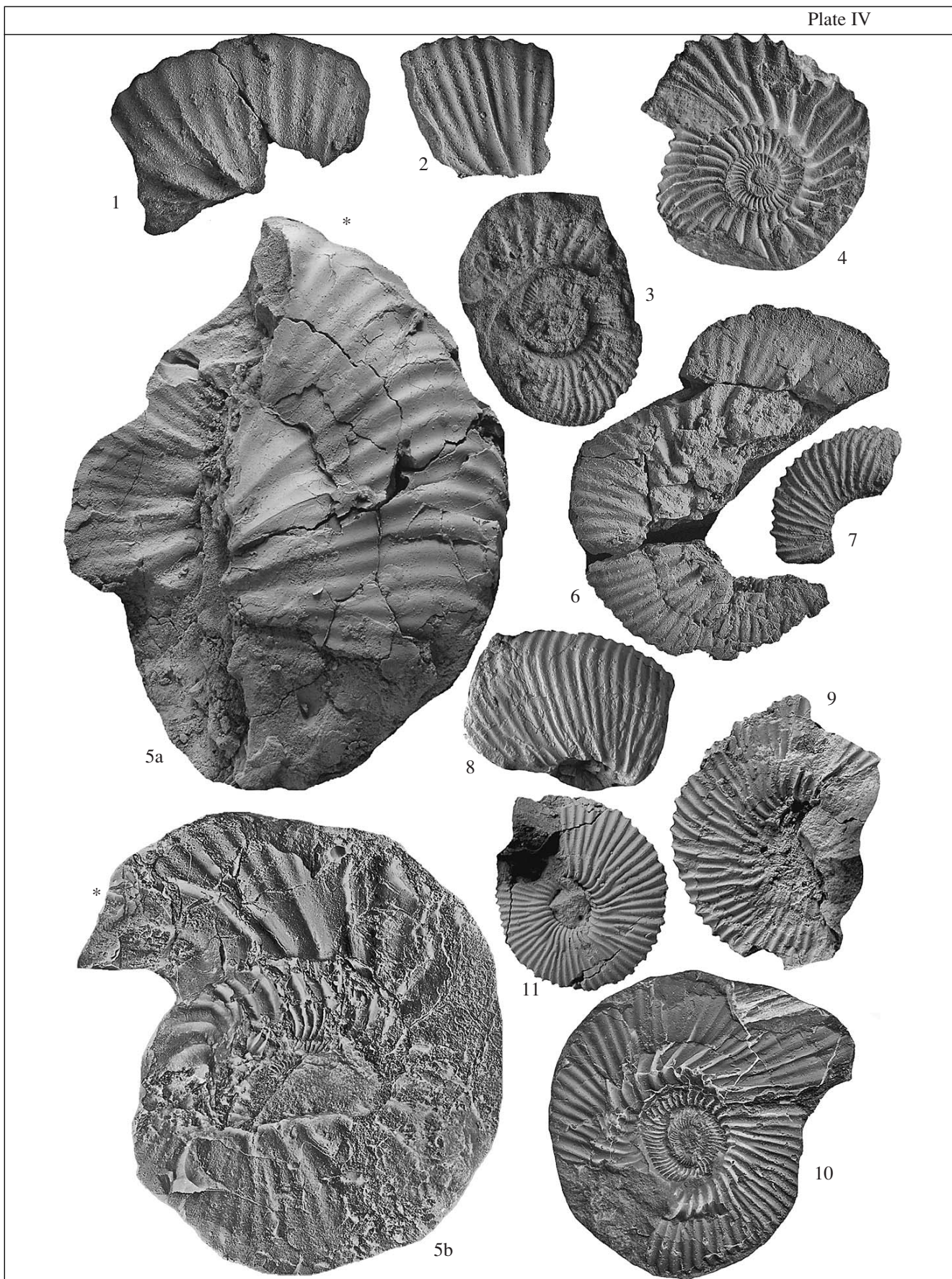
C. elatmae. In his opinion, the main feature of the former that differs it from the latter is later appearance of smooth shell in ontogenesis. Accordingly, *C. anabarense* is of a more archaic morphotype. Meanwhile, amount of tubercles in *C. anabarense* is 1.5 times greater than in *C. elatmae*. Therefore, in terms of the phylogenetic trend, the TBC of *C. anabarense* is of a more advanced morphotype.

The number of bullae on the TBC of *C. anabarense* corresponds to that of primary ribs on *C. elatmae* shells 20–45 mm across, and its umbilicus is 70–75 mm in diameter. This likely means that the *C. anabarense* morphotype (as well as *C. glabrum* and *C. multiforme*) could appear owing to bradygenesis (retardation in development) of *C. (Paracadoceras)* species, which were at the point of phylogenetic trend close to that of *C. elatmae*. *C. chisikense* Imlay that was at the same

Plate IV. Cardioceratidae from the Bathonian–Callovian boundary sediments of the Prosek section

(1, 2) *Cadoceras (Paracadoceras)* cf. *bodylevskiyi* Frebold: (1) YarGPU Pr5-2. Bed 5, 0.4 m above the base, (2) YarGPU Pr5-5. Bed 5, 0.55 m above the base. Upper Bathonian, *bodylevskiyi* Biohorizon; (3) *Cadoceras (Catacadoceras)* *inifumum* Gulyaev et Kiselev: YarGPU Pr4-2. Bed 4, 0.15 m above the base. Upper Bathonian, *Calix* Zone, *inifumum* Biohorizon; (4) *Pseudocadoceras (Costacadoceras)* aff. *mundum* (Sasonov): YarGPU Pr7-6. Bed 7, 1.2 m above the base. *Elatmae* Zone, *fearsi* Biohorizon; (5) *Cadoceras (Catacadoceras)* cf. *nordenskoeldi* Callomon et Birkelund: YarGPU Pr6-3. Specimen with the terminal aperture (half destroyed) and constriction shown by asterisk: (a) deformed cast with an impression fragment, (b) impression (tone of the image is inverted). Bed 6, 0.05 m above that base. *Elatmae* Zone, *Breve* Biohorizon; (6) *Cadoceras (Paracadoceras)* cf. *breve* Blake: YarGPU Pr6-1. Bed 6, 0.25 m above the base. *Elatmae* Zone, *breve* Biohorizon; (7) *Pseudocadoceras (Costacadoceras)* cf. *pisciculus* (Gulyaev): YarGPU Pr6-1. Bed 5, 0.3 m above the base. *Elatmae* Zone, *bodylevskiyi* Biohorizon; (8–10) *Cadoceras (Paracadoceras)* cf. *quenstedti* Spath: (8) YarGPU Pr8-10. Bed 8, 0.83 m above the base, (9) YarGPU Pr8-7. Bed 8, 0.02 m above the base, (10) YarGPU Pr8-6. Bed 8, 0.32 m above the base. All the specimens from the *Elatmae* Zone, *quenstedti* Biohorizon; (11) *Cadoceras (Paracadoceras)* *elatmae* (Nikitin): YarGPU Pr9-1. Bed 9, 2.6 m above the base. *Elatmae* Zone, *elatmae* Biohorizon.

Plate IV



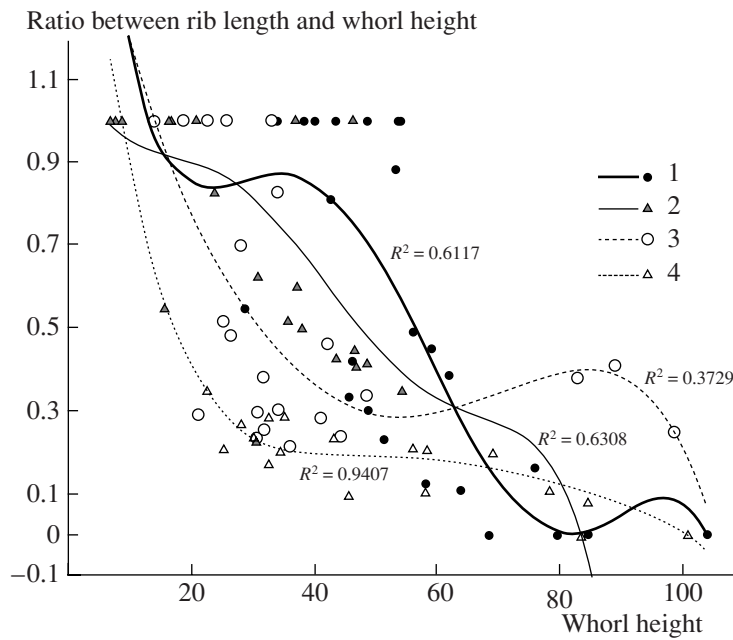


Fig. 9. Changes in the ornamentation reduction degree in Bathonian–Callovian *Macrocephalites* species belonging to the *M. triangularis*–*M. pavlowi* lineage.

(1) *M. triangularis*; (2) *M. jacquoti*; (3) *M. prosekense*; (4) *M. pavlowi*.

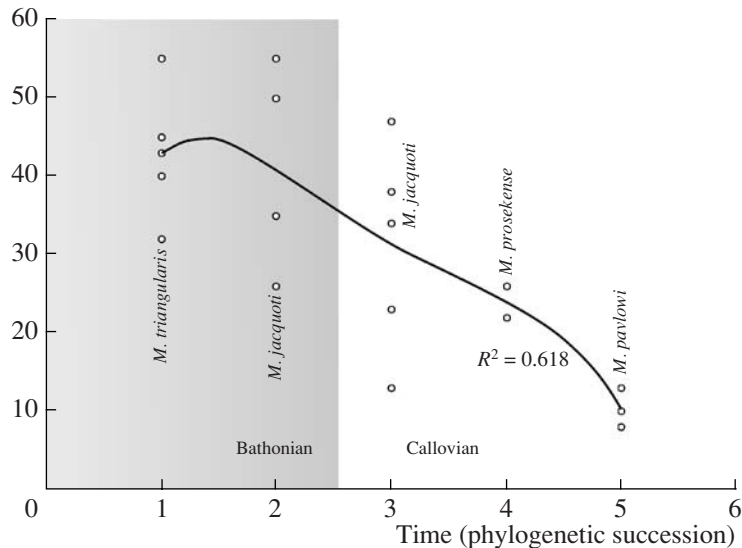


Fig. 10. Gradual reduction of the stage with the ornamented periumbilical segment of the shell in *Macrocephalites* species belonging to the *M. triangularis*–*M. pavlowi* lineage. Age is shown along the abscissa (numerals designate evolutionary stages from *M. triangularis* to *M. pavlowi*).

point can be considered as a true ancestor of *C. anabarsense*.

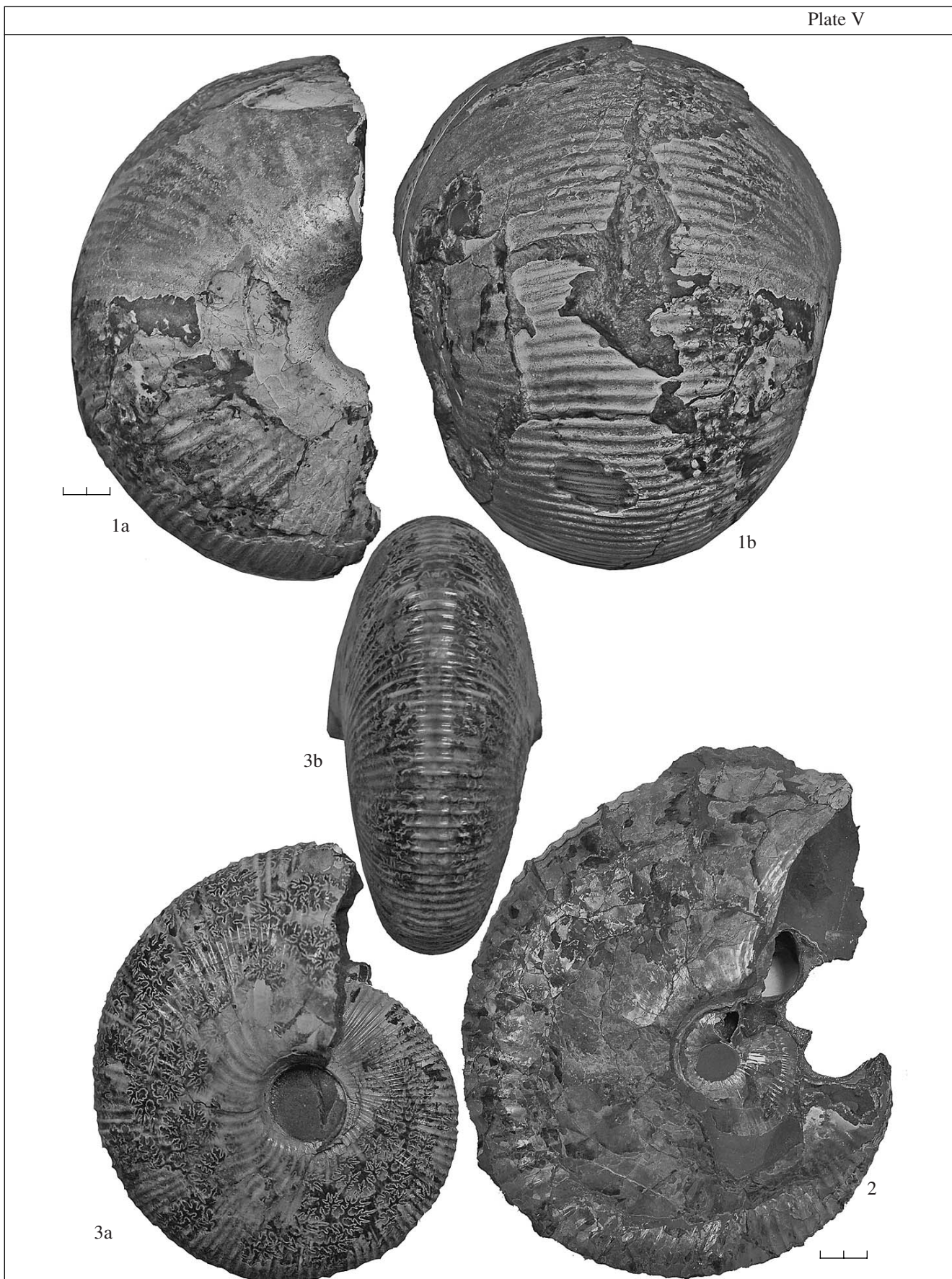
Thus, beginning from the *C. frearsi* chron, younger *C. (Paracadoceras)* forms from the Central Russian sea

represent largely the autonomous Cadoceratinae group distributed from West Europe (Germany) to the northern Caucasus. Its appearance was probably caused by expansion of the Central Russian sea during the early

Plate V. *Macrocephalites* from Bed 11 (concretions from the *elatmae* Biohorizon of the *Elatmae* Zone) of the lower Callovian Prosek section. Figures 1 and 2 are diminished (bar is 1 cm)

(1) *Macrocephalites (Pleurocephalites)* cf. *terebratus* (Phillips): NGPU-1: (a) side view, (b) ventral view; (2) *Macrocephalites (Macrocephalites) prosekensis* Gulyaev: NGPU-2; (3) *Macrocephalites (Macrocephalites) versus* Buckman: NGPU-3: (a) side view, (b) ventral view.

Plate V



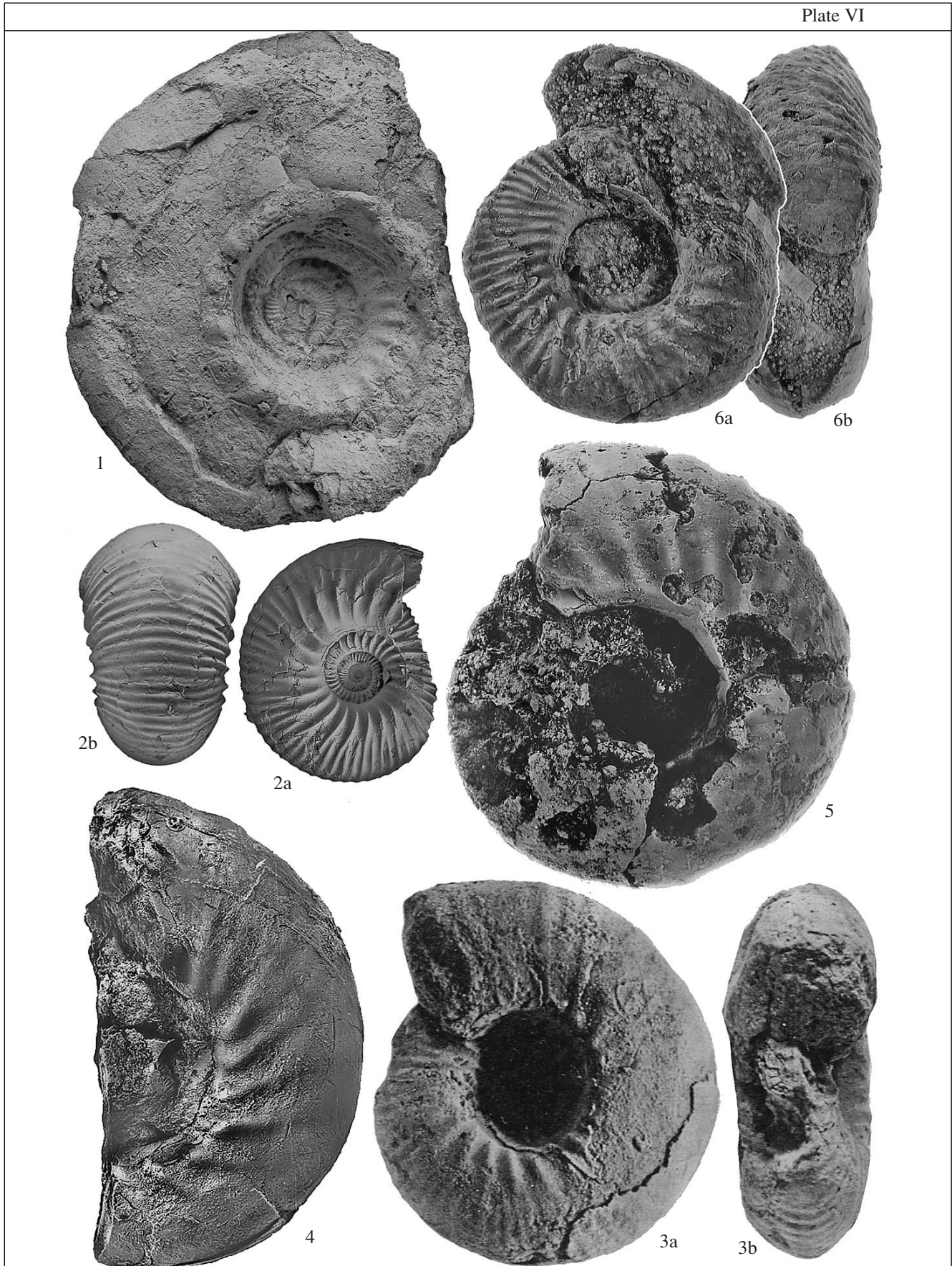


Table 4. Infracal stratigraphy of the Bathonian–lower Callovian sediments in European Russia

		Gulyaev and Kiselev, 1999a, 1999b; Gulyaev, 2001, 2005		Mitta, 2000, 2004a, 2004b, 2005a, 2005b, 2006		This work				
L.C.	Elatmae	<i>Paracadoceras elatmae elatmae</i>		Lower Callovian	Elatmae	<i>Cadoceras elatmae</i>				
		<i>Paracadoceras elatmae anabarensis</i>				<i>Cadoceras falsum</i>				
		<i>Macrocephalites jacquoti</i>	<i>Paracadoceras primaevum</i>			<i>Keplerites keplerii/Cadoceras frearsi</i>	<i>C. frearsi</i>			
			<i>Paracadoceras poultoni</i>				<i>C. breve</i>			
Upper Bathonian	Infimum	<i>Paracadoceras</i> “ <i>infimum</i> subsp. nov.”		Upper Bathonian	Keuppi	<i>K. trail-lensis</i>	<i>C. bodylevskiyi</i>			
							<i>C. nordenskjöldi</i>	<i>C. bodylevskiyi</i>		
		<i>Paracadoceras infimum infimum</i>				Unnamed		Hiatus?		<i>C. infimum</i>
								<i>Cadoceras apertum</i>		
								<i>Keplerites vardekloeftensis</i>		
								<i>Keplerites aff. peramplus</i>		
		<i>Paracadoceras keuppi</i>		<i>?C. keuppi</i>						
		<i>Paracadoceras nageli</i>		<i>C. nageli</i>						

Note: In Tables 4 and 5, boundary between the Bathonian and Callovian stages is shown by triple line; boundaries between biohorizons are shown by double line and between zones and subzones, by simple line; (L.C.) lower Callovian.

Callovian transgression maximum. Development of *C. (Paracadoceras)* lineages in Arctic regions and Central Russia presumably was concurrent and independent. Phylogenetic transformation of the TBC in two lineages was different: ammonites of Central Russia evolved in line with the gerontogenesis (de Beer, 1958) or prolongation of ontogenesis, whereas development of Arctic taxa corresponded to bradygenesis (a variety of paedogenesis after Ivanov, 1969) avoiding last ontogenetic stages. Evolution of the second type led to origin of morphotypes combining plesiomorphic and apomorphic features. The last type of evolution characteristic of the Arctic Cadoceratinae up to the middle Callovian.

Macrocephalites

Representatives of this genus from the basal Callovian zone are the only ones of the Tethyan origin and offer opportunity for remote correlation up to Madagascar and Indonesia. At the same time, frequent parallelism, wide variation spectrum, low rate of morphologi-

cal changes in many lineages (Callomon and Dietl, 1990), and, as a result, wide stratigraphic ranges of some species diminish their stratigraphic significance. It became clear recently that some *Macrocephalites* species considered previously as reliable stratigraphic markers are of wide stratigraphic ranges, for instance, the Indian–Madagascar forms such as *M. triangularis*, *M. madagascariensis*, and *M. formosus* (see Westermann and Callomon, 1988; Datta et al., 1996; Jain, 2007). Diagnosis of *Macrocephalites* forms meets additional difficulties because of different specialization ways of these ammonites. For example, the main trend in evolution of this group toward more flattened cross-section (Lominadze, 1967) was probably accompanied by development of lineages terminating with morphotypes having low cross-sections. As Callomon et al. (1992, p. 20) noted, “The easily apprehensible characters of whorl-inflation, size, strength of ribbing and density of ribbing seemed to occur in all combinations.”

It seems that evolution of the genus *Macrocephalites* progressed without significant morphological

Plate VI. Lower Callovian *Cadoceras*

(1, 2) *Cadoceras (Paracadoceras) elatmae* (Nikitin): (1) YarGPU Pr1-12. Bed 11, 0.95 m above the base, (2) YarGPU Pr1-14. Bed 11, from concretions: (a) side view, (b) ventral view. All the specimens are from the *Elatmae* Zone, *elatmae* Biohorizon; (3–6) *Cadoceras (Paracadoceras) breve* Blake: (3) Holotype BM C11763 (cast of the original; the image is kindly donated by K. Page). England, Dorset, near Weymouth, East Fleet. Lower Callovian, Fleet Member: (a) side view, (b) apertural view; (4) Sample 1158, collection by T.A. Lominadze (=holotype of *Cadoceras tschegemicum* Lominadze). North Caucasus, Chegem River. Bed 3, lower Callovian (after Lominadze, 1982, p. 228); (5) Sample 12/1528, collection by D.B. Gulyaev. Chuvashia Republic, Khvadukasy Village. Lower Callovian, *Elatmae* Zone; (6) Sample 8/1353, collection by D.B. Gulyaev. Komi Republic, Pizhma River, Churkino Village. Churkinskaya Shchel'ya section, Bed 3 (after Gulyaev, 2005), lower Callovian, *Elatmae* Zone, *breve* Biohorizon: (a) side view, (b) apertural view.

Table 5. Correlation of Bathonian–Callovian infrazonal scales of Europaen Russia, Germany, and East Greenland. Correlation of the largest part of the *Elatmae* Zones with the *Apertum* Zone is based on phylogenetic analogues

East Greenland ¹			European Russia				West Europe (Germany) ²				
Lower Callovian	Apertum	cf./aff. <i>breve</i>	Lower Callovian	<i>Elatmae</i>	<i>Elatmae</i>		<i>suevicum</i> α, β		<i>Keppleri</i>	<i>Herveyi</i>	Lower Callovian
		<i>tenuifasciculatus</i>			<i>jacquoti</i>	<i>quenstedti</i>		<i>jacquoti</i>			
		<i>apertum</i> γ				<i>frearsi</i>	<i>kepleri</i>				
		<i>apertum</i> β				<i>breve</i>					
Upper Bathonian	Calyx	<i>apertum</i> α	Upper Bathonian	Unnamed	<i>bodylevskyi</i>	By position	<i>Discus</i>	<i>Discus</i>	Upper Bathonian		
		<i>vardekloeftensis</i>		Calyx	<i>Infimum</i>		<i>Hannoveranus</i>				
	<i>peramplius</i>	<i>Keuppi</i>			<i>keuppi</i>	By position	<i>Blanasense</i>				
	<i>rosenkrantzi</i>			<i>nageli</i>							
	Variable			<i>inflatus</i>							

¹ Callomon, 1993.

² Dietl, 1994; Callomon and Dietl, 1990, 2000; Callomon et al., 1989.

changes during the Bathonian–Callovian transitional period. At any rate, all the species known from the uppermost Bathonian (*M. triangularis*, *M. madagascariensis*, *M. lamellosus*, *M. formosus*, and *M. subcompressus* in India, Indonesia, and Madagascar; *M. jacquoti* in West Europe) occur also at the base of the Callovian Stage. Despite this fact, even insignificant morphological changes should be taken into account in order to substantiate boundaries of biostratigraphic units based on well-manifested morphological trend in numerous specimens (see below).

Macrocephalites species from the Russian platform are interpreted in different works less controversially significant than in the genera considered above. Of prime importance for our purpose is the phyletic lineage *M. jacquoti* (Plate II, figs. 3–7)–*M. prosekense* (Plate V, fig. 2)–*M. pavlowi* and finds of *M. verus* and *M. terebratus*. Gulyaev (1999) was first to outline this phyletic lineage connecting *M. ex gr. jacquoti* (= *M. prosekense*) and *M. pavlowi*. Owing to subsequent finds of abundant *M. jacquoti* at the base of the *Elatmae* Zone (Gulyaev, 2001), the lineage acquired accomplished form with distinct morphological trend of progressively earlier disappearance of primary ribs and gradual narrowing of the ventral side. Other sculptural features, a high rib ratio in internal whorls inclusive, remain unchanged in this group of species (Plate II, figs. 3–7; Gulyaev, 1999, Plate 1, figs. 1, 4). Later on, Gulyaev (2005) added *M. cf./aff. jacquoti* characteristic of the “*elatmae anabarensis*” (here = *quenstedti*) Biohorizon and placed it between *M. jacquoti* and *M. prosekense*. In our collection, similar forms are either missing or cannot be discriminated from *M. jacquoti*. We do not exclude that these ammonites are close to forms that combine features of *M. jacquoti* and

M. verus known from the same stratigraphic level in southern Germany (Callomon and Dietl, 1990). Mitta defined the genus *Eckhardites* Mitta, 1999, with the type species *Macrocephalites pavlowi* referred to the subfamily Arctocephalitinae. He also attributed to the new genus the close or identical species *Chamoussetia menzeli* described from approximately the same stratigraphic level (Mönnig, 1995). Presenting extended description of the genus a year later, Mitta (2000, p. 34) noted some similarity between *Eckhardites* and *Macrocephalites jacquoti*: “...morphogenesis of ornamentation in representatives of this genus is fairly typical of Cardioceratidae being unknown in Macrocephalitinae (development of ‘ventral’ ribs along with general smoothing of ornamentation is repeatedly observable in the Cardioceratidae phylogeny).” Nagel and Pirkl (2001, pp. 294–295) presented almost the same diagnosis in their article. However, the ornamentation smoothing around umbilical part of the shell is characteristic of most Stephanocerataceae similar in morphotype to “*Eckhardites*.” The same feature is widespread in *Macrocephalites* forms. Disappearance of ornamentation in lower part of the lateral surface is already typical of many Bathonian species at different stages of their ontogeny: near the TBC (*M. madagascariensis*, *M. triangularis*, see Thierry, 1978, Plate 18, fig. 1; Krishna and Westermann, 1987, Plate 1; Westermann and Callomon, 1988, Plate 15, fig. 3; Datta et al., 1996, Plate 1; and others) or in phragmocone (*M. mantataranus*, see Thierry, 1978, Plate 24, fig. 5; Westermann and Callomon, 1988, Plate 10, figs. 1–5). Many Callovian species with high oval whorl sections, the forms with relatively wide whorls such as *M. verus* included, are lacking ornamentation in the peri-umbilical area, and in their macroconchs there is a stage, when only ventral

ribs are observable. Proximity between external segments of septal suture in “*Eckhardites*” and *Chamoussetia* (Mönnig, 1995, fig. 19) cannot be an argument favoring attribution of “*Eckhardites*” to a particular family. The matter is that external segments of septal suture in different Stephanocerataceae are very similar in form, frequently depending on shape of the whorl section rather than on taxonomic affinity (see for comparison septal sutures in *Kosmoceras* (*Catasigaloceras*) and *Macrocephalites tcherekensis* in Lominadze, 1967, fig. 29). On the other hand, even neighboring septal sutures in representatives of the same *Macrocephalites* species may differ significantly from each other. In other words, “... the intraspecific variability of the septal suture in representatives of Macrocephalitidae is so strong that it is difficult to find two specimens with identical septal sutures” (Lominadze, 1967, p. 74). Substantial difficulties in attributing the *pavlowi* species to the Arctocephalitinae subfamily are connected with the significant stratigraphic gap (almost a half of stage) between these taxa.

Unfortunately, almost all the *M. jacquoti* and *M. prosekense* specimens available in our collection are deformed, and published data on changes in whorl section of ammonites of this group during ontogenesis are scarce. Hence, only the reduction degree of peri-umbilical ribs can be used for discriminating between taxa. Although the last feature is also variable and depends, in addition, on preservation of ammonites, it seems to be most useful.

The morphological analysis of the Bathonian–Callovian *Macrocephalites* species with narrow whorl sections in adult stages shows the following:

(1) There is a distinct morphological trend of reducing degree of ornamentation observable from *M. jacquoti* to *M. pavlowi*. It should be noted that despite significant morphological similarity, which allowed Dietl (1994, p. 14) to note that “Die Macrocephalen ‘Population’ aus dem hochstetteri-Horizont unterscheidet sich nur geringfügig von der des kepleri-Horizonts... Auch hier ist also der Evolutionsschritt innerhalb einer Ammonitengruppe von einem zum anderen Faunenhorizont sehr klein, wahrscheinlich kleiner als die Zeitdauer eines einzigen Faunenhorizonts,” and similar trend in development of Bathonian and Callovian *M. jacquoti* specimens, the Callovian species loss ornamentation earlier than the Bathonian ones (Fig. 9). This is clearly seen in the plot demonstrating changes in the whorl height, at which ornamentation begins reducing within the same lineage (Fig. 10).

(2) Despite its “older” morphotype, Indian–Madagascar *M. triangularis* is very close to *M. jacquoti* that was noted previously (Westermann and Callomon, 1988, p. 16; Dietl, 1994, p. 13). Nevertheless, owing to less frequent and coarser ribs in internal whorls (Datta et al., 1996, Plate 1, figs. 3, 4) and peculiar subrectangular cross-section in adult whorls, *M. triangularis* is readily distinguishable from European species.

(3) *M. pavlowi* should be attributed to the family Macrocephalitidae.

Macrocephalites verus (Plate VI, figs. 4, 5) appears in West Europe in the *quenstedti* Biohorizon and is also characteristic of the overlying *suevicum* Biohorizon (Callomon et al., 1989; Dietl and Gygi, 1998). In the East European platform, this species is widespread in the *elatmae* Biohorizon (Mitta, 2000; Gulyaev, 2005). This is consistent with correlation based on Cardiocerataceae species. It is also noteworthy that some researchers (Gulyaev, 2005) consider *Cadoceras suevicum* and *C. elatmae* as synonyms. Rare finds of *M. cf. terebratus* (Plate V, fig. 1) at the same level concretions in the Prosek section, where *M. verus* occurs, are also important for correlation. In England (Rage, 1989), these *Macrocephalites* forms are accepted for index species of neighboring faunal horizons. The level with concretions inside the *elatmae* Zone in the Prosek section corresponds likely to the boundary between these biohorizons.

BIOSTRATIGRAPHIC UNITS

Principles of Definition

Two biostratigraphic zonations have been suggested recently for the upper Bathonian–basal lower Callovian of European Russia (Table 4). They differ in ranges of the *Elatmae* Zone and upper Bathonian, as far as it concerns infrazonal units, and in position of the Bathonian–Callovian boundary.

The stratigraphic scale considered below is based on the synthesis of available scales and data of this study. The following modifications are introduced:

(1) The *Calyx* Zone is included into the upper Bathonian zonal scale to replace the previous *Infimum* Zone taking into consideration the priority principle.

(2) Three previous biohorizons of the infazonal scale are renamed based on revision of their index species: *brevi* (= *poultoni* Gulyaev 2002, 2005); *frearsi* (= *primaevum* Gulyaev 2002, 2005); *quenstedti* (= *falsum* Mitta and Starodubtseva, 1998; Mitta, 2000; = *elatmae anabarensis* Gulyaev 2002, 2005).

(3) The Bathonian–Callovian boundary is defined at the top of the *bodylevskiyi* Biohorizon in contrast to Mitta (2000) who correlated it with the biohorizon base.

These modifications are introduced because of the following reasons:

(A) The validity of infazonal units is determined by the triple priority and subordinate principles (Gulyaev, 2002) of (1) resolution degree, (2) succession, and (3) seniority. According to the second principle, the scale of biohorizons should be based, if possible, on links of the phylogenetic succession. This determines the resolution degree of the scale (first principle) and its completeness. In accord with the second principle, the succession of biohorizons in suggested scale is deter-

mined on successive species of the phyletic lineage *C. (Catacodoceras)–C. (Paracadoceras)*. Species *Cadoceras (Bryocadoceras) falsum* Voronetz 1962 that was selected (Mitta and Starodubtseva, 1998; Mitta, 2000) for index species of one biohorizons of the *Elatmae* Zone, the equivalent of our *quenstedti* Biohorizon, does not belong to this phyletic lineage and cannot be used as an index species our scale.

(B) In the standard scale, the Bathonian–Callovian boundary is defined at the base of the *kepleri* Biohorizon (Callomon et al., 1988). This universally recognized position corresponds approximately to the base of the *jacquoti* Biohorizon (Thierry et al., 1997), although in southern Germany these levels differ notably. Accordingly, the biostratigraphic boundary unit defined or established below the base of the *kepleri (jacquoti)* Biohorizon should be attributed to the Bathonian and the higher unit to the Callovian. Taking this into consideration, we referred the *bodylevskiyi* Biohorizon to the Bathonian, whereas Mitta (2000) considered it as the basal faunal horizon of the Callovian.

Problems of Correlation

Recently, the suggested scale can be correlated at the infrazonal level only with scales of Germany and East Greenland, which are of a high resolution and based in some intervals on similar ammonites successions.

Correlation with the German scale, primarily for the lower Callovian, is the least controversial (Table 5). Infrazonal units are directly correlative based on identical index species (*jacquoti* and *quenstedti* biohorizons), which can be considered as isochronous geographic subspecies (*elatmae* Biohorizon in Russia and *suevicum* α , β in Germany), and on associated species of the ammonite assemblage (*Calyx* Zone and *Hannoveranus* Subzone, see below). Other intervals of the scales under consideration are lacking species in common in ammonite assemblages, being correlated according to their stratigraphic position.

Correlation between infrazonal scales of European Russia and East Greenland is more difficult. The direct correlation is admissible only for the upper Bathonian *Calyx* and, to a lesser extent, for *Variabile* zones based on identical or close index and associated species. The overlying interval equivalent to *Apertum* and *Nordenskjöldi* is almost lacking species in common.

Two alternative versions can be proposed now for correlation between infrazonal scales of European Russia and East Greenland using different approaches and index species.

(A) Correlation based on phylogenetic analogues (Table 5). The *Apertum* Zone entirely or almost entirely corresponds to the *Elatmae* Zone. This version accords with available ideas on the phylogenetic affinity between index species *Cadoceras apertum* and *Cadoceras frearsi* from East Greenland and Central

Russia, respectively (Callomon, 1993). As is mentioned, morphological similarity between these species appears to be real according to characteristic features of their TBCs (Fig. 7).

Correlation between the *Apertum* and *Elatmae* zones is based on species from the *Keplerites kepleri–plenus* group occurring in both of them and characteristic of the *Kepleri* Subzone. *K. kepleri* and *K. traillensis* (= *plenus*) are usually considered as close and, consequently, almost isochronous species (Callomon, 2001; Callomon and Dietl, 1990, 2000) that is substantiated in this work by morphometric data (Fig. 6). As is shown, they are not identical however in detail: *K. traillensis* is a transitional morphotype between *K. kepleri* and true Bathonian *Keplerites* forms.

(B) Correlation based on identical or close index species. The *Nordenskjöldi* Zone is correlated with the basal part of the *Elatmae* Subzone and, correspondingly, the *Apertum* Zone is attributed to the Bathonian Stage. This version was first proposed by Mitta (2004b, 2005a, 2005b) who took into consideration the joint occurrence of *Cadoceras* form morphologically similar to *C. nordenskjöldi* and *K. traillensis* in the Yazykovo–Lekarevka section (Sura River basin). We found in the Prosek section a form close to *C. nordenskjöldi* (Plate V, figs. 5, 12) along with first *M. jacquoti*, and this indicates as well that the *Nordenskjöldi* Zone should be at substantially lower level than it is usually thought.

This version is favored also by close stratigraphic occurrence of *C. nordenskjöldi* and *C. breve*. In Callomon's scale, they represent index species of neighboring biohorizons. In the Prosek section, both species (determined in open nomenclature) are found in the *breve* Biohorizon. The forms identified by Callomon as *C. cf./aff. breve* are probably similar to *Cadoceras* forms of the underlying *bodylevskiyi* Biohorizon, but this is only a suspicion, since the specimens have not been figured.

It is reasonable to think also that the top of the *Nordenskjöldi* Zone in East Greenland is marked by hiatus corresponding to the largest part of the *Elatmae* Zone. In section 43 Fossilbjerget, at the top of Bed 26 with Fauna 30 (*nordenskjöldi* β) there is a sharp boundary and abundant concretions near it (Alsen and Surlyk, 2004; Callomon, 2004). This may indicate a condensed interval of sediments. We accept the traditional correlation model, which seems best substantiated.

Given below is description of biostratigraphic units located immediately near the Bathonian–Callovian boundary (*Calyx* Zone, *bodylevskiyi* and *breve* biohorizons).

We omit description of other biohorizons established in the Prosek section (*infimum*, *fearsii*, *quens-taedi* (= *falsum* Mitta and Starodubtseva, 1998; = Gulyaev, 2005); = *elatmae anabarensis* Gulyaev, 2005). They are described in other works: *infimum* in

Table 6. Ammonite assemblages of the *Calyx* Zone

Ammonites	European Russia		East Greenland ²	Northern Siberia ³
	Prosek	Alatyr II ¹		
1. <i>Cadoceras</i> (<i>Bryocadoceras</i>) <i>calyx</i> Spath		?	h	
2. <i>C. (Catacadoceras) infimum</i> Gulyaev et Kiselev	h	?		
3. <i>C. victor</i> Spath			h	
4. <i>C. franciscus</i> Spath			h	
5. <i>C. ammon</i> Spath			h	
6. <i>C. cf. franciscus</i> Spath				
7. <i>C. cf. victor</i> Spath				
8. <i>C. aff. variabile</i> Spath				
9. <i>C. perrarum</i> Voronetz				
10. <i>Pseudocadoceras</i> (<i>Costacadoceras</i>) <i>pisciculus</i> (Gulyaev)	h			
11. <i>Kepplerites</i> (<i>Kepplerites</i>) <i>svalbardensis</i> Sokolov et Bodylevsky				
12. <i>K. (K.) peramplus</i> Spath			h	
13. <i>K. (K.) antiquus</i> Spath			h*	
14. <i>K. (K.) nobilis</i> Spath			h*	
15. <i>K. (K.) vardekloeftensis</i> Spath		?	h	
16. <i>K. (K.) rosenkrantzi</i> Spath				
17. <i>K. (K.) aff. peramplus</i> Spath		?*		
18. <i>K. (K.) aff. dietli</i> Schairer				
19. <i>Toricellites pauper</i> (Spath)			h	

Note: Asterisk designate forms identified here as *Kepplerites* (*K. svalbardensis* Sokolov et Bodylevsky. Question mark in Tables 6–8 indicates species identified with uncertainty.

¹ Mitta, 2004b, 2005a, 2005b, 2006. ² Callomon, 1993. ³ Knyazev et al., 2006.

(Gulyaev and Kiselev, 1999; Gulyaev, 2001; and others); *frearsi* in (Gulyaev, 2005 (as *primaevum*); *quenstedti* in (Gulyaev, 2005 as *elatmae anabarensis*); *elatmae* in (Mitta, 2000; Gulyaev, 2001, 2005; and others). The *frearsi* (= *primaevum* Gulyaev, 2005) Biohorizon is renamed for new index species (*C. frearsi* (Orb.) and *C. primaevum* Sazonov are considered as synonyms); their nomenclature is discussed in Callomon, 1993; Mitta, 2000). The *quenstedti* Biohorizon (Callomon et al., 1989) is introduced instead of the former one (*elatmae anabarensis*) because of the other reason: *C. anabarensis* Bodylevsky is widespread in Arctic regions only (see above) and cannot be considered as ancestor of *C. elatmae* (*C. quenstedti* Spath is accepted for index species in this work).

Upper Bathonian

CALYX Zone Callomon and Birkelund 1973 (in Surlyk et al., 1973) emend Callomon 1993

Infimum Zone (pars): Gulyaev and Kiselev, 1999a, 1999b; Gulyaev, 2001, 2005

Keuppi Zone (pars): Mitta, 2005a, 2005b

Index species: *Cadoceras* (*Bryocadoceras*) *calyx* Spath. Holotype is figured in Spath, 1932, Plate 20, fig. 1; East Greenland, near the Constable Point, Vardkloft Formation, *K. tychonis* Horizon.

Stratotype: East Greenland, Jamson Land, western coast of Hurry Inlet, Mount Zackenbjerg, Section 12 (after Callomon, 1993).

Range: in East Greenland biohorizons *Kepplerites peramplus* (Fauna 22; Callomon, 1993) and *Kepplerites vardekloeftensis* (Fauna 23; Callomon, 1993); *Cadoceras infimum* Biohorizon (Gulyaev and Kiselev, 1999) in European Russia.

Ammonites: see Table 6

Correlation. In European Russia, the zone is established based on species in common in the ammonite assemblage of the *Calyx* Zone of East Greenland. In the Alatyr River basin, the zone is recognizable in the upper part of the *Keuppi* Zone, primarily in the Alatyr II section, where Mitta (2005) defined preliminarily the

K. vardekloeftensis faunal horizon and defined the *K. aff. peramplus* unit. Mitta (2004, Plate I, fig. 2; 2005, p. 641, Plate 8, fig. 1) described and figured *Cadoceras calyx* from the same stratigraphic level.

In West Europe (Germany, Swabian Alb), the *Calyx* Zone can be correlated with the upper part of the *Orbis* Zone (*Hannoveranus* Subzone) containing *Kepplerites* forms close to the index species of the *peramplus* Biohorizon (Dietl and Callomon, 1988). It is conceivable that the lower part of the *Calyx* Zone corresponds also to the upper part of the *Blanasense* Subzone, which yields *Kepplerites* species close to forms from the *peramplus*–*K. dietli* Schairer 1990 Biohorizon.

Remarks. The *peramplus* and *vardekloeftensis* biohorizons of East Greenland are unrecognizable in the Prosek section for several reasons.

First, identification of *K. peramplus* and *K. vardekloeftensis* is quite difficult. Figures of *K. peramplus* topotypes are reproduced in two works only. The holotype (Spath, 1932, Plate 24, fig. 1) corresponds to S-morphotype, and the TBC cast is therefore lacking secondary ornamentation that is the most important feature. After first description of the holotype by Spath, two topotypes have been figured under the same name (Dietl and Callomon, 1988). They differ from the holotype in quantity of primary ribs on the terminal whorl: 32–33 instead of 45 in the holotype. Since we accept this feature for parameter of the phylogenetic trend in the genus *Kepplerites*, such a difference is significant.

When defining *K. vardekloeftensis*, Callomon (1993, p. 102) distinguished holotype (Spath, 1932, Plate 25, fig. 2) and paratype (Spath, 1932, Plate 25, fig. 1). Description of the species is missing from publications, and species diagnosis cannot be established based on Spath's specimens because of their poor preservation (ornamentation is eroded); the holotype is unsuitable therefore for counting ribs on the TBC.

Second, according to Callomon, *Kepplerites svalbardensis* and *Cadoceras calyx* occur in East Greenland at different levels: the first species in the *peramplus* Biohorizon and second one in the *vardekloeftensis* Biohorizon. In the Prosek section, they are found in one concretion.

Third, the aforementioned species are found in association with *K. rosenkrantzi* Spath, the index species of biohorizon in the *Variabile* Zone that is below the *Calyx* Zone. This species is probably of a wider stratigraphic range than that suggested by Callomon. Ammonites, which we determined as *K. rosenkrantzi*, bear coarse ribs with distinct tubercles at their furcation points on middle whorls. This morphotype corresponds to specimen of Spath, which is the species paratype (Spath, 1932, Plate 19, fig. 3). Callomon (1993, Plate 1) identified this specimen with *K. cf. vardekloeftensis* referring to the same species also the holotype *K. nobilis* Spath (Spath, 1932, Plate 23, fig. 4). The latter form is considered as an "anomalously involute variety of *K. vardekloeftensis*." The holotype *K. nobilis* has coarse ribs in

internal whorls as well. Unfortunately, ammonites found in situ in the *Calyx* Zone stratotype were figured after Spath only occasionally. Hence, the taxonomic status of species under consideration remains ambiguous.

bodylevskiy Biohorizon Callomon 1984

= fauna C11. *Cadoceras bodylevskiy* (pars): Callomon, 1984

= *Kepplerites* ex gr. *svalbardensis*–*Cadoceras* ex gr. *frearsi* Beds (pars): Mitta and Starodubtseva, 1998

= *Cadoceras bodylevskiy* faunal horizon (pars): Mitta, 2000

Index species: *Cadoceras (Paracadoceras) bodylevskiy* Frebold. The holotype is figured by Frebold (1964, Plate 17, fig. 1); Canadian Arctic Archipelago, Axel Heiberg Island, Strand Fiord; Savik Formation, lower *Cadoceras* Beds.

Stratotype is undefined. The type locality of index species can be considered as representing the latter.

Ammonites: see Table 7

Correlation. When defining the *bodylevskiy* Biohorizon, Callomon (and, subsequently Mitta, 2000) suggested its occurrence in the northern Yukon region (the *Bodylevskiy* Zone, Poulton, 1987) in addition to the Canadian Arctic Archipelago. As is shown, specimens figured by Poulton and Frebold and named *C. bodylevskiy* belong to different, although close species of the *Paracadoceras* phyletic lineages: *C. bodylevskiy* Frebold and *C. breve* Blake. The first of them marks the top of the Bathonian Stage, while the second one is confined to the Callovian basal strata. The *bodylevskiy* Biohorizon belongs to the Bathonian Stage, as it is below the *Kepplerites keppleri*–*Macrocephalites jacquoti* Beds, which determine the base of the Callovian Stage. The overlying *breve* Biohorizon bears *M. jacquoti* found in several sections of European Russia (see below) and should be attributed to the Callovian Stage.

The biohorizon correlation with the standard *Discus* Zone and *apertum* α Biohorizon in East Greenland is conditional since ammonite assemblages from these units are lacking species in common.

Remarks. The *Kepplerites* specimens from the Yazykovo–Lekarevka section (Sura River basin) are figured and identified by Mitta (2000, 2004b) as *Kepplerites traillensis*. Morphometric comparison shows that one of the specimens falls into the morphological field of the *K. plenus* (= *traillensis*); the other one into the field of *K. svalbardensis*. In any case, both specimens from the same stratigraphic interval are morphologically closer to the Bathonian *Kepplerites* forms. Hence, the *bodylevskiy* Biohorizon is certainly subdivision of the Bathonian Stage.

Table 7. Ammonite assemblages of the *bodylevsky* Biohorizon

Ammonites	European Russia		Arctic Canada
	Prosek	Sura River basin ¹	
1. <i>Cadoceras (Paracadoceras) bodylevskyi</i> Frebold		?	h
2. <i>C. (P.) cf. bodylevskyi</i> Frebold			
3. <i>C. (Catacadoceras) nordenskjoldi</i> Callomon et Birkelund			
4. <i>Pseudocadoceras (Costacadoceras) cf. pisciculus</i> Gulyaev			
5. <i>Keplerites (Keplerites) cf. kepleri</i> (Oppel)	?		
6. <i>Toricellites pauper</i> (Spath)			

Note: ¹ Mitta, 2000, 2004. (h) holotype

LOWER CALLOVIAN

ELATMAE Zone

Breve Biohorizon (Callomon 1984) emend
(Gulyaev 2002)

= *Paracadoceras breve* + *Keplerites kepleri*
(fauna): Callomon, 1984

= fauna C11. *Cadoceras bodylevskyi* (pars): Cal-
lomon, 1984

?= Fauna 28. *Cadoceras (Paracadoceras) cf. or aff.*
breve: Callomon, 1993

= *Cadoceras variabile* Beds: Meledina and
Zakharov, 1996

= *Cadoceras bodylevskyi* Horizon (pars): Mitta,
2000

= *Cadoceras poultoni* Biohorizon: Gulyaev, 2002
(in Gulyaev et al., 2002), 2005

Index species: Cadoceras (Paracadoceras) breve
Blake 1905. Holotype is figured by Blake (1905, Plate 5,
fig. 1) and reproduced in unpublished dissertation
(Page, 1988, Plate 17, fig. 3) and in this paper (Plate VI,
fig. 3). England, Dorset, near Weymouth, East Fleet.
Lower Callovian.

Synonymy of *C. breve* includes ammonites
described under names *C. bodylevskyi* Frebold 1964
(Poulton, 1987, Plates 27, 28), *C. tschegemicum* Lominadze
2004 (Lominadze, 2004, Plate 1, figs. 4, 5; Plate 2,
fig. 1; this paper, Plate VI, fig. 4), *C. variabile* Spath
(Meledina, 1994, Plate 8, figs. 1, 2); *C. poultoni*
Gulyaev 2005 (= *C. bodylevskyi* Frebold sensu Poulton;
holotype in Poulton, 1987, Plate 27, figs. 4–6). The
holotype *C. breve* is represented by adult whorls lack-
ing the terminal body chamber. The morphotype of this
specimen is characterized by peculiar features: primary
ribs half-transformed into tubercles cover not only
umbilical but also lateral sides of whorls, being
obliquely oriented. Slightly above the umbilical shoul-
der, the bullae-shaped primary ribs bifurcate into three
secondary ribs. The morphotype is characteristic of
adult whorls (although not of the TBS) in all the speci-
mens figured by Poulton (1987, Plate 28) and of the

holotype *C. tschegemicum* (Lominadze, 2004, Plate 1,
fig. 5).

The terminal body chamber of *C. breve* is similar to
that of *C. bodylevskyi* Frebold, being different from it
in several phylogenetic features of the *C. (Paraca-*
doceras) trend, i.e., in greater number of ribs and wider
umbilicus (see above). Gulyaev who was first to note
these differences regarded specimens figured by Poul-
ton as species different from *C. bodylevskyi*. The TBC
of the *C. tschegemicum* paratype (Lominadze, 2004,
Plate 2, fig. 1) fits parameters of the *C. breve* mor-
phological field like *C. poultoni* (Poulton, 1987, Plate 27,
figs. 4–6), and both forms can be considered as identi-
cal species and, consequently, as junior synonyms of
C. breve.

Ammonites: see Table 8

Stratotype is defined by Gulyaev (2005) in the Chur-
kinskaya Shchel'ya site (Pizhma River, Komi, Repub-
lic); lower Callovian, *Elatmae* Zone, Bed 3 (silt with
large siltstone concretions). The type locality of the
index species holotype (one specimen found in
England) is unsuitable for stratotype, since exact posi-
tion of the found specimen inside the Fleet Member of
the Upper Cornbrash is unknown.

Stratigraphic position and correlation. As is known,
the holotype is confined to the Fleet Member of the
Upper Cornbrash spanning the *Kepleri*, *Terebratus*,
and basal *Kamptus* zones in the Weymouth area (Page,
1989). Callomon (1984) suggested joint occurrence of
this species with *K. kepleri* found below the
Cadoceras elatmae Beds. Later on, he assumed that the
holotype originates from the upper part of the *Kepleri*
Zone (Callomon, 1993), or more precisely from the *tere-*
bratus α Biohorizon (Callomon et al., 1988) of the
Terebratus Subzone (Page, 1989). These are hypotheti-
cal speculations, however, and the real position of holo-
type inside the Fleet Member remains unclear.

When studying Bathonian and Callovian sections in
the Pizhma River basin, Gulyaev (2005) established
that this species (identified as *Paracadoceras poultoni*,

Table 8. Ammonite assemblages of the *breve* Biohorizon

Ammonites	European Russia		North Caucasus ²	England	East Greenland ³	Arctic Canada ⁴
	Prosek	Pizhma River basin ¹				
1. <i>Cadoceras</i> (<i>Paracadoceras</i>) <i>breve</i> Blake				h		
2. <i>C. (P.)</i> cf. <i>breve</i> Blake					?	
3. <i>C. (Catacadoceras)</i> cf. <i>nordenskoeldi</i> Callomon et Birkelund					?	
4. <i>Pseudocadoceras</i> (<i>Costacadoceras</i>) cf. <i>pisciculus</i> Gulyaev						
5. <i>Kepplerites</i> (<i>Kepplerites</i>) ex gr. <i>keppleri</i> (Oppel)				?		
6. <i>Macrocephalites jacquoti</i> Douville				?		
7. <i>M. tumidus</i> (Rein.)			?			
8. <i>M. pila</i> (Nikitin)			?			

Note: (h) holotype. ¹ Gulyaev, 2005; Meledina, 1994; ² Lominadze, 1982; ³ Callomon, 1993; ⁴ Poulton, 1987.

Plate VI, fig. 6) occurs in association with first *Macrocephalites* forms of the *Macrocephalites jacquoti* group between the *P. infimum* subsp. nov. and *P. primae-vum* (= *frearsi* in this paper) biohorizons. The latter units contains *Macrocephalites* forms of the given type as well. Thus, the species characterizes the basal lower Callovian, namely the lower part of the *jacquoti* Biohorizon, an equivalent of the *keppleri* Biohorizon. As is noted above however, *M. jacquoti* occurs in southern Germany in two upper Bathonian biohorizons (*hollandi* and *hochstetteri*) (Callomon et al., 1989; Dietl, 1994). According to reduction degree of ornamentation, *M. jacquoti* differs from Bathonian species and falls into the morphological field of Callovian forms. *Kepplerites* ex gr. *keppleri* found in association with this taxon proves the assumption that *M. jacquoti* marks the base of the Callovian Stage in the Prosek section. In addition, the ammonite assemblage of the *Keppleri* Subzone in England is “dominated by compressed and fine-ribbed macrocephalid macroconchs belonging to the species *M. jacquoti* (Douville) and *M. verus* Buckman” (Page, 1989, p. 369). Thus, it can be assumed that appearance of *M. jacquoti* in different areas of the Subboreal Realm (England and European Russia) was synchronous most likely.

It is relatively difficult to correlate the *breve* Biohorizon with the fauna cf./aff. *breve* from East Greenland. First, specimens of this species from East Greenland have not been figured and originate, according to Callomon (1993), from different localities of different ages. Some of them may originate from the *Apertum* Zone. We correlate conditionally this biohorizon with the *Apertum* Zone based on morphological affiliation of both species with the indicated phylogenetic trend.

In the northern Caucasus, the biohorizon in question is recognizable only in the lower part of “*Macrocephalites macrocephalus* Beds” (nomenclature of Lominadze, 1982) in two sections, where *C. tschegemicum*

(defined here as *C. breve*) was found in situ: in the Chegem River basin (Bed 3, 1.8–2.2 m above the base) and in Cherek Balkarskii–Psygansu watershed (approximately, in the lower 9 m above the base of Bed 1) (Lominadze, private communication, 2006). The index species is accompanied in these sections by different Macrocephalitidae forms, which are more diverse in the Chegem section (*M. tumidus*, *M. pila*, according to Lominadze). First Macrocephalitidae representatives are found in Bed 2 of the Chegem section; these are *Indocephalites sphaericus tschegemensis* Lominadze (Lominadze, 1967, Plate XVIII, fig. 2; = ?*Bullatomorphites* sp.) and *Kamptokephalites grantanus* (Opp.) (Lominadze, 1967, Plate IV, fig. 4 = *Macrocephalites* sp. (m). Consequently, this bed also belongs to the *breve* Biohorizon, although it can be of the Bathonian age as well.

CONCLUSIONS

The complete succession of ammonite zones and biohorizons of the terminal upper Bathonian and basal lower Callovian, which are characteristic of European Russia, is established in the Prosek section. The *infimum* Biohorizon corresponding to the *Calyx* Zone of East Greenland is distinguished in the upper Bathonian. The Bathonian–Callovian boundary is defined at the base of the *breve* (*jacquoti*) Biohorizon. Infrazonal biostratigraphic units of the Bathonian–Callovian boundary interval established in the section are of the wide geographic distribution and high correlation potential in the Panboreal Superrealm, i.e., in European Russia, northern Caucasus, West Europe, East Greenland, Arctic Canada (*breve* and, to a lesser extent, *bodylevskiyi* biohorizons) and in the Tethyan Superrealm, the adjacent European areas inclusive (*jacquoti* Biohorizon).

The section studied meets most requirements concerning the GSSP selection (Remane et al., 1996) and

can be considered as a candidate for the GSSP of the Callovian Stage. The Bathonian–Callovian boundary strata are represented here by marine facies containing abundant and diverse ammonoids throughout the interval under consideration. The section is lacking significant biostratigraphic hiatuses and reveals the ammonite succession similar in many aspects with those known in West Europe (largely for the lower Callovian) and East Greenland (for the upper Bathonian).

Ammonites precisely sampled from the section are used to substantiate the modified succession of biohorizons in the Bathonian–Callovian boundary sediments of the East European platform. The Boreal and Tethyan ammonoids found in association near the Bathonian–Callovian boundary ensure possibility to reliably correlate the defined succession of biohorizons with biostratigraphic scales of West Europe and East Greenland.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research (project no. 06-05-64284) and by the Russian Science Support Foundation. We express our gratitude to the participants of the field observations in October of 2006 (A.A. Sudovykh, L.A. Glin-skikh, S.Yu. Malenkina, M.V. Pimenov, A.V. Manikin). We thank also our colleagues, who provided published data and materials on structure of the Bathonian–Callovian boundary sediments in the northern Caucasus (T.A. Lominadze, Georgia), India (S. Jain, the United States), and Germany (G. Dietl). We are grateful also to V.A. Zakharov (Geological Institute of the RAS) and V.V. Mitta (Paleontological Institute of the RAS), who reviewed carefully the manuscript.

Reviewers V.A. Zakharov and V.V. Mitta

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