Paleontological Journal, Vol. 39, Suppl. 5, 2005, pp. S629–S644.

Late Bathonian Cardioceratidae (Ammonoidea) from the Middle Reaches of the Volga River

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Received April 5, 2005

Abstract—Three new cardioceratid species with an abnormally short (0.5–0.6 whorls) body chamber were found while studying the coevolution of early Cardioceratidae and Kosmoceratidae (*Paracadoceras keuppi, P. nageli*, and *P. efimovi*). The interval marked by the occurrence of these ammonites is proposed as a new *keuppi* Zone, subterminal in the Upper Bathonian in the Russian Platform. This zone is apparently equivalent to the *variabile* and *calyx* zones of the Boreal (Eastern Greenland) scale and is represented in the basin of the Sura River by a series of quartz sands referred to the upper part of the Prialatyrskaya (=Lukoyanovskaya) Group. The Late Bathonian *Cadoceras apertum* Callomon et Birkelund and *C. calyx* Spath are described. The stratigraphic scheme of the Bathonian of the Russian Platforms and its correlation with the Boreal standard are proposed.

Key words: Late Bathonian, Cardioceratidae, Ammonoidea, Middle Volga River.

INTRODUCTION

The base of the Jurassic in the middle reaches of the Volga River (Srednee Povolzh'e) is generally composed of light and yellow fine-grained quartz sands and siltstones, frequently obliquely bedded, with interbeds and nodules of sandstone, up to 20–30 m thick. This series occurs over virtually the entire basin of the Alatyr River and sometimes outside it (Alatyr Uplift, Sura–Moksha dislocations). There are old records of the discovery of a fragment of a "shoulder bone, apparently of a plesiosaur" in these sands (Möller, 1875, p. 49). However, Möller (1875, p. 84–85) regarded these sands as "diluvial," i.e., Quaternary. The expedition of V.V. Dokuchaev describing the soils of the Nizhnii Novgorod Region determined that the series of sand was overlain by the Lower Callovian clay, which allowed the determination of the Jurassic age of this series (Zemyatchenskii and Dokuchaev, 1884; Sibirtsev, 1886). Based on the position in the section and scarce plant remains, this so-called Prialatyrskaya Series (termed as such by Sibirtsev, 1886) was tentatively dated Bathonian. In the *Unified Stratigraphic Scheme of the Jurassic of the Russian Platform* (1993), it was regarded as the upper member of the Lukoyanovskaya Group. Until recently no documented macrofaunal remains have been known from the Prialatyrskaya Series.

However, recently these "paleontologically silent formations" (descriptive name given by Sibirtsev) "broke the oath of silence." In 1999, in the vicinity of the town of Saransk, V.M. Efimov discovered vertebrae of ichthyosaurs and ammonite shells in sandstone bullion. These shells were passed on to me for study. The study of these shells showed that they belong to Late Bathonian members of the genus *Kepplerites*. Taking into account the importance of this discovery, from 2000 to 2003 I undertook systematic field work in the Alatyr River basin. By now, four localities in Mordovia and the Nizhnii Novgorod Region (the area studied is shown in Fig. 1) have yielded considerable material, represented by fossils of marine invertebrates and reptiles (Mitta and Efimov, 2004).

Fossils of marine reptiles are infrequently found in this area and include isolated vertebrae, fragments of ribs and teeth, and isolated skull bones. Invertebrates are represented by bivalves, belemnites, or accumulations of serpulid tubes. Ammonite shells (sometimes excellently preserved) are especially numerous. They belong to two families Kosmoceratidae (genus *Kepplerites* s. str.) and Cardioceratidae (subfamily Cadoceratinae, genera *Paracadoceras* and *Cadoceras*).

The outcrops are mainly sand pits dug for local needs, less commonly relatively large quarries. They are mainly located on the slopes of watersheds. The sections cut through the series of light and yellow fine-grained (in places medium-grained or silty micaceous) quartz sand with a few nodules and interbeds of sandstone. The sandstone varies from light-colored and yellowish red to dark brown, is irregularly cemented, from loose to compact, and ferruginous. The thickness is at least 8–12 m, but the lower parts of the sections are usually covered by talus. The top of the sand series frequently contains nodules and reddish yellow limonitized sandstone, up to 1 m in diameter, sometimes forming a plate covering the sandy series (Fig. 2).

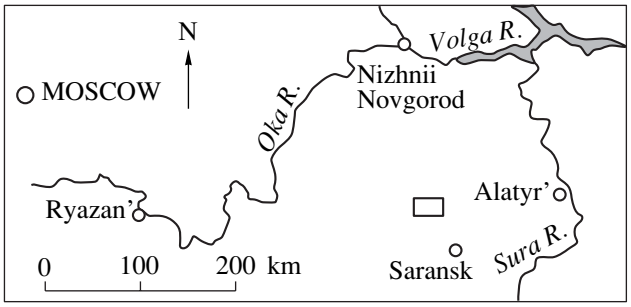


Fig. 1. Map showing the location of the Alatyr I–IV sections (the area under study is shown by a rectangular).

In Alatyr I, most shells come from the interval of 1.2–1.7 m below the top of the sand and are represented by ammonoids of the subfamily Cadoceratinae, sharply different from the known species in the short body chamber (0.5–0.6 of the external whorl instead of 0.75–1.00 in younger members of the subfamily, i.e., *Cadoceras* and *Rondiceras*). These shells are described below as new species, *Paracadoceras keuppi* and *P. nageli.* Shells of *Kepplerites*, which have been found here in situ, are very poorly preserved and cannot be identified to species. The material collected loose from the talus requires preparation.

The ammonite occurrences in the Alatyr II locality are found in the interval 1.0–5.5 m below the top of the sand series. The topmost occurrences contain *Kepplerites vardekloeftensis* Callomon, 1993. Two meters below the top, there are ammonites similar both to this species and to *K. peramplus* Spath, to specimens figured by Dietl and Callomon (1988, text-figs. 3–5) (see *K.* aff. *peramplus*; Mitta, 2004, pl. 2, figs. 1, 2), and a single specimen of *Paracadoceras* sp. (Pl. 7, fig. 5). Below these, the occurrence contained *Kepplerites* (mostly not yet prepared) and three species of *Paracadoceras* (*P. nageli, P. efimovi*, and *P. keuppi*), described below. From the same locality (no exact details of occurrence known), Efimov found *Kepplerites svalbardensis* Sokolov et Bodylevsky and *Cadoceras calyx* Spath (Mitta, 2004, pl. 1, figs. 1, 2, respectively).

The Alatyr III locality is interesting in that all records of ammonites are restricted here to a very narrow (less than 0.4 m thick) interval of limonitized sandstones at the top of the Prialatyrskaya series. The oryctocoenosis of ammonites is monospecific. It is composed of macro- and microconches of *Cadoceras apertum* Callomon et Birkelund.

In the Alatyr IV locality the ammonites are found in the interval of about 2.5 m. Ammonites are represented by well-preserved microconches *Kepplerite*s; numer-

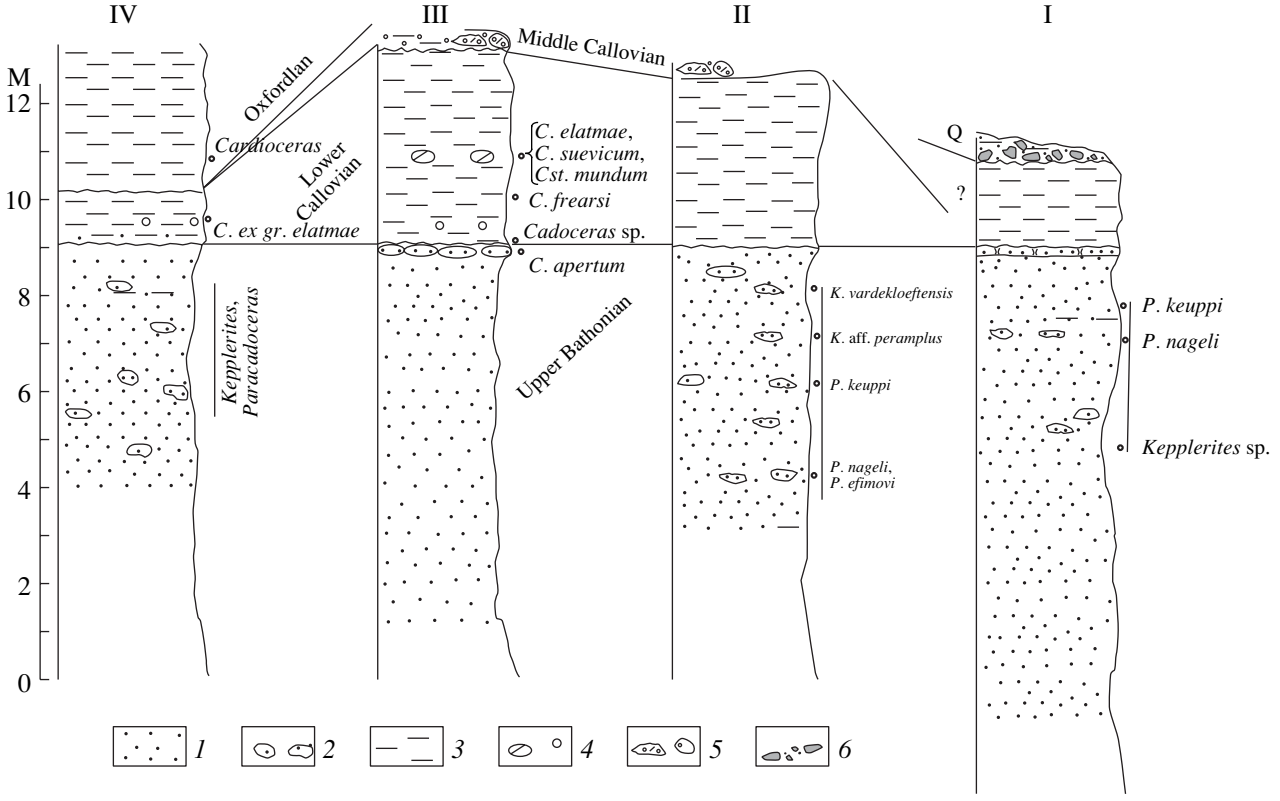


Fig. 2. Middle Jurassic sections in the basin of the Alatyr River (localities I–IV). Explanations: (*1*) sand, (*2*) sandstone nodules, (*3*) clay, (*4*) carbonate nodules, (*5*) oolitic marl, and (*6*) conglomerate. Vertical lines show the intervals of the ammonoid occurrences; circles show the levels of the occurrences of ammonites identified to species.

ous, although poorly preserved macroconches of this genus; and a few small *Paracadoceras* sp.

In most places, the Prialatyrskaya Series is transgressively overlain by the clay of the Uzhovskaya Series, typical of the Lower Callovian *elatmae* Zone of dark gray clay with carbonate nodules, sometimes containing complete shells of *Cadoceras* and *Costacadoceras*. The lower 0.2–04 m are usually strongly sandy because of the erosion of the sandy series. The basal part of the Prialatyrskaya Series contained poorly preserved *Cadoceras* cf. *bodylevskyi* Frebold (section Alatyr III). About 1 m above the base, the series contained spherical carbonate nodules about 10–15 cm in diameter. These nodules are difficult to break ("cannon balls") and do not contain faunal remains. The nodules are similar to those in the faunal horizon *Kepplerites keppleri*, in the outcrop near the village of Khvadukassi in the basin of the Sura River (Mitta, 2000). The beds 2–2.5 m above the base in the same locality contain frequent large elliptical carbonate nodules with excellently preserved *Cadoceras elatmae* (Nikitin), *C. elatmae suevicum* Callomon *et al.*, and *Costacadoceras mundum* (Sazonov). A similarly preserved shell of *Cadoceras frearsi* (d'Orbigny) was found in a similar matrix somewhat lower in the section.

Thus, in the Lower Callovian clay series (overlain by Middle Callovian oolitic clay and marl or gray clay of the Oxfordian), it is possible to recognize the faunal horizons *bodylevskyi, keppleri/frearsi*, and *elatmae*, i.e., lower faunal horizons of the *elatmae* Zone, established in the basin of the Sura River. Hence, the entire underlying sandy Prialatyrskaya Series is Bathonian. The topmost covering sandstone bed (some portions of which are platelike and others are closely spaced large nodules) belongs to the lower faunal horizon *Cadoceras apertum* of the uppermost Bathonian terminal zone, as yet unnamed in the Russian Platform. The interval of the cooccurrence of *Kepplerites, Cadoceras*, and *Paracadoceras* observed below in the sand series is possible to identify as a new Upper Bathonian *Paracadoceras keuppi* Zone of Central Russia with a stratotype of the Alatyr II section (Fig. 2). The *Kepplerites vardekloeftensis* Horizon is the upper faunal horizon of this zone. Its lower boundary is determined by the appearance of *Paracadoceras nageli* and *P. efimovi.* Four faunal horizons may be recognized in the new zone. The basal layers of the zone contain *Paracadoceras nageli, P. efimovi, Kepplerites* sp. nov. (faunal horizon *nageli*). The beds above contain *P. keuppi, Kepplerites* ex gr. *svalbardensis* Sokolov et Bodylevsky and apparently *Cadoceras calyx* Spath collected by V.M. Efimov (faunal horizon *keuppi*). Beds above contain *Kepplerites* aff. *peramplus* Spath and *Paracadoceras* sp. (pl. 4, fig. 5). The zone is terminated by the faunal horizon with *Kepplerites vardekloeftensis* Callomon. This horizon contains only *Kepplerites* (partly transitional from the index species to *K*. ex gr. *keppleri*).

It is noteworthy that the material is not sufficient for the positive recognition of faunal horizons in the *keuppi* Zone. Therefore, they are established only preliminarily, until new data are obtained, including the successions of *Kepplerites*, while their boundaries are shown by dashed lines. The accumulation of the sediments of the Prialatyrskaya Series was apparently relatively rapid, while the observed changes in the distribution of ammonites, in the interval of a few meters, were likely not to be connected with significant age differences.

The stratigraphic succession of the Late Bathonian cardioceratids is studied in the greatest detail in eastern Greenland. The *keuppi* Zone is an approximate equivalent of two eastern Greenland zones of the so-called Boreal Bathonian (*variabile* and *calyx*), each of which is subdivided into two faunal horizons (Callomon, 1993).

As a result of the new study the emended scheme of the Bathonian stratigraphy in the Russian Platform and its correlation with the Boreal scale established by Callomon for eastern Greenland is proposed (table). The stratigraphy and correlation of the Lower Bathonian are cited from those of the Saratov Povolzhye (Mitta *et al.*, 2004). Altogether the Bathonian of the Russian Platform contains seven correlation levels, shown depending on the level of certainty by different arrows:

(1) based on the specimen of *Arctocephalites* ex gr. *freboldi* found not in situ but most likely coming from the *besnosovi* Zone (Mitta and Seltzer, 2002, pl. 4, fig. 1);

(2) based on the occurrence of the index species *Arcticoceras harlandi* (Mitta and Seltzer, 2002, pl. 1, fig. 1);

(3) based on the occurrence of the index species *Arcticoceras ishmae* (Mitta and Seltzer, 2002, pl. 3, fig. 1);

(4) based on the similarity of *Paracadoceras nageli* to the unpublished cardioceratids from this faunal horizon of eastern Greenland in the collection of Callomon;

(5) based on the occurrence of ammonites similar to *Kepplerites peramplus* (Mitta, 2004, pl. 2, figs. 1, 2);

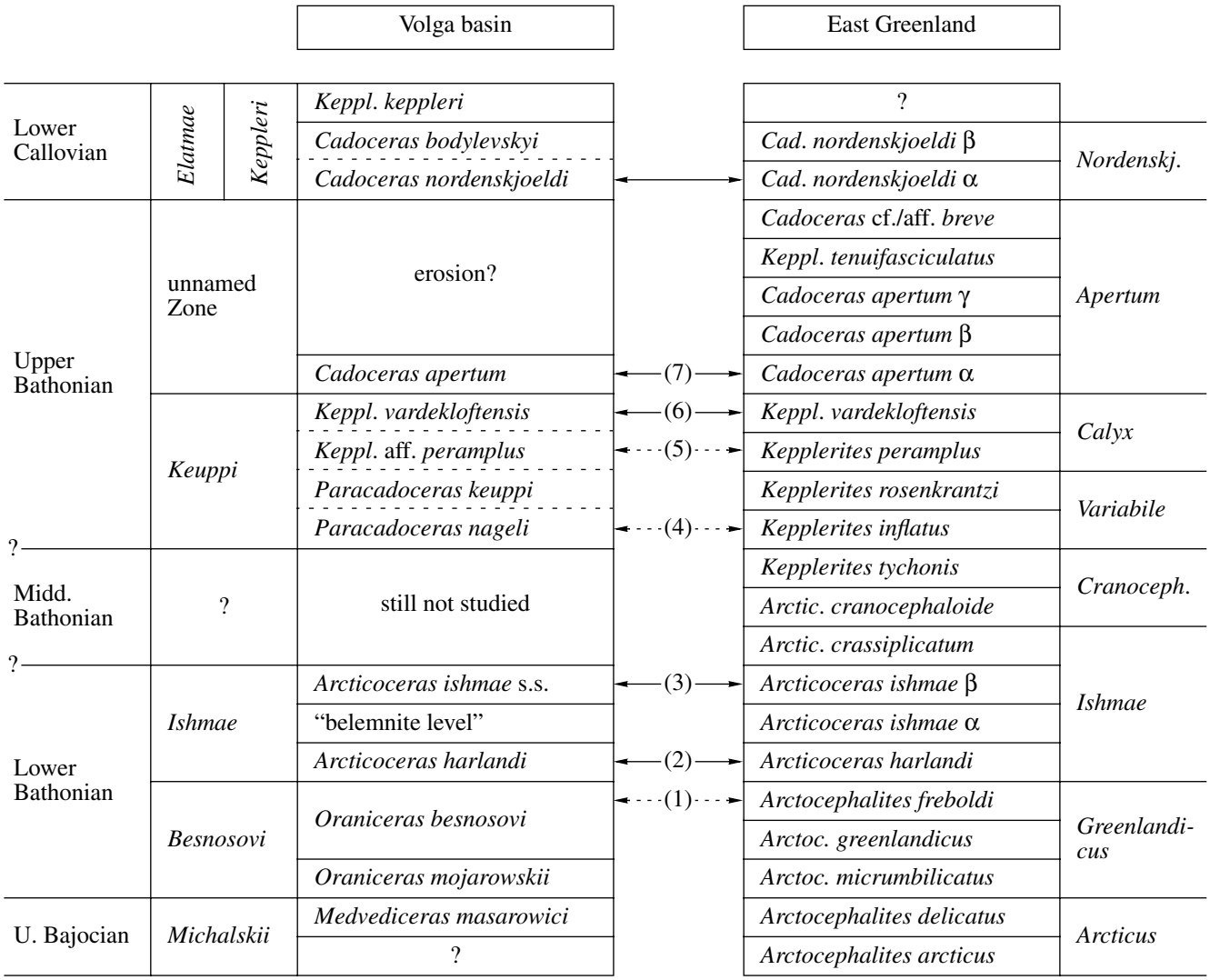
(6) based on the occurrence of the index species *Kepplerites vardekloeftensis*; and

(7) based on the occurrence of *Cadoceras apertum* (Pl. 7, figs. 1–4).

Correlation with the Lower Callovian faunal horizon *nordenskjoeldi* of Greenland is based on the occurrence of the index species *Cadoceras nordenskjoeldi* (Mitta, 2004, pl. 4, figs. 1, 2).

The observations made in the large and excellently organized but only partly published collection of John Callomon housed in the Geological Museum of the University of Copenhagen allowed me to directly compare the Greenland and Central Russian material rather than base comparisons on the few published figures. This comparison showed that the morphology of cardioceratids with an abnormally short body chamber from the basin of the Alatyr' River is the most similar to that of ammonites transitional from the last members of the subfamily Arcticoceratinae (genera *Arcticoceras* and *Arctocephalites*) to the subfamily Cadoceratinae (genus

Chronostratigraphic subdivision of the Bathonian Stage of the Russian Platform (Volga River basin) and its correlation with the boreal standard (eastern Greenland)



Cadoceras). Three species with a short body chamber described below most likely evolved directly from arcticoceratins and represent a separate trend in the phylogeny of cardioceratids. This conclusion is also based on the study of microconches found together (unfortunately not associated with respective species of macroconches). They can also be subdivided into three morphogroups (Pl. 5, fig. 4; Pl. 6, figs. 2–4) and are generally more similar to the microconches of arctocephalitins than to those of cadoceratins. Taking into account the existing diversity of generic and subgeneric names for the Bathonian–Callovian members of the family Cardioceratidae, we could not establish a new generic name and preferred to assign these species to the genus *Paracadoceras*. The type species of this genus (*P. harveyi* Crickmay) is described based on a single specimen from British Columbia (Crickmay, 1930, p. 55, pl. 16, figs. 1, 2; the holotype was refigured by Imlay, 1953, pl. 43, fig. 12; Frebold, 1964, pl. 40, fig. 3). The stratigraphic distribution of *Paracadoceras* is restricted to the Upper Bathonian–Lower Callovian. The species composition (most often regarded as a subgenus of *Cadoceras*) is debatable. Various authors assign to it up to 20 species from the entire Boreal Realm, from northern North America and northern Siberia to northern regions of European Russia, Siberia, and eastern Greenland. Apparently *Paracadoceras* is a typical polyphyletic genus containing Bathonian–Callovian cardioceratids of different origins. It has juvenile whorls similar to those of *Cadoceras* but differs in less strongly inflated, more evolute adult whorls that have a more rounded cross section. *Cadoceras* species mostly have a cadiconic shell. *Paracadoceras* s. str. includes serpenticones with a weakened ornamentation. Based on these characters, the new species described below mainly agree with the diagnosis of *Paracadoceras*.

Fig. 3. *Platychamoussetia funifera* (Phillips, 1829), specimen no. 5029/034, mold of the adult shell with a complete body chamber and aperture; lateral view, ×1; Moscow Region, quarry near the Peski Station; Upper Callovian, not in situ, coll. by A.G. Sennikov.

In contrast, the body chamber length is quite different. According to L. Longridge and P. Smith, who by my request reexamined the holotype of the type species of the genus, *Paracadoceras* has a long body chamber. The holotype shows only two sutures, while the body chamber apparently had only seven-eighths of the external whorl. Certain *Paracadoceras*, such as *P. moffiti* and *P. chisikense* described from the Chinitna Formation of Alaska (Imlay, 1953), are represented by incomplete specimens that give no information on the length of the body chamber.

The length of the body chamber in cardioceratids varies strongly. Different workers considered this character to be either of generic or specific rank. It is thought that the length of the body chamber affected the position of the ammonite shell in the water. The longer the body chamber, the greater the rotational mobility of the mollusk about the horizontal axis. Thus, ammonites with a short body chamber had a better fixation of the shell in the water. The best studied cadoceratins from the lower portion of the Callovian (species of *Cadoceras* and *Rondiceras*) had a long body chamber,

Plate 4

2a

*

2b

1b

1a

*

usually from 0.75 to 1.1 whorls (Mitta, 2000). The *Cadochamoussetia* had a slightly shorter body chamber. In derivates of *Cadoceras*, the body chamber occupied 0.75–0.8 whorls. The last representatives of *Chamoussetia* (a genus that evolved from *Cadochamoussetia*) had a body chamber of only 0.5 whorls. The last representatives of the genus *Platychamoussetia*, homeomorphic to *Chamoussetia*, from the upper Callovian also have a body chamber of a half of the external whorl (Fig. 3). It is interesting that these two genera with a short body chamber represented a blind alley in evolution.

In early species of cardioceratids this character also varies. The genus *Cranocephalites* had short body chambers up to 0.65 whorls. Their phylogenetic and stratigraphic successors (*Arctocephalites* and *Arcticoceras*) usually have the body chambers from three-quarters to a complete whorl. One of the last *Arcticoceras* (*A. cranocephaloide* Callomon et Birkelund) had a distinctly shortened body chamber compared to other species (0.65 whorls). The shell morphology and morphogenesis of the ornamentation of this species is very much different from the Central Russian *Paracadoceras*. However, its stratigraphic and phylogenetic descendant (figured as *"Arcticoceras/Cadoceras* sp. nov. ? aff. *variabile* Spath" by Callomon and Birkelund, 1980, pl. 1, fig.1 [= *Arcticoceras* aff. *cranocephaloide* sensu Callomon, 1993]) is similar to Central Russian species but differs in the noticeably narrower umbilicus and body chamber up to 0.7 whorls. In later succession, the length of the body chamber of cardioceratins increases.

Thus, the combination of morphological characters and stratigraphic distribution of the new species suggests their assignment to a short, possibly very short, evolutionary trend at the point of divergence of arctocephalins and cadoceratins. This cardioceratid lineage existed in the Central Russian Bathonian Sea along with typical cadoceratins (*Cadoceras calyx*) and apparently completed its existence during this stage.

Apart from the new species, specimens of *Cadoceras calyx* and *C. apertum* that were recorded for the first time outside eastern Greenland are described below. Material described is housed in the Paleontological institute of the Russian Academy of Sciences (PIN), coll. no. 5029.

ABBREVIATIONS

(Dm) shell diameter, (WH) whorl height, (WW) whorl width, and (UW) umbilical width.

SYSTEMATIC PALEONTOLOGY

Family Cardioceratidae Siemiradzki, 1891

Subfamily Cadoceratinae Hyatt, 1900

Genus *Paracadoceras* Crickmay, 1930

***Paracadoceras keuppi* Mitta, sp. nov.**

Plate 4, fig. 2; Plate 5, figs. 2 and 3; Plate 8, fig. 3

?*Paracadoceras* sp.: Poulton, 1987, p. 57, pl. 29, figs. 1–6.

Cadoceras (Streptocadoceras) variabile: Meledina, 1994, pl. 12, fig. 2; ? pl. 8, figs. 1 and 2.

Etymology. In honor of H. Keupp, specialist in paleopathology and paleobiology of cephalopods.

Holotype. PIN, no. 5029/12; Middle Volga Region, interfluve area between the Alatyr and Insar rivers, Alatyr II Section; Upper Bathonian, *keuppi* Zone, Prialatyrskaya Series 2.7–3.0 m below its top.

Description. The shell is medium-sized (about 100 mm in diameter), with inflated whorls circular in cross section. The umbilicus is wide, less commonly stepped. The umbilical wall is almost vertical. The umbilical shoulder is rounded. The body chamber is 0.5–0.6 whorls. The aperture is simple, with a ledge-shaped ventral projection.

In juvenile whorls, the ribs are regularly prominent, bifurcating, simple and intercalating, with a branching point in the lower third or at the mid-flank. They cross the flanks and the venter, slightly slanting forward. With age, the primary ribs become more strongly raised. Their branches, in contrast, become weaker, and at the end of the body chamber appear as wrinkles. In the apertural part of the body chamber of adult shells, the primary ribs usually also become weaker.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW/Dm	WH/Dm	WW/Dm	UW/Dm
Holotype 5029/12	106	36	48	43	0.34	0.45	0.41
	80	26	40	33	0.33	0.50	0.41
5029/18	94	34	37	34	0.36	0.39	0.36
	76	26	31	27	0.34	0.41	0.36
5029/24	92	36	37	33	0.39	0.40	0.36
5029/25	91	37	40	30	0.41	0.44	0.33
5029/19	86	30	38	31	0.35	0.44	0.36
5029/26	78	30	31	27	0.38	0.39	0.35

Comparison. This species is distinguished from *P. nageli*, which has similar juvenile whorls, by the

Explanation of Plate 4

All figures are of natural size. The asterisk marks the beginning of the body chamber.

Fig. 1. *Paracadoceras nageli* sp. nov.; holotype. no. 5029/11, adult shell with a complete body chamber and preserved aperture: (1a) lateral view, (1b) ventral view.

Fig. 2. *Paracadoceras keuppi* sp. nov.; holotype no. 5029/12, adult shell with a complete body chamber and preserved aperture: (2a) lateral view, (2b) ventral view.

Both from the outcrop Alatyr II; *keuppi* Zone; collected by the present author.

Plate 5

more rounded whorl cross section, the generally wider umbilicus, and by the smoothened ventral ribs on the body chamber. It differs from *Paracadoceras* sp. (Pl. 8, fig. 5) in the ventral ribs smoothening on the body chamber.

R e m a r k s. The species described is the most morphologically similar to *Arcticoceras/Cadoceras* sp. nov. ? aff. *variabile* Spath (Callomon and Birkelund, 1980, pl. 1, fig. 1) = *Arcticoceras* aff. *cranocephaloide* sensu Callomon, 1993. The latter was found in Milne Land, in the interval that Callomon correlates with the upper part of the *cranocephaloide* Zone of eastern Greenland, which was mainly described from the sections of Jameson Land. In my opinion, this form represents a new species, transitional from *Arcticoceras* to *Cadoceras*. *P. keuppi*, most likely, is contemporary to this species, which should indicate younger beds (faunal horizon 20 of the *variabile* Zone of Jameson Land). This is suggested by the presence of very similar ammonites collected there by Callomon and identified as "*Cadoceras* cf. or aff. *variabile* Spath" (Callomon, 1993, p. 102).

This species is very similar to the fragmentary material from the Yukon Territory (Canada) described by T. Poulton from the loose material from the Late Bathonian *Cadoceras barnstoni* Zone (see the synonymy list). However, the state of preservation of Canadian ammonites does not allow their positive identification.

The ornamentation of the species described resembles "*Gonolkites* ex gr. *convergens*" from the Pechora River basin (Meledina, 1994, pl. 7, figs. 2, 3). The specimens in my collection differ in their generally wider umbilicus. In any event, the specimens from the Pechora belong to the Cardioceratidae but certainly not to the genus *Gonolkites* (Family Parkinsoniidae). Specimens described from the Pizhma River as *Cadoceras variabile* (see synonymy list) can be assigned (all or in part) to the new species.

O c c u r r e n c e. Upper Bathonian, *keuppi* Zone of the Middle Volga Region and the Pechora River basin.

M a t e r i a l. Seven specimens: five specimens from the Alatyr I section (1.2 m below the top of the Prialatyrskaya Series) and two specimens (holotype and one specimen without exact data on its occurrence in the section) from the same series of the Alatyr II section.

Paracadoceras nageli Mitta, sp. nov.

Plate 4, fig. 1; Plate 5, fig. 1; Plate 8, fig. 2

? *Cadoceras (Catacadoceras) perrarum*: Meledina, 1999, p. 1403, pl. 2, figs. 6–8.

non *Cadoceras* ? *perrarum*: Voronets, 1962, p. 55, pl. 15, fig. 1.

E t y m o l o g y. In honor of O. Nagel, who participated in the fieldwork on the Jurassic sections in European Russia in 1998–2004.

H o l o t y p e. PIN, no. 5029/11; Middle Volga River Region, interfluve area between the Alatyr and Insar rivers, Alatyr II section; Upper Bathonian, *keuppi* Zone, Prialatyrskaya Series, 4.5–5.0 m below its top.

D e s c r i p t i o n. The shell is medium-sized (up to 120 mm in diameter). The last whorls of the phragmocone are inflated, less commonly strongly inflated. The body chamber of the adult shells is inflated or of medium width. The whorl cross section is rounded quadrangular, with the greatest width near the umbilicus. The flanks are weakly convex. The venter is usually flattened-rounded. The umbilicus is wide in the juvenile whorls to become moderately wide in the body chamber. The umbilical wall is steep, weakly inclined. The umbilical shoulder is well developed. The body chamber occupies 0.5–0.6 whorls. The aperture is simple with a ledge-shaped projection.

In the young whorls, the ribs are regularly bifurcating, with a bifurcation point near the mid-flank. Less commonly the ribs are simple or intercalating. With age, the primary ribs are raised. Their branches also become wider. They are not smoothened. Their branches also become wider and are not smoothened on the body chamber.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen no.	Dm	WH	WW	UW/Dm	WH/Dm	WW/Dm	UW/Dm
5029/17	117	39	46	36	0.33	0.39	0.31
	86	33	42	34	0.38	0.49	0.39
Holotype 5029/11	107	40	48	37	0.37	0.45	0.34
	91	30	50	29	0.33	0.55	0.32
5029/27	95	31	37	35	0.33	0.39	0.37

V a r i a b i l i t y. Variability is mostly seen on the body chamber in the degree of flattening of the venter and in the variations of the coefficient of rib branching (from 2.3 to 3.4).

C o m p a r i s o n. This species is most similar to some specimens of *Cadoceras* ex gr. *variabile* Spath in the collection of Callomon from eastern Greenland but is readily distinguished by the generally wider umbilicus. It is distinguished from the single occurrence of *Paracadoceras* sp. (Pl. 7, fig. 5) by the more angular whorl cross sections.

E x p l a n a t i o n o f P l a t e 5

All figures are of natural size. The asterisk marks the beginning of the body chamber.

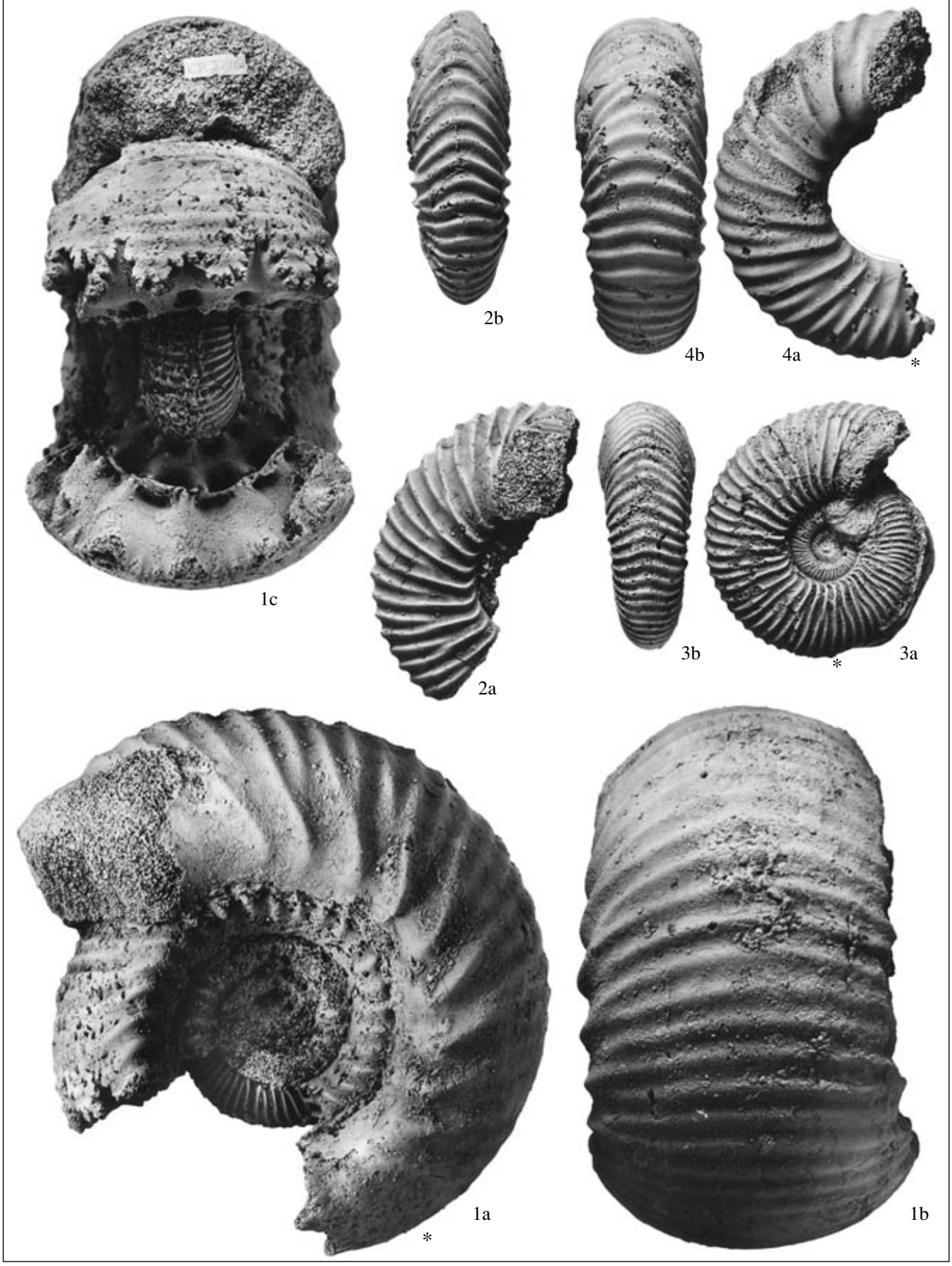
Fig. 1. *Paracadoceras nageli* sp. nov.; paratype no. 5029/17, adult shell with a complete body chamber and preserved aperture: (1a) lateral view, (1b) ventral view.

Figs. 2 and 3. *Paracadoceras keuppi* sp. nov.; (2) paratype no. 5029/19, young shell with a complete body chamber and broken aperture; lateral view; (3) paratype no. 5029/18, young shell with an aperture: (3a) lateral view, (3b) ventral view.

Fig. 4. *Costacadoceras* sp., morph 3; specimen no. 5029/29, young shell: (4a) lateral view, (4b) ventral view.

All from the *keuppi* Zone; (1–3) outcrop Alatyr I, (4) outcrop Alatyr II; collected by the present author.

Plate 6



R e m a r k s. The new species resembles *Cadoceras perrarum* (Voronets, 1962, pl. 15, fig. 1), described based on a single specimen from the Lena River (Siberia), in the whorl cross section and ornamentation. The length of the body chamber of the Siberian species is unknown; however, the new species is readily distinguished by the wider umbilicus. The body chamber of ammonites described by Meledina from Kotel'nyi Island as *C. perrarum* (see the synonymy list) occupies nearly one-half whorl, but the poor preservation of those ammonites does not allow a more precise comparison.

Some specimens of the species described resemble ammonites from northern Siberia identified by Meledina (1994, pl. 5, figs. 1, 2) as *Arcticoceras ? cranocephaloide* Callomon et Birkelund and previously described as the Lower Callovian *Cadoceras aff. kialagvikense* Imlay (Meledina, 1977, p. 86, pl. 24, fig. 2; pl. 25, fig. 1), differing from them in the more angular cross section and less frequent ribs at the end of the phragmocone.

O c c u r r e n c e. Upper Bathonian, *keuppi* Zone of the Middle Volga River Region and the New Siberian Islands.

M a t e r i a l. Nine specimens of various state of preservation: three specimens from the Alatyr I section (1.7 m below the top of the Prialatyrskaya Series), two specimens collected loose from the talus at the base of the section, and four specimens from the Alatyr II section (4.5–5.0 m below the top of the Prialatyrskaya Series).

Paracadoceras efimovi Mitta, sp. nov.

Plate 6, fig. 1

E t y m o l o g y. In honor of the paleontologist V.M. Efimov, who first collected ammonites from the Prialatyrskaya Series.

H o l o t y p e. PIN, no. 5029/13; Middle Volga River Region, interfluve area between the Alatyr and Insar rivers, Alatyr II section; Upper Bathonian, *keuppi* Zone, Prialatyrskaya Series, 4.5–5.0 m below its top.

D e s c r i p t i o n. The shell is medium-sized (about 100 mm in diameter). The last whorls of the phragmocone are very strongly inflated. The body chamber is strongly inflated. The whorl cross section is bud-shaped. The flanks fuse with the wide venter. The umbilicus is wide and deep. The umbilical wall is sloping and covered with ribs, which, with age, step back on its upper half. The body chamber occupies 0.5 whorls; the aperture is simple and ledge-shaped, with a pronounced apertural constriction.

The phragmocone mainly possesses bifurcating, prominent ribs (branching coefficient is 2.0), crossing the umbilical wall with a pronounced inclination forward. Near the umbilical shoulder, the ribs somewhat increase and cross the venter, noticeably bending forward. On the body chamber, the umbilical parts of the ribs increase even more, the ribs are more widely spaced, while the branching coefficient increases up to 2.5 due to the appearance of the tripartite and intercalating ribs.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen no.	Dm	WH	WW	UW/Dm	WH/Dm	WW/Dm	UW/Dm
Holotype 5029/13	105	32	58	47	0.30	0.55	0.45
	88	25	61	38	0.28	0.69	0.43

C o m p a r i s o n. This species is distinguished from other species of this genus by the low, bud-shaped whorls of the phragmocone and generally strongly inflated shell.

R e m a r k s. The shape of the juvenile whorls in the species described is identical to that of some other (geochronologically younger) *Cadoceras* species (Late Bathonian and Early Callovian). It is possible that this species marks the beginning of the evolutionary trend *Paracadoceras efimovi* ⟶ *Cadoceras calyx* ⟶ *C. apertum* and, hence, marks the beginning of the divergence of the derivates of the Arctocephalitinae into the clades *Cadoceras a*nd *Paracadoceras* in the Russian Platform.

M a t e r i a l. Apart from the holotype, one more specimen, the poor preservation of which allows only a tentative assignment to this species, from the same locality.

Genus *Cadoceras* Fischer, 1882

Cadoceras apertum Callomon et Birkelund, 1985

Plate 7, figs. 1–4

Cadoceras apertum: Callomon and Birkelund, 1985, p. 80, pl. 2, fig. 1; pl. 3, figs. 1–6.; Callomon, 1985, text-fig. 8L, l.

Explanation of Plate 6

All figures are of natural size. The asterisk marks the beginning of the body chamber.

Fig. 1. *Paracadoceras efimovi* sp. nov.; holotype. no. 5029/13, adult shell with the aperture preserved on one side: (1a) lateral view, (1b) ventral view, (1c) apertural view.

Fig. 2. *Costacadoceras* sp., morph 1; specimen no. 5029/14, fragment of the body chamber with a preserved aperture: (2a) lateral view, (2b) ventral view.

Fig. 3. *Costacadoceras*, morph 2; specimen no. 5029/15, young shell with a complete body chamber and partly broken aperture.

Fig. 4. *Costacadoceras* sp., morph 3; specimen no. 5029/16, body chamber of the adult shell with a preserved aperture; lateral view and ventral view.

All from the Alatyr II section; Upper Bathonian, *keuppi* Zone; collected by the present author (figs. 1–3) and V.M. Efimov (fig. 4).

Plate 7

Holotype. Geological Museum of the Copenhagen University, no. MGUH 16574 (JHC 2444), Callomon and Birkelund, 1985, pl. 2, fig. 1; eastern Greenland, Jameson Land; Upper Bathonian?, *apertum* Zone.

Description. The shell is medium-sized. The population from Central Russia reaches 110 mm in diameter. The young whorls are inflated. The whorl cross section of the young whorls is rounded, gradually becoming rounded-trapezoid. The last whorl of the phragmocone and the body chamber are strongly inflated. The umbilicus is wide or moderately wide, deep, and funnel-shaped. The body chamber occupies about 0.9 whorls. The aperture is simple with a wide apertural constriction disguised by the shell.

The ribs are prominent, mostly bipartite, less commonly tripartite, and slanting forward. As the shell grew, the umbilical parts of the ribs are raised to form crestlike structures; the ventral branches become noticeably weaker, although they do not disappear entirely.

The microconchs associated reach 40 mm in diameter. They have an elliptical or oval whorl cross section of medium width, with a moderately wide (on the phragmocone) and wide (on the body chamber) umbilicus, with a sloping wall. The ribs are thin, threadlike, bipartite, simple, intercalating, and slanting forward. The aperture is simple, with a ventral projection.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW/Dm	WH/Dm	WW/Dm	UW/Dm
5029/20	109	45	69	31	0.41	0.63	0.28
	86	34	56	28	0.40	0.65	0.33
5029/21	55	22	26	19	0.40	0.47	0.35
5029/22	32	12	15	10	0.38	0.47	0.31
5029/23 [m]	32	12	10	12	0.38	0.30	0.38
	27	11	8	9	0.41	0.30	0.33

Comparison. This species is distinguished from similar species by the relatively high, rounded trapezoid cross section of the young whorls and by the weakly pronounced ribs on the venter of the body chamber. It differs from *C. calyx* in the less inflated whorls, narrower umbilicus, and in the generally later smoothening of the ventral ribs on the body chamber.

Remarks. In the original description of this species, its authors noted that the species contains three successive morphs (α, β, and γ), differentiated in a 1.5-m-thick member of glauconitic clay at three nodule-bearing levels. The latest morph is characterized by the most evolute whorls. Russian ammonites are more involute than the holotype, which represents the morph β; hence, the Alatyr specimens more likely belong to the initial morph α of this species. Note that individuals of the Central Russian population of the species described (and some Late Bathonian *Kepplerites*) are noticeably smaller than the specimens of the type series, representatives of which reach 150 mm (microconches reach 55 mm) in diameter. This may be considered to be an indirect indication of the warmer-water environment of the Central Russian Basin compared with the Eastern Greenland basin.

Occurrence. Upper Bathonian? of eastern Greenland and the Middle Volga River Region.

Material. Eighteen specimens, mainly juvenile shells, and six microconchs from the Alatyr III section; bed of the limonitized sandstone at the top of the Prialatyrskaya Series.

Cadoceras calyx Spath, 1932

Plate 8, fig. 1

Cadoceras calyx: Spath, 1932, p. 69, pl. 20, fig. 1; Callomon, 1985, text-fig. 8K, k.

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

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

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

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

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

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

Holotype. Geological Museum of the University of Copenhagen; no. MGUH 9263, Spath, 1932, pl. 20, fig. 1; eastern Greenland, Jameson Land; Upper Bathonian, *calyx* Zone, Vardekloft Formation, "Horizon with calcareous nodules."

Description. The shell is medium-sized, up to 100 mm in diameter, with strongly inflated whorls, horizontally oval in cross section. The umbilicus is wide. The umbilical wall is almost vertical. The umbilical shoulder merges with the ventrolateral shoulder. The body chamber occupies 0.9 of the external whorl.

At the end of the phragmocone–beginning of the body chamber, the ribs begin from the middle of the umbilical wall to become smoothened on the wall. The primary ribs are prominent, slanting forward on the

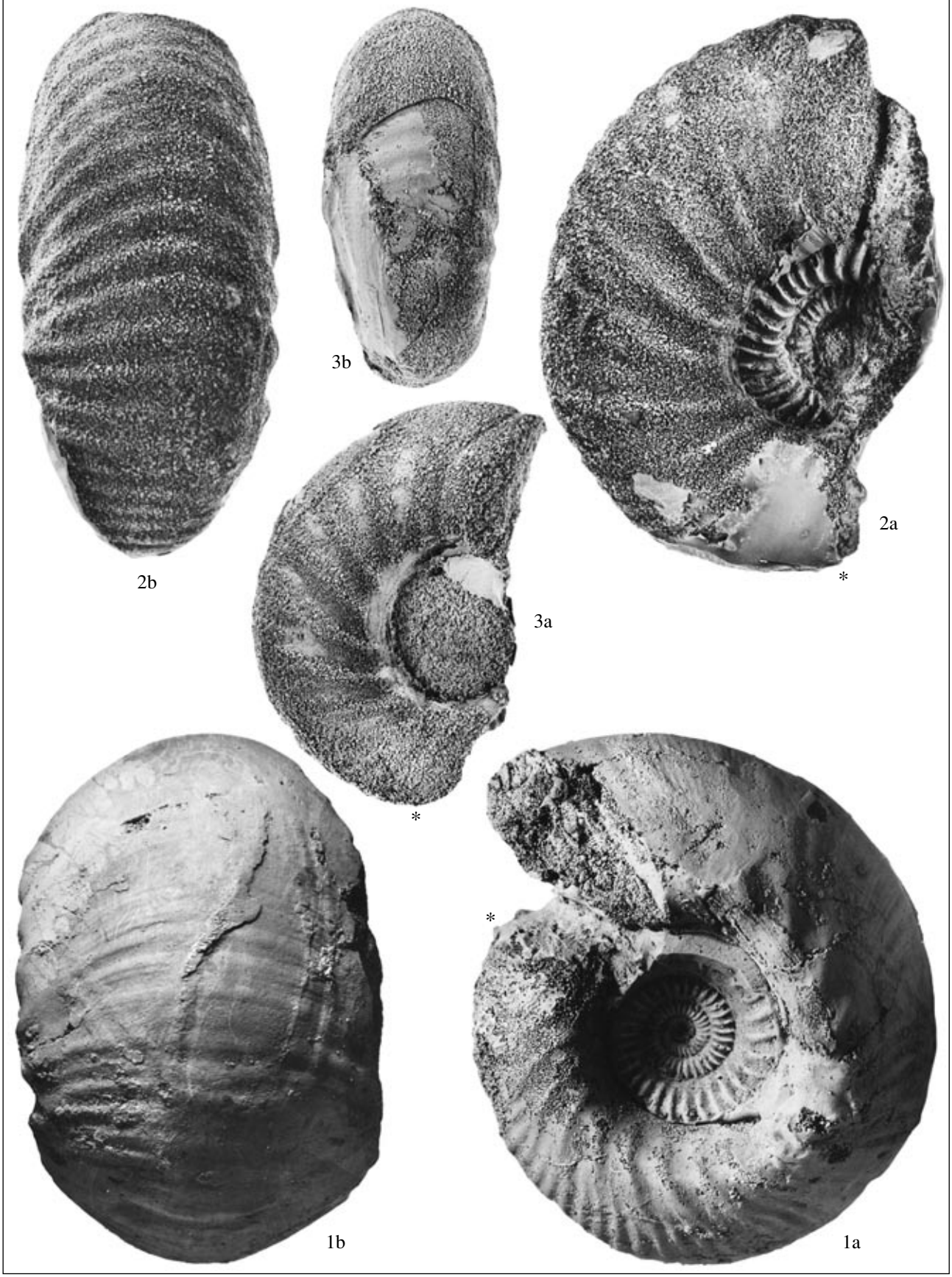
Explanation of Plate 7

All figures are of natural size. The asterisk marks the beginning of the body chamber.

Figs. 1–4. *Cadoceras apertum* Callomon et Birkelund, 1985; (1) specimen no. 5029/20, adult shell with a complete body chamber and preserved aperture: (1a) lateral view, (1b) ventral view; (2) specimen no. 5029/21, phragmocone: (2a) lateral view, (2b) apertural view; (3) specimen no. 5029/22, juvenile shell: (3a) lateral view, (3b) ventral view; (4) specimen no. 5029/23, microconch with a complete body chamber and aperture preserved on one side: (4a) lateral view, (4b) ventral view. All from the Alatyr III section, Upper Bathonian, unnamed zone, faunal horizon *apertum*; collected by the present author.

Fig. 5. *Paracadoceras* sp.; specimen no. 5029/28, young shell: (5a) lateral view, (5b) ventral view. Alatyr II section; Upper Bathonian, *keuppi* Zone; collected by the present author.

Plate 8



Explanation of Plate 8

All figures are of natural size. The asterisk marks the beginning of the body chamber.

Fig. 1. *Cadoceras calyx* Spath, 1932; specimen no. 5029/2, adult shell with a complete body chamber and aperture: (1a) lateral view, (1b) ventral view; the exact level of the occurrence is unknown.

Fig. 2. *Paracadoceras nageli* sp. nov.; paratype no. 5029/32, adult shell with a complete body chamber and preserved aperture: (2a) lateral view, (2b) ventral view; not in situ.

Fig. 3. *Paracadoceras keuppi* sp. nov.; paratype no. 5029/26, young shell with an aperture: (3a) lateral view, (3b) ventral view.

All from the *keuppi* Zone: (1) Alatyr II section, collected by Efimov; (2, 3) from the Alatyr I, collected by the present author.

flanks. They are subdivided into two or three branches, crossing the venter with a strong inclination forward. The intercalating ribs (unconnected with the primary ribs) commonly occur between the secondary ribs. At the end of the body chamber, the secondary ribs become transformed into densely spaced, well-pronounced wrinkles.

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW/Dm	WH/Dm	WW/Dm	UW/Dm
5029/2	98	33	70	38	0.34	0.71	0.39
5029/30	92	35	62	31	0.38	0.67	0.34
5029/31	79	26	52	32	0.33	0.66	0.41

Comparison. This species differs from the similar *C. apertum* first of all in the secondary ribs more pronounced on the venter.

Remarks. Spath described this species based on a single well-preserved specimen. Callomon (1993) assigned some of the other ammonites figured by Spath, including those identified by Spath as the new species *Cadoceras franciscus* and *C. victor*, to this species. Following Callomon, I tentatively placed these species in the synonymy of the species described.

Occurrence. Upper Bathonian of eastern Greenland and the Middle Volga River Region.

Material. Three specimens with a body chamber and partly preserved phragmocone, without inner whorls (in the specimen figured in Pl. 8, fig. 1, the inner whorls are cast in plaster based on the umbilicus imprint) from the Alatyr II section, Prialatyrskaya Series, the exact position in the section is unknown (coll. by V.M. Efimov).

ACKNOWLEDGMENTS

Iraida Starodubtseva (Moscow), Oliver Nagel (Radeberg), Viktor Pirkl (Herlingen), and Andrei Stupachenko (Moscow) took part in the field work in the basin of the Alatyr River. I am grateful for invaluable consultations of John Callomon (London) and for the opportunity to study his collections from eastern Greenland made possible by friendly assistance of Peter Alsen and David Harper (Copenhagen). Louise Longridge and Paul Smith (Vancouver) provided additional information on the type specimen of the genus *Paracadoceras*. I am extremely grateful to all these people and indebted to V.M. Efimov for the ammonites donated and for the indication of the original localities.

The study is supported by Program no. 25 of the Presidium of the Russian Academy of Sciences "Origin and Evolution of the Biosphere," project "Coevolutionary Processes in the Marine Pelagic Biota and Its Response to the Abiotic Changes in the Critical Epochs of the Paleozoic and Mesozoic."

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