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Kepplerites keppleri (Ammonoidea: Kosmoceratidae), an Index Species of the Lowermost Subzone of the Callovian Standard Scale, in Localities of the Russian Platform

V. V. Mitta[a], *, V. V. Kostyleva[b], and A. N. Lebedev[c]

[a] *Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117647 Russia*
[b] *Geological Institute, Russian Academy of Sciences, Moscow, 119017 Russia*
[c] *Independent Researcher, Ulyanovsk, 432072 Russia*
**e-mail: mitta@paleo.ru*

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Abstract—The species *Kepplerites keppleri* (Oppel), first described from southern Germany, is an index species of the lowermost subzone of the Callovian standard scale. This and the wide geographical distribution of this taxon determine its importance for interregional correlation. At the same time, *K. keppleri* is the ancestor of all the Callovian representatives of the genus *Kepplerites* (and the family Kosmoceratidae) in a vast territory of Boreal, Subboreal and Peri-Tethyan marine basins. The paper discusses the finds of this species in Central Russia (Middle Volga area) and their significance for systematics and biostratigraphy. The Bathonian-Callovian boundary on the Russian Platform is proposed to be drawn based on the first appearance of *Kepplerites keppleri*, as is customary in southern Germany.

Keywords: ammonites, Keppleritinae, biostratigraphy, Middle Jurassic, Lower Callovian, Central Russia
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INTRODUCTION

The species *Kepplerites keppleri* (Oppel, 1862) is the type species of the genus *Kepplerites* Neumayr et Uhlig, 1892 and is ancestral to the Callovian representatives of this genus, which in turn is the ancestor of the extensive family Kosmoceratidae Haug, 1887, which existed from the middle Bathonian to the late Callovian inclusive. In addition, *K. keppleri* is an index species of the lowermost subzone of the standard (Western European) Callovian scale, which determines its importance for biostratigraphy.

J.H. Callomon suggested a very wide geographic distribution for *K. keppleri*—Germany, England, the Northern Caucasus, Japan, East Greenland, Alaska, etc. (Callomon, 2001, text-fig. 4). The lower boundary of the *keppleri* Subzone in southern Germany (Albstadt-Pfeffingen section) was put forward as a candidate for the GSSP of the base of the Callovian (Callomon and Dietl, 2000).

Although Callomon's identifications of *K. keppleri* for some regions were subsequently challenged, the extensive range of this species in the Lower Callovian of the Boreal, Subboreal, and Peri-Tethyan regions was confirmed. In particular, *K. keppleri* was identified for the first time from Central Russia, both from new collections (Mitta, 2000) and from museum collections (Mitta and Starodubtseva, 2000).

Over the past decade, our colleagues from Germany have published new data on both the genus *Kepplerites* as a whole and *K. keppleri*, including the position of this species in the phylogeny of the Bathonian–Callovian representatives of the genus (Mönnig and Dietl, 2017). In addition, ammonite associations of the *keppleri* faunal horizon were studied in the Lower Callovian reference section in the Swabian Alb in southern Germany (Dietl et al., 2021) and in the type locality of *K. keppleri* (Dietze and Franz, 2023).

Recently, new data on *Kepplerites keppleri* have been obtained on the Russian Platform. This paper presents information on the geographic and stratigraphic distribution of this species in Central Russia; some published conclusions on the taxonomy of the species *K. keppleri* are discussed.

LOCALITIES AND MATERIAL

The specimens described in this paper are housed in the Paleontological Institute of the Russian Academy of Sciences (PIN RAS), collection no. 5029.

All *Kepplerites keppleri* finds from the Russian Platform come from the lower horizons of the Elatma Formation of the Middle Volga region (Sursko-Mokshinskaya and Simbirskaya structural-facies zones of the Ulyanovsk–Saratov Trough according to: *Unifit-*

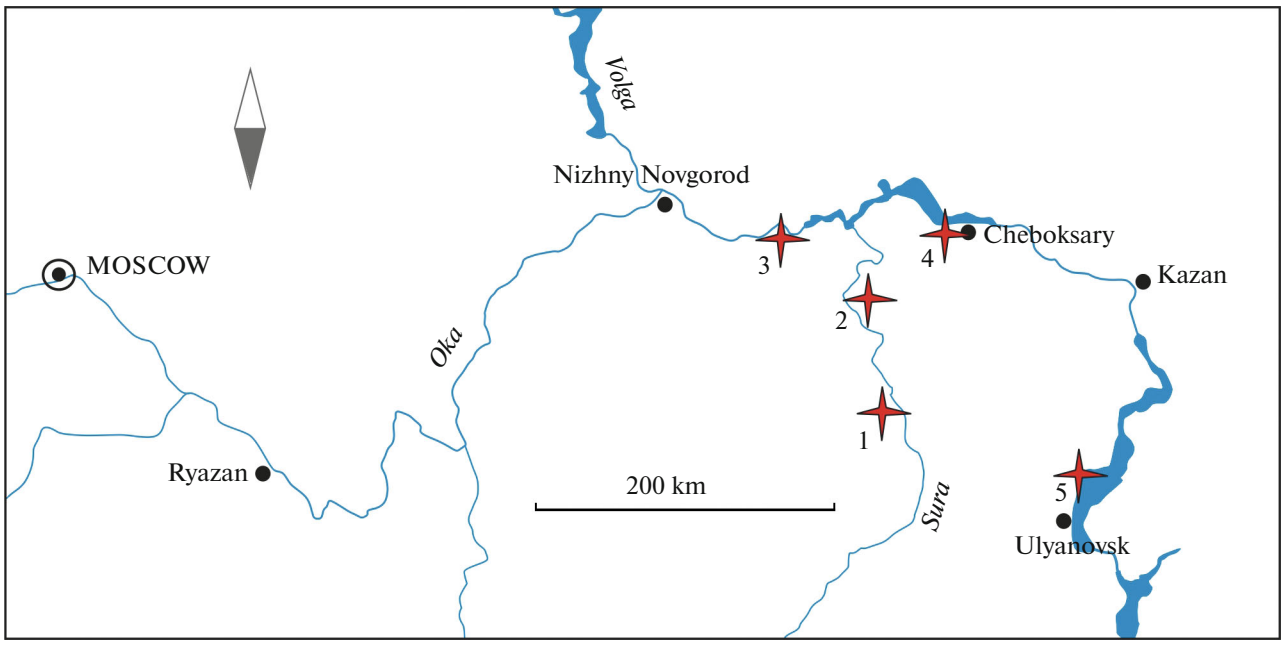

Fig. 1. Localities with *Kepplerites keppleri* (Oppel) in the Middle Volga region: (1) Kisha, (2) Khvadukasy, (3) Prosek, (4) Hyrkasy, (5) Verkhnetarkhanskaya Pristan.

sirovannaya..., 2012). In the modern administrative division, this territory is located within the northwestern part of Chuvashia, the eastern part of the Nizhny Novgorod Region and the part of Tatarstan bordering the Ulyanovsk Region (Fig. 1).

The lower part of the Elatma Formation is represented by dark-gray clays, often with large concretions of clayey limestone and pyrite nodules (the *Cadoceras elatmae* Zone is the basal zone of the Central Russian Callovian). It is noteworthy that to the south, in the Lower Volga region (near Saratov), and to the west, in the Oka River basin (near Elatma), similar rocks of the same age are present, but no *K. keppleri* shells are present in collections from these localities. At the same time, the Lower Callovian outcrops downstream of the town of Elatma have been intensively studied by geologists and paleontologists for many decades, especially from the late 19th to the first third of the 20th centuries. However, only *Cadoceras* (numerous) and *Macrocephalites* (single finds) are present in museum collections and mentioned in publications.

The first published finds of the species under discussion were made *in situ* in a ravine near the village of Khvadukasy, Krasnochetaysky District, Chuvashia (Fig. 1). Here, in association with *Cadoceras frearsi* (d'Orbigny) [M], *Pseudocadoceras* aff. *mundum* (Sasonov) [m], *Eckhardites* cf. *menzeli* (Mönnig) [M], macroconchs *Kepplerites* (*Kepplerites*) *keppleri* (Oppel) and microconchs *K.* (*Toricellites*) sp. (Mitta, 2000, p. 18, pl. 12, fig. 2; pl. 60, figs. 1–4) were found. This interval was assigned to the *keppleri* faunal horizon. Higher up the section, intervals of the *falsum* and *elatmae* faunal horizons were established, without any *Kepplerites* finds.

During analysis of collections made by predecessors in the Vernadsky State Geological Museum of the Russian Academy of Sciences, ammonites very similar to *Kepplerites keppleri* were discovered. Their study showed that these shells really belong to the macroconchs and microconchs of this species (Mitta and Starodubtseva, 2000). Based on the surviving original labels and card index, it was possible to establish that these were collected from Nizhny Novgorod Province by V.A. Stchirowsky.

According to the collector, the ammonites were found on the Kisha River: "Along the bottom of the dried-up river, there are scattered a large number of spherical concretions (up to two quarters in diameter) of dark-gray limestone. These concretions, resembling cannonballs, are filled with perfectly preserved fossils. They contain fragments of crayfish claws and *Pentacrinus* stems, pieces of wood, numerous shells from the genera *Turbo, Pinna, Pecten*, *Avicula*, etc., small belemnite phragmocones and large specimens of *Cadoceras modiolare* Nik., *Cadoceras elatmae* Nik., *Cosmoceras Gowerianum* Sow., and forms close to them" (Stchirowsky, 1892, pp. 153–154). The forms that Stchirowsky identified as "*Cosmoceras Goweria-num* Sow. and forms close to them" were later revised and published as *Kepplerites keppleri* [M] and *K.* (*Toricellites*) sp. [m] (Mitta and Starodubtseva, 2000, p. 14, pl. 3, figs. 1, 2; pl. 4, figs. 1–4).

During a visit to the site on the Kisha River in 2002 by a field team from the All-Russian Research Geo-

logical Oil Institute (VNIGNI), headed by V.V. Mitta, it was discovered that beavers had inhabited the river for over a century, and their dams had raised the water level to at least 1 m. Nevertheless, several spherical concretions of gray clay limestone were retrieved from the river bottom, one of which contained a well-preserved adult shell of *Cadoceras falsum* Voronetz.

Two fragments of ammonite shells from the top of the Bathonian and the base of the Lower Callovian of the section near the village of Prosek in the Lyskovsky District of the Nizhny Novgorod Region were identified as *Kepplerites* (*Kepplerites*) ex gr. *keppleri* (Oppel) (Kiselev and Rogov, 2007, pl. 1, figs. 5, 6).

A new location with *K. keppleri* is a quarry for the extraction of expanded clays near the village of Hyrkasy, Cheboksary urban district. In early 2024, one of us (A.N. Lebedev) received several ammonites from the quarry administration staff, including a *Kepplerites* shell. In September of the same year, the authors of this article jointly studied the geological section exposed by the quarry. From bottom to top, the lower part of the Elatma Formation is exposed here. The description and lithological column of the section (Fig. 2) were compiled by V.V. Kostyleva:

(1) Clay gray, on the weathered surface light gray, silty-sandy, with interbeds of light beige fine-grained sand. Visible thickness 2.0 m.

After a gap of ca. 3 m the following beds crop out:

(2) Clay gray, light gray on the weathered surface, silty, with interbeds of light beige silt and rare pyrite concretions. In the middle part there is a concretionary lenticular interbed (0.1–0.15 m) of fine-grained clayey limestone. The shell *Kepplerites keppleri* (Oppel) (Pl. 5, fig. 2) probably comes from this interval; its matrix is light grey clayey limestone. Visible thickness is 4 m.

(3) After a gap of ca. 11 m the following beds crop out:

(4) Clay dark grey, grey on the weathered surface, silty, with rare pyrite concretions and fragments of carbonized wood. Numerous pyritized cores of *Cadoceras falsum* Voronetz (Fig. 3) and the shell of *Kepplerites keppleri* (Oppel) (Pl. 5, fig. 1) come from this bed. Thickness is about 4 m.

These beds are unconformably overlain by Quaternary reddish-yellow loam.

Lebedev also found another Lower Callovian locality with *Kepplerites*, which we referred to as Verkhnetarkhanskaya Pristan. To the south of the village of Verkhnie Tarkhany in the Tetyushi District of Tatarstan, when water is released from the Kuibyshev Reservoir in early spring and late fall, a narrow strip of the bedrock coast becomes accessible for study. Black clay is exposed here, dark gray on the weathered surface, slightly silty, with small fragments of carbonized and often pyritized detritus and numerous pyritized nodules, with a visible thickness of 0.2–0.3 m.

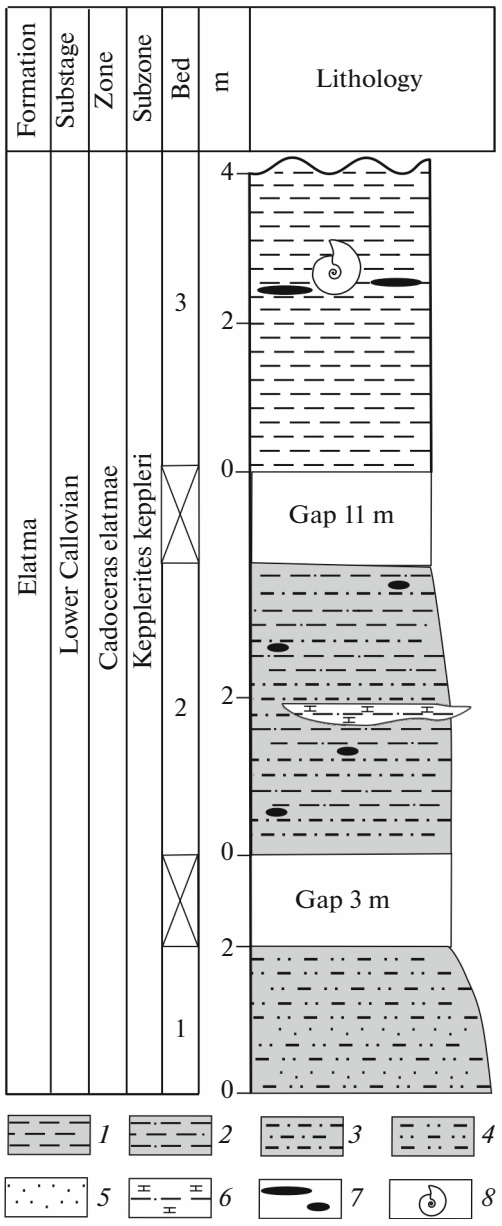

Fig. 2. Lower Callovian section in a quarry near the village of Hyrkasy. Designations: (*1*) clay, (*2*) silty clay, (*3*) silt, (*4*) silty-sandy clay, (*5*) fine-grained sand, (*6*) calcareous concretion bed, (*7*) pyrite nodules, (*8*) ammonites.

Most of the nodules (picked up mainly on the beach) contain ammonites of varying degrees of preservation, including those with a shell. These are mainly *Cadoceras falsum* Voronetz, as well as *C. elatmae* (Nikitin), *C. tschernyschewi* Sokolov (Fig. 4) and *Pseudocadoceras* ex gr. *mundum* (Sasonov); in addition, several *Kepplerites* shells were found. The latter are heavily covered with pyrite or preserved in fragments, but the sculpture (sickle-shaped primary ribs ending in a distinct node at the branching point) allows us to identify them as undoubtedly *K. keppleri* (Oppel) (Fig. 5).

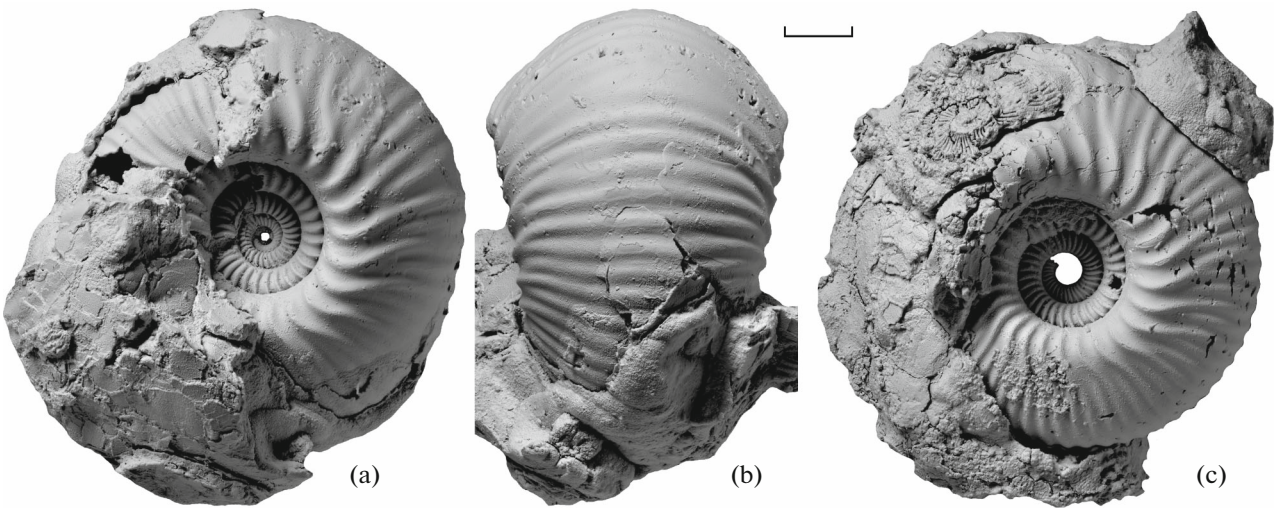

Fig. 3. *Cadoceras falsum* Voronetz: (a, b) specimen PIN, no. 5029/199, phragmocone with a deformed initial part of the body chamber: (a) lateral view, (b) ventral view; (c) specimen PIN, no. 5029/200, phragmocone with the initial part of the body chamber, lateral view; Chuvashia, Cheboksary urban district, quarry near the village of Hyrkasy; Lower Callovian, *Elatmae* Zone, *Keppleri* Subzone; coll. by A.N. Lebedev, 2024. Scale bar 10 mm.

It is noteworthy that only six to seven km upstream (the Tarkhanskaya Pristan area), the Lower Callovian is represented by a thin condensation horizon or even limonite and phosphorite pebbles with ammonite fragments (Mitta, 2003; Mitta et al., 2014).

DISCUSSION

As already mentioned above, a very wide geographic distribution was assumed for the species *Kepplerites keppleri* (Callomon, 2001). Subsequent studies showed that this species characterizes the basal Callovian beds not only in southern Germany, England and the Northern Caucasus, but also in central Russia (Mitta, 2000; Mitta and Starodubtseva, 2000). These data are generally fully presented in the publication by Mönnig and Dietl (2017), but some clarifications and comments are necessary. In particular, Mönnig and Dietl (2017) mention the article by T. Kobayashi on *Kepplerites* from Japan (Kobayashi, 1947), but this involves redefining the holotype of *K.* (*Seymourites*) *japonicus* Kobayashi as *K.* cf. *rionensis*, in the caption (Mönnig and Dietl, 2017, text-fig. 6).

The species *K. rionensis* was first described (based on the holotype) from the Callovian of the vicinity of the village of Tsesi (Georgia) by Khimshiashvili (1957), later than Kobayashi's publication, so *K. japonicus* cannot be treated as synonymy of the junior name *K. rionensis* even in open nomenclature. The Japanese species *K.* (*Seymourites*) *japonicus* Kobayashi, *K.* (*S.*) *acuticostatum* Kobayashi and *K.* (*S.*) *kuzuryuensis* Kobayashi (Kobayashi, 1947, pp. 27–29, pl. 7, figs. 1–3) were established based on single specimens, with sickle-shaped primary ribs with nodes at the branching point at the adult stage. Apparently, all three of these species, as well as *K.* (*K.*) *rionensis* Khimshiashvili, should be considered as junior subjective synonyms of *K.* (*Kepplerites*) *keppleri*. The synonymy of *K. keppleri*, as presented in Mitta and Starodubtseva (2000, p. 14), also includes other Caucasian representatives of *Kepplerites*, published under different (often new) names.

The preservation of the ammonite from the Lower Callovian *Bullatus* Zone of France, identified as *K.* (*K.*) *keppleri* (Branger, 2009, pl. 2, fig. 4) and as *K.* (*K.*) *radiatus* (Mönnig and Dietl, 2017, text-fig. 12.2), is, in our opinion, insufficient for species assignment. A fragment of *Kepplerites* identified as *K.* sp. aff. *K. japonicus* (Nakada et al., 2019, p. 38, text-fig. 5.5), also cannot be more accurately identified.

K. (*K.*) *radiatus* Lominadze et Sakharov was established based on the holotype, a well-preserved adult shell (Lominadze and Sakharov, 1985, p. 7, pl. 3, fig. 1) and the remaining fragments that were not depicted; its description noted that the ribs were radial at all stages and did not form nodes. The type material comes from the Gerchech Pass (Ingushetia), from a thin condensation horizon at the top of the Bathonian (sheet 3 in: Mitta, 2011). Other ammonites from the same locality are described by Lominadze and Sakharov (1985, p. 5, pl. 1, fig. 2; pl. 2, fig. 1) as *K.* (*K.*) *keppleri* and quite reasonably attributed by Mönnig and Dietl to *K.* (*K.*) *radiatus*. In contrast, fully mature shells from the Macrocephalen-Oolith Formation of southern Germany, attributed to *K.* (*K.*) *radiatus* (Mönnig and Dietl, 2017, p. 257, figs. 15, 16.1), show forward-bent primary ribs with pronounced nodes at the branching point, which indicates that they belong to *K.* (*K.*) *keppleri*.

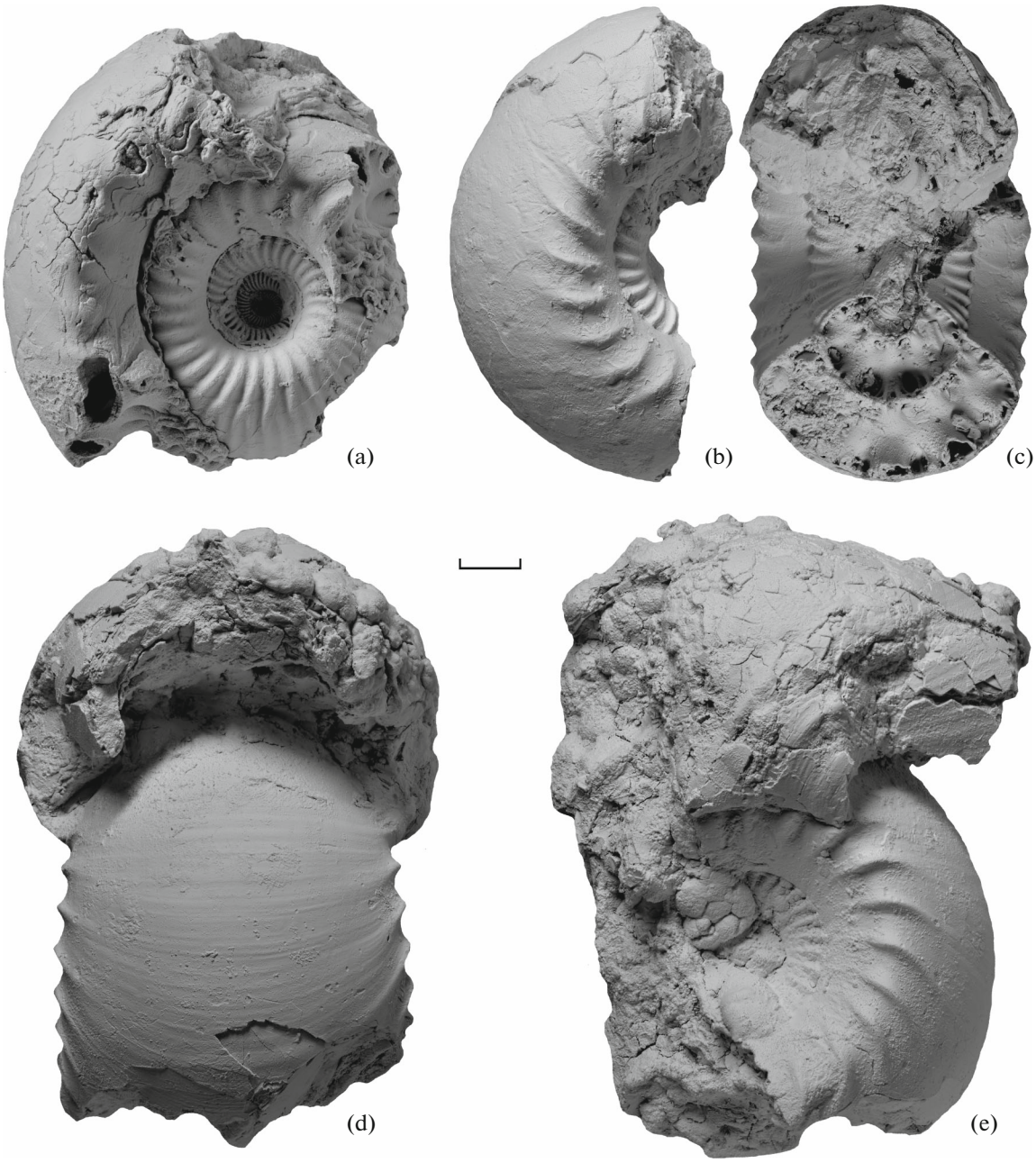

Fig. 4. *Cadoceras* from the Verkhnetarkhanskaya Pristan area: (a) *C. tschernyschewi* Sokolov, specimen PIN, no. 5029/197, phragmocone, lateral view; (b–d) *C. elatmae* (Nikitin): (b, c) specimen PIN, no. 5029/196, fragment of the body chamber with partially preserved previous whorl of the phragmocone: (b) lateral view, (c) cross-section; (d, e) specimen PIN, no. 5029/198: (d) apertural view, (e) lateral view; Tatarstan, Tetyushi District, bank of the Volga River south of the village of Verkhnie Tarkhany; Lower Callovian, *Elatmae* Zone, *Keppleri* Subzone; coll. by A.N. Lebedev, 2024. Scale bar 10 mm.

The inclusion by German authors of ammonites described from the Kisha River (Mitta and Starodubtseva, 2000) as *K.* (*K.*) *keppleri,* in the synonymy of the late Bathonian species *K.* (*K.*) *radiatus,* is most likely a misunderstanding—the shells from this locality have sculpture on the body chamber represented by sickle-shaped curved primary ribs terminating in more or less developed nodes, which is characteristic of *K. keppleri*. Occurrences of *Cadoceras falsum* (Voronetz) in this locality in concretions similar to those described by Stchirowsky suggest that the *Kepplerites* shells from this locality come from the Lower Callovian *falsum* faunal horizon. This is confirmed by the co-occurrences of *Cadoceras falsum* and *Kepplerites keppleri* in the Hyrkasy locality and, additionally, by the presence of *K. keppleri* in the ammonite assemblage collected in the Verkhnetarkhanskaya Pristan area.

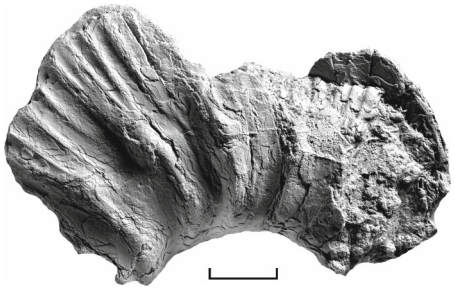

Fig. 5. *Kepplerites keppleri* (Oppel), specimen PIN, no. 5029/203, fragment of the initial part of the body chamber, lateral view; Tatarstan, Tetyushi District, bank of the Volga River south of the village of Verkhnie Tarkhany (Verkhnetarkhanskaya Pristan locality); Lower Callovian, *Elatmae* Zone, *Keppleri* Subzone; coll. by A.N. Lebedev, 2024. Scale bar 10 mm.

This certainly also applies to the redefinitions by Kiselev and Rogov (2007, p. 53), who attributed one specimen of the eight illustrated *Kepplerites* shells from the Kisha River (Mitta and Starodubtseva, 2000, pl. 3, fig. 1) to the Late Bathonian *K. svalbardensis* Sokolov et Bodylevsky.

In discussing the new finds, it is necessary to note their significance for a detailed subdivision of the *Elatmae* Zone. According to Mitta (2000) and other authors, this zone is understood to comprise two subzones and nine faunal horizons (Fig. 6). The *keppleri* faunal horizon was first established on the Russian Platform at the base of the Callovian based on the joint occurrence of the index species, *Cadoceras* sp. (sp. nov.?) [M] and *Pseudocadoceras* sp. ex gr. *mundum* (Sasonov) [m] (Mitta and Starodubtseva, 1998, p. 6). A little later, the identifications of the cardioceratid taxa from this interval (in the Khvadukasi section) were refined: *Cadoceras frearsi* (d'Orbigny) [M], *Pseudocadoceras* aff. *mundum* (Sasonov) [m], *Eckhardites* aff. *menzeli* (Mönnig) (Mitta, 2000, p. 18). Up the section, numerous *Cadoceras falsum* Voronetz and a few *C. elatmae* (Nikitin) were found (*falsum* faunal horizon).

The joint findings of *Kepplerites keppleri* and *Cadoceras falsum* in the Hyrkasy section clearly show that the species *K. keppleri* also continues into the *falsum* faunal horizon; this is indirectly confirmed by its findings in other localities (Kisha and Verkhnetarkhanskaya Pristan).

In the upper part of the Keppleri Subzone (*elatmae* and *tschernyschewi* faunal horizons), *Kepplerites* representatives in the Central Russian sections (Unzha River, Kostroma Region) are represented by juvenile whorls and fragments that cannot be determined to species. Most of the next subzone, *Subpatruus* (three faunal horizons), is characterized by one dimorphic pair of kosmoceratids—*Kepplerites* (*Gowericeras*) *russiensis* Mitta [M] and *K.* (*Toricellites*) *unzhensis* Mitta [m] (Mitta and Starodubtseva, 1998, pl. 4, figs. 1–3; Mitta, 2000, pl. 61, figs. 1–5; Mönnig and

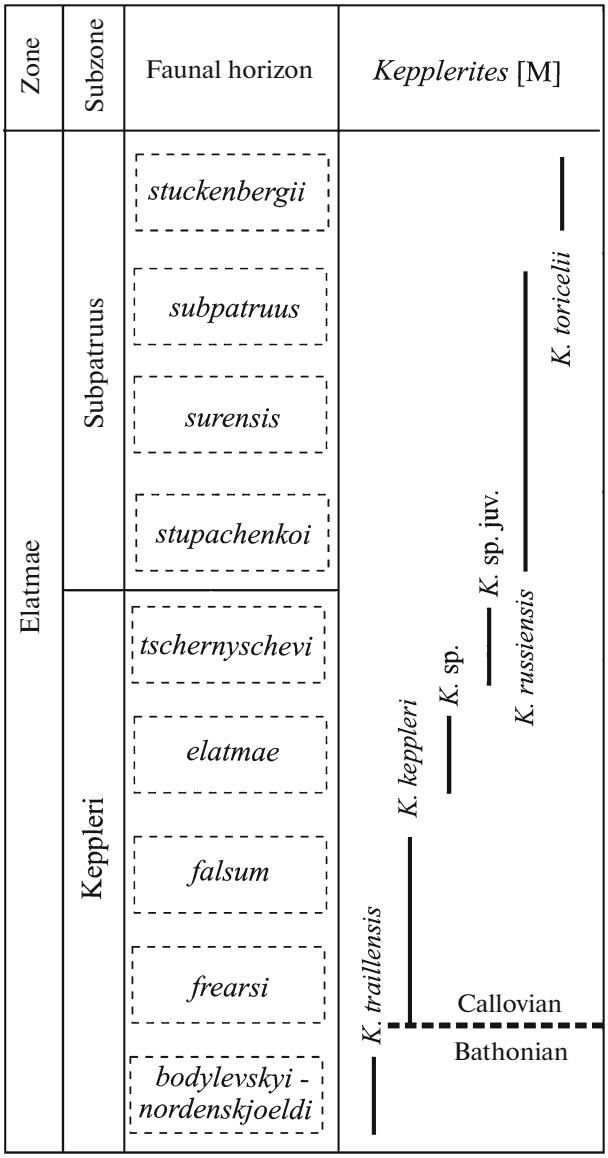

Fig. 6. Stratigraphic distribution of *Kepplerites* in the Lower Callovian Zone of the Russian Platform. The dotted line shows the proposed Bathonian–Callovian boundary.

Explanation of Plate 5

Figs. 1, 2. *Kepplerites keppleri* (Oppel): (1) phragmocone, specimen PIN, no. 5029/201: (1a) apertural view, (1b) lateral view, (1c) ventral view; (2) adult shell, specimen PIN, No. 5029/202: (2a) apertural view, (2b) lateral view, (2c) ventral view; Chuvashia, Cheboksary urban district, quarry near the village of Hyrkasy; Lower Callovian, *Elatmae* Zone, *Keppleri* Subzone; from the collection of A.N. Lebedev. Scale bar 10 mm.

Plate 5

Dietl, 2022, text-fig. 11, 1–3; etc.). The shells of these ammonites are clearly distinguished from those of *K. keppleri* by their rounded cross-section and nodes present on the flanks at the branching point of the ribs on the last whorl of the phragmocone—the beginning of the body chamber between one or two, rarely three primary ribs.

Another dimorphic pair of kosmoceratids occurs at the top of the *Subpatruus* Subzone (*stuckenbergii* faunal horizon): *K.* (*Gowericeras*) *toricellii* (Oppel) [M] and *K.* (*Toricellites*) *uhligi* (Parona et Bonarelli) [m] (Mitta, 2000, pl. 62, figs. 1–7). On the phragmocone of the macroconchs of these ammonites, nodes at the branching point are already observed on each primary rib, but on part of the body chamber, ribs with nodes still alternate with ribs without nodes. The shell morphology strongly suggests that these are direct descendants of the dimorphic pair *K.* (*Gowericeras*) *russiensis/K.* (*Toricellites*) *unzhensis* and ancestors of the large group *K.* (*G.*) *gowerianus* (Sowerby), occuring higher up, in the Lower Callovian *Gowerianus* Zone of the Russian Platform.

K. traillensis Donovan, a species first described from East Greenland (holotype: Donovan, 1953, pl. 17, fig. 1) is here considered as the direct ancestor of *Kepplerites keppleri*. In the Central Russian sections, *K. traillensis* is indicated in the very bottom of the Callovian together with *Cadoceras bodylevskyi* Frebold and *C. nordenskjoeldi* Callomon et Birkelund (Mitta, 2000, 2004, 2008).

The lowest part of the Callovian on the Russian Platform was recognized as the *bodylevskyi* faunal horizon, with *Cadoceras bodylevskyi* and *Kepplerites* ex gr. *svalbardensis* Sokolov et Bodylevsky (Mitta, 2000, p. 26, pl. 9, 59). Further study of the ammonites of this interval showed that it is characterized by *K. traillensis* Donovan, *Cadoceras bodylevskyi* Frebold, *C. nordenskjoeldi* Callomon et Birkelund and their microconchs (Mitta, 2004, pls. 3, 4). Considering that the last species was found only in the scree (but together with *Kepplerites traillensis*), there remained understandable doubts that this association was of the same age. As a result, taking into account the morphology of representatives of *Cadoceras*, the interval under discussion was subdivided into the *nordenskjoeldi* (bottom) and *bodylevskyi* (top) levels, both assigned to the *traillensis* faunal horizon (Mitta, 2004, fig. 2). In subsequent publications (Mitta, 2005, p. S632; Mitta, 2008, table 1) the levels of occurrences of *C. nordenskjoeldi* and *C. bodylevskyi* were indicated as successive faunal horizons, for which *Kepplerites traillensis* was considered as transitional one.

CONCLUSIONS

The above data show that the succession of species of the family Cardioceratidae (genus *Cadoceras*) at the beginning of the Callovian (in the *Elatmae* Chron) occurred much faster than the change of species of the family Kosmoceratidae (genus *Kepplerites*). For nine to ten faunal horizons of cardioceratids in this interval there are only five to six species of kosmoceratids; at the same time, the species in both families are connected by transitional forms, which confirms the continuity of both phyletic lines.

Species-level identification of ammonites from different regions and localities, especially near stage boundaries, can often lead to disagreement among specialists. Only a few controversial concepts of the taxa under discussion have been mentioned above.

The best-defined and most stable taxonomic units are rightly considered to be taxa of genus rank. The discussed kosmoceratids (genus *Kepplerites* in the subfamily Keppleritinae) are represented in the *Elatmae* Zone by two subgenera—*Kepplerites* s. str., characteristic of the *Keppleri* Subzone, and *K.* (*Gowericeras*), quite definitely characterizing the *Subpatruus* Subzone (and the *Gowerianus* Zone higher in the section).

In contrast, the evolution of cardioceratids (subfamily Cadoceratinae) in the same interval of geological time occured much faster. In the *Keppleri* Subzone, there are only species of the genus *Cadoceras* Fischer with a cadiconic shell, which are replaced at the base of the *Subpatruus* Subzone by species of the genus *Cadochamoussetia* Mitta, with a pronounced tendency for the umbilicus to narrow and the cross-section to increase, ultimately leading to the appearance of *Chamoussetia* R. Douvillé with an oxyconic shell—a dead-end iteration that continued for some time in the *Gowerianus* Chron (Mitta, 1999, 2016; etc.). Accordingly, the sequence of faunal horizons established for the *Elatmae* Zone exclusively based on cardioceratids is more detailed. At the same time, cardioceratid species from different regions and locations of the Bathonian–Callovian boundary interval are often identified differently by different authors.

Possibly, the previously published proposal (Mitta and Starodubtseva, 1998) that first appearance of *Kepplerites keppleri* should define the base of the Callovian on the Russian Platform should be accepted. In our understanding, this corresponds to the *frearsi* faunal horizon (Fig. 6). Most authors agree on the concept of *Cadoceras frearsi* (d'Orbigny, 1845) (neotype: Sazonov, 1957, pl. 4, figs. 1, 1a; proposed by Callomon and Birkelund, 1985, p. 82). This also agrees with the opinion of Callomon and Dietl (2000) and Mönnig and Dietl (2017), who accept the first appearance of *Kepplerites keppleri* as the base of the Callovian in southern Germany.

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CONFLICT OF INTEREST

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

REFERENCES

Branger, P., Buffevent (Deux-Sèvres), une nouvelle coupe de référence pour la base du Callovien, *Rev. Natur. Deux-Sèvres Nat. Environnement*, 2009, no. 2, pp. 52–58.

Callomon, J.H. and Birkelund, T., Description of three new species, *Spec. Pap. Palaeontol.*, 1985, vol. 33, pp. 78–86.

Callomon, J.H. and Dietl G. On the proposed basal boundary stratotype (GSSP) of the Middle Jurassic Callovian Stage, in *Advances in Jurassic Research*, Hall, R.L. and Smith, P.L., Eds., Trans Tech Publ., 2000, pp. 41–54 (*GeoResearch Forum*, vol. 6).

Callomon, J.H., Fossils as geological clocks, in *The Age of the Earth: from 4004 BC to AD 2002*, Lewis, C.L.E. and Knell, S.J., Eds., London: Geol. Soc., 2001, pp. 237–252 (*Geol. Soc. Spec. Publ.*, no. 190).

Dietl, G., Mönnig, E., and Schweigert, G., The ammonites of the *keppleri* Horizon (basal Callovian, Middle Jurassic) of Albstadt-Pfeffingen (Swabian Alb, Germany)—biostratigraphy and correlation, *N. Jb. Geol. Paläontol. Abh.*, 2021, vol. 302, no. 1, pp. 1–33.

Dietze, V. and Franz, M., Nachtrag zur Ammonitenfauna in Grenzbereich Bathonium/Callovium (Mittlerer Jura in Eningen unter Achalm (Mittlere Schwäbische Alb, SW Deutschland), der Typus-lokalität der Ammonitenart *Kepplerites keppleri* (Oppel, 1862), *Jh. Ges. Naturk. Württ.*, 2023, vol. 179, pp. 173–184.

Donovan, D.T., The Jurassic and Cretaceous stratigraphy and palaeontology of Traill Ø, East Greenland, *Medd. Grønland.*, 1953, vol. 111, no. 4, pp. 1–150.

Khimshiashvili, N.G., *Verkhneyurskaya fauna Gruzii (Cephalopoda i Lamellibranchiata)* (Upper Jurassic Fauna of Georgia (Cephalopoda and Lamellibranchiata)), Tbilisi: Akad. Nauk. Gruz. SSR, 1957.

Kiselev, D.N. and Rogov, M.A., Stratigraphy of the Bathonian–Callovian boundary deposits in the Prosek section (Middle Volga Region). Article 1. Ammonites and infrazonal biostratigraphy, *Stratigr. Geol. Correl.*, 2007, vol. 15, no. 5, pp. 485–515.

Kobayashi, T., On the occurrence of *Seymourites* in Nippon and its bearing to the Jurassic palaeogeography, *J. Japan. Geol. Geogr.*, 1947, vol. 20, pp. 1–19.

Lominadze, T.A., and Sakharov, A.S., *Kosmotseratidy Kavkaza* (Kosmoceratids of the Caucasus), Tbilisi: Metsniereba, 1985.

Mitta, V.V. and Starodubtseva, I.A., Field work of 1998 and biostratigraphy of the Lower Callovian of the Russian Platform, *Vernadsky Mus. Novit.*, 1998, no. 2, pp. 1–20.

Mitta, V.V., The genus *Cadochamoussetia* in the phylogeny of the Jurassic Cardioceratidae (Ammonoidea), Advancing Research on Living and Fossil Cephalopods, Oloriz, F. and Rodriguez-Tovar, F.J., Eds., N.Y.: Kluwer Acad.—Plenum Publ., 1999, pp. 125–136.

Mitta, V.V. and Starodubtseva, I.A., W.A. Stchirowsky and study in the Mesozoic of Alatyr–Kurmysh area (basin of the Middle Volga), *Vernadsky Mus. Novit.*, 2000a, no. 5. pp. 1–20.

Mitta, V.V., Ammonites and biostratigraphy of the Lower Callovian of the Russian Platform, *Bull. KF VNIGNI*, 2000b, no. 3, pp. 1–144.

Mitta, V.V., On the boundary deposits of the Callovian and Oxfordian of the Volga Basin, *Vernadsky Mus. Novit.*, 2003, no. 11, pp. 1–21.

Mitta, V.V., On the evolution of ammonites and stratigraphy of Bathonian–Callovian boundary deposits in the Volga basin, in *Ekosistemnye perestroyki i evolyutsiya biosfery* (Ecosystem Restructurings and Evolution of the Biosphere), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 2004, no. 6, pp. 125–136.

Mitta, V.V., Late Bathonian Cardioceratidae (Ammonoidea) from the middle reaches of the Volga River, *Paleontol. J.*, 2005, vol. 39, Suppl. 5, pp. S629–S644.

Mitta, V.V., The genus *Kepplerites* Neumayr et Uhlig (Kosmoceratidae, Ammonoidea) in the Bathonian–Callovian beds (Middle Jurassic) of the Russian Platform, *Paleontol. J.*, 2008, no. 1, pp. 5–14.

Mitta, V.V., Ammonites of the genus *Cadoceras* (Cardioceratidae) from the uppermost Bathonian-lowermost Callovian of the Northern Caucasus (Ingushetia), *Paleontol. J.*, 2011, vol. 45, no. 6, pp. 609–619.

Mitta, V.V., On the phylogeny of early Cardioceratidae (Ammonoidea) and Cadoceratinae of Central Russia at the Bathonian–Callovian boundary, *Paleontol. J.*, 2016, vol. 50, no. 4, pp. 358–368.

Mitta, V.V., Kostyleva, V.V., Glinskikh, L.A., et al., Middle Jurassic Stratigraphy of the southwestern part of the Republic of Tatarstan, *Stratigr. Geol. Correl.,* 2014, vol. 22, no. 1, pp. 28–43.

Mönnig, E. and Dietl. G., The systematics of the ammonite genus *Kepplerites* (upper Bathonian and basal Callovian, Middle Jurassic) and the proposed basal boundary stratotype (GSSP) of the Callovian Stage, *N. Jb. Geol. Paläontol. Abh.*, 2017, vol. 286, no. 3, pp. 235–287.

Mönnig, E. and Dietl, G., Die Ammonien-Gattung *Kepplerites* in der obersten Herveyi- und der Koenigi-Zone

(Unter Callovium, Mittel Jura) von Nord- und Süddeutschland, *Geol. Paläontol. Westfalen*, 2022, vol. 95, pp. 3–84.

Nakada, K., Nakayama, K., Sakai, Y., and Noda, Y., Middle Jurassic fossil molluscan assemblage from the Itoshiro River in Kaizara, Ono City, Fukui Prefecture, *Mem. Fukui Pref. Dinosaur Mus.*, 2019, vol. 18, pp. 1–42.

Sazonov, N.T., *Yurskiye otlozheniya tsentral'nykh oblastey Russkoy platformy* (Jurassic Beposits of the Central Kegions of the Russian Platform), Leningrad: Gostoptekhizdat, 1957.

Stchirowsky, V., Brief outline of the south-eastern part of Kurmysh district and adjacent parts of Alatyr district of Simbirsk Province, *Izv. Geol. Kom.*, 1892, vol. 11, no. 6, pp. 147–161.

Unifitsirovannaya stratigraficheskaya skhema yurskikh otlozheniy Vostochno-Yevropeyskoy platformy, Ob''yasnitel'naya zapiska (Unified Stratigraphic Scheme of the Jurassic Deposits of the East European Platform, Explanatory Note), Mitta, V.V., Alekseev, A.S., and Shik, S.M., Eds., Moscow: Paleontol. Inst.– VNIGNI, 2012.