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'PARAINOCERAMYA' PSEUDORETRORSA (INOCERAMIDAE, BIVALVIA) FROM THE DORSOPLANITES PANDERI ZONE (VOLGIAN STAGE, UPPER JURASSIC) OF EUROPEAN RUSSIA

LEV E. SHILEKHIN[1,2*] & MIKHAIL A. ROGOV[1]

[1]Geological Institute of RAS, 119017 Moscow, Russia. E-mail: levia4an@mail.ru
[2]Moscow State University, 119991 Moscow, Russia
[*]Corresponding author.

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Abstract. The bivalve species *'Parainoceramya' pseudoretrorsa* (Gerasimov, 1955) is redescribed. All occurrences of the species are summarized, including those from localities previously unreported. *'P.' pseudoretrorsa* is widely distributed in the *Dorsoplanites panderi* Zone of the Middle Volgian Substage from the coast of the Barents Sea in the north to the Saratov Volga Region and northern Kazakhstan in the south. It has a narrow stratigraphic range within the Zarajskensis ammonite Subzone, and most of the finds of the species are confined to black shales. Thus, the range of this species is considerably narrower than that of any species of the genus *Buchia* and is comparable to those of the most rapidly evolving ammonoid species. The *'P.' pseudoretrorsa* biohorizon is proposed here for this event; this is the first case of establishing this type of biostratigraphic unit based on bivalves. Furthermore, the Late Jurassic evolution of the superfamily Inoceramoidea is briefly reviewed and the prospects for identifying biostratigraphic units in the Upper Jurassic based on Inoceramoidea are evaluated.

Introduction

The bivalves of the superfamily Inoceramoidea flourished in the second half of the Cretaceous period. Rapid rates of evolution, cosmopolitan distribution, and high resistance to dysoxic conditions allowed them to become one of the most important biostratigraphic tools for Upper Cretaceous deposits on a global scale (Dhondt 1992; Harries et al. 1996; Ifrim 2017). The Early to Middle Jurassic (pre-Callovian) representatives of this superfamily are an important group primarily for the Boreal and Notal (Gondwanian) biogeographic regions (Koshelkina 1974; Damborenea 1990; Shurygin 2005), although at this time they also occurred at low latitudes.

From the Callovian to the beginning of the Early Cretaceous, inoceramoids declined in diversity and became relatively rare (Pergament 1967). The currently documented record of Inoceramoidea from this interval is confined to several discrete stratigraphic levels and does not span the entire Callovian to earliest Cretaceous succession. This patchy record was probably related mainly to ecological and facies controls, particularly bottom-water oxygenation, while possible competition with Bu-

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chiidae cannot be excluded as an additional factor (Zakharov 1966, 1981; Pokhialainen 1974). The previously noted alternation of intervals dominated by Buchiidae and Inoceramidae in Ryazanian strata of Northern Siberia (Zakharov & Turbina 1979), in the Jurassic–Cretaceous sedimentary succession of Western Siberia (Panchenko et al. 2015), and in Middle Volgian succession of the Timan–Pechora region (Shilekhin & Rogov 2024) may reflect differences in environmental tolerance between these groups, particularly with respect to oxygenation.

At present, the Late Jurassic is the least studied interval for the evolution of the Inoceramoidea. Late Jurassic representatives of the superfamily are characterized by a predominantly high-latitude distribution. From the Southern Hemisphere, they are known from Antarctica (Thomson & Willey 1972; Quilty 1977; Crame 1982), India (Jaitly et al. 1995; Fürsich et al. 2022), New Zealand (Speden 1970), and Argentina (Sokolov 1946). A separate monograph was devoted to the Jurassic Inoceramoidea of Japan (Hayami 1960). In the Panboreal Superrealm (Westermann 2000), comprehensive information on Late Jurassic Inoceramoidea is available for Western Siberia (Braduchan et al. 1986), Eastern Siberia (Koshelkina 1962; Zakharov 1966; Zakharov & Turbina 1979), and England (Arkell 1933; Kelly 1984; Clausen & Wignall 1990). Surprisingly, only a few finds are known from North America (Imlay 1964; Villaseñor et al. 2005). Rare finds of Inoceramoidea are also known from the Upper Jurassic of southern Europe (Spain, southeastern France, Switzerland), as well as Saudi Arabia (Howarth & Morris 1998). However, information on the Tethyan Inoceramoidea of the Upper Jurassic of Europe is often either limited to figures of not always precisely stratigraphically referenced finds in 19th-century publications (e.g., Thurmann & Etallon 1862), or to simple mentions of taxa without images in newer publications (Weber 1955; Checa & Sequeiros 1990). From the Late Jurassic Middle Russian Sea only two species of Inoceramoidea have been described, both of which are known from a single figure, and not revised (Ilovaisky 1903; Gerasimov 1955).

Most Upper Jurassic inoceramids are referred to the genus *Parainoceramya* Ros-Franch, Damborenea, Márquez-Aliaga et Manceñido, 2015 in recent literature, which was established for Jurassic taxa previously assigned to the genus *Parainoceramus* Voronetz, 1936. It was already established more than 40 years ago that the type species of the genus *Parainoceramus*, *P. bukurensis* Voronetz, 1936, is of Permian age and belongs to the genus *Kolymia* (Muromtseva & Guskov, 1984). Nevertheless, the name *Parainoceramus* was applied to Jurassic species for a long time. When discussing the family Kolymiidae, Biakov (2013, p. 149) pointed out that "Mesozoic representatives assigned to the genus *Parainoceramus* should be considered within another genus". The type species of the genus *Parainoceramya*, *Crenatula ventricosa* J. de C. Sowerby, 1823, originates from the Lower Jurassic, and Middle Jurassic to Lower Cretaceous species were assigned to that genus merely by convention. *Parainoceramya* sensu stricto is characterized by a multivincular ligament attached to the inner nacreous/lamellar layer. In contrast, several Late Jurassic forms, including *'P.' cramei* and the material described here, show a ligament area developed on a thickened prismatic calcite layer. These differences, previously noted for Upper Jurassic inoceramoids (Knight & Morris 2009; Ros-Franch et al. 2015), indicate that the studied taxon is not *Parainoceramya* in the strict sense. The assignment of the Upper Jurassic inoceramids studied here to the genus *Parainoceramya* is therefore retained only provisionally, because the available material is insufficient for formal genus-level taxonomy.

Although finds of Inoceramoidea in Upper Jurassic deposits are relatively rare, in some stratigraphic intervals they occur in great quantities, forming marker horizons (Panchenko et al. 2015; Shilekhin & Rogov 2024). Representatives of this group, apparently, could episodically inhabit the bottom of marine basins and reach high population densities. This allows us to consider inoceramids as a promising group for stratigraphy of the Upper Jurassic.

Of particular interest in this respect is the species '*Parainoceramya*' *pseudoretrorsa* (Gerasimov, 1955). We use quotation marks following the proposal of Bengtson (1988, p. 224), who stated "that the species is thought to belong to a new genus related to the named genus, but the material available is insufficient for the formal erection of a new genus". This species has been repeatedly mentioned in publications about the Middle Volgian of European Russia and adjacent Kazakhstan but has only been illustrated sporadically. First mentioned in

Table 1 - Localities of *'Parainoceramya' pseudoretrorsa.*

Number in Fig. 1	Locality	Latitude	Longitude	Host rock	Age	References
1	Borehole 3, district of Naryan-Mar, Nenets region	67.649426	53.205165	Black shales	Panderi Zone	Firer & Chernyavskiy 1964; this paper
2	Borehole Kharyaginskaya 260, Nenets region	67.189535	56.659127	Black shales	Panderi Zone	This paper
3	Izhma river, Komi Republic	63.917506	53.747353	Black shales, clays	Panderi Zone	Stratigraphy of the Jurassic System…, 1976; Repin et al. 2006
4	Ayuva river, Ayuva-7 section, Komi Republic	63.699264	54.226558	Black shales, clays	Zarajskensis Subzone; *regularis* biohorizon	Ippolitov et al. 2023; this paper
5	Vonyu river, Komi Republic	63.640939	54.259794	Black shales, clays	Zarajskensis Subzone; *regularis* biohorizon	Ippolitov et al. 2023; this paper
6	Borehole 338 (depth 35.5-39.15 m), Chim-Loptyuga field, Arkhangelsk region	63.135221	48.310352	Black shales	Panderi Zone	This paper
6	Borehole 353 (depth 11.2 m), Chim-Loptyuga field, Arkhangelsk region	63.131558	48.269967	Black shales	Panderi Zone	This paper
7	Sysola river, Yb section, Komi Republic	61.0798	50.3389	Black shales	Panderi Zone	The collection of L.I. Lutugin; Khudyaev 1927
8	Vizinga river, Komi Republic	60.966757	49.807055	Black shales	Panderi Zone	Khudyaev 1927; this paper
9	Koygorodok, Komi Republic	60.445227	50.999838	Siltstones	Panderi Zone	This paper
10	Kazhimsky factory, Sysola river, Komi Republic	60.331679	51.533301	Marls	Panderi Zone	This paper
11	Loyno, Kirov region	59.721966667	52.653897222	Sandstone, sands, shaly silts	Zarajskensis Subzone	This paper
12	Sinegor'ye, Kirov region	59.703055556	50.684166667	Black shales, clays, silt,	Zarajskensis Subzone; *pilicensis* biohorizon	This paper
13	Letka river, Komi Republic	59.520677	49.490821	Clays	Panderi Zone	Krotov 1887
14	Kobra river, Kirov region	60.027907	50.761353	Sandy marls	Panderi Zone	Jirmunski 1918; Kazakov 1927; Kassin 1928, 1941; this paper
15	Vyatka river, Kirov region	59.339972	52.241434	Sandy marls	Panderi Zone	Nikitin 1886; Kassin 1928; this paper
16	Neya river, Kostroma region	58.533786	44.834089	Black shales	Panderi Zone	Krom 1933
17	Ivkino, Kostroma region	58.2433	44.658	Black shales, clays, marls	Zarajskensis Subzone; *kuteki* biohorizon	Sokolov 1929; Gerasimov 1955; Rogov 2021; this paper
18	Borehole 52 (depth 62-68 m), Kostroma region	58.472567	42.654742	Clays	Panderi Zone	Kuznetsova 1965
18	Borehole 1 (depth 188.4-197.6 m), Kostroma region	58.422097	42.309289	Clays	Panderi Zone	Kuznetsova 1965
19	Unzha river, near the village of Ugory, Kostroma region	58.129583	44.359761	Black shales	Panderi Zone	Krom 1933
20	Gorka, Kostroma region	58.04769	44.07011	Siltstones	Zarajskensis Subzone; *regularis* biohorizon	Rogov 2021; this paper
21	Bula river, Chuvash Republic	55.078061	47.734183	Black shales	Panderi Zone	Gerasimov & Kazakov 1939; Mitta 1986
22	Kilna river, Republic of Tatarstan	54.800476	48.612332	Black shales, clays	Zarajskensis Subzone	Zonov 1939
22	Sviyaga river, Republic of Tatarstan	54.734539	48.338310	Black shales	Zarajskensis Subzone	Zonov 1939
23	Borehole 1, Republic of Tatarstan	54.554405	47.383131	Black shales, clays	Panderi Zone	Zorina 2007
24	Gorodischi, Ulyanovsk region	54.574209	48.417261	Black shales	Zarajskensis Subzone; *kuteki, regularis* and *pilicensis* biohorizons	Kuleva et al. 2004; this paper
25	Kashpir, Samara region	53.043506	48.446059	Black shales, clays	Panderi Zone	Gerasimov 1955
26	Yablonovy ravine, burnt shales quarry, Samara region	52.84404	50.41025	Black shales	Zarajskensis Subzone; *kuteki* biohorizon	This paper
27	Borehole 559 (depth 63.9-121.1 m), Samara region	52.158263	50.4315	Black shales, clays	Zarajskensis Subzone; *kuteki, regularis* and *pilicensis* biohorizons	Bukina et al. 1985; Kuleva et al. 2004; this paper
28	Borehole 120 (depth 46-55.5 m), Saratov region	52.341	48.61	Black shales	Panderi Zone	Molostovsky et al. 2004; this paper
29	Ivanikha, Saratov region	51.916866	50.6559833	Black shales	Panderi Zone	This paper
30	Borehole 121, Saratov region	51.798060	50.162623	Black shales	Panderi Zone	This paper
31	Borehole 1038 (depth 37.1-50.4 m), Saratov region	51.753983	50.650902	Black shales, clays	Panderi Zone	Bukina et al. 1985
32	Ozinsky shale mine, Saratov region	51.168820	49.639393	Black shales	Panderi Zone	This paper
33	Near the city of Uralsk, Kazakhstan	51.31	51.96	Black shales, clays	Panderi Zone	Sokolov 1921
34	Borehole Aleksandrovogayskaya-1 (depth 2050-2055 m), Saratov region	50.141	48.61	Black shales	Zarajskensis Subzone; *regularis* biohorizon	This paper

the late 19th century (Nikitin 1886; Krotov 1887), the Late Jurassic specimens were erroneously assigned to the Middle Jurassic species *Inoceramus retrorsus* Keyserling, 1848 (Bodylevsky 1948; Voronets & Laptinskaya 1954). At the beginning of the 20th century, most researchers believed that this was a taxon characteristic of the Portlandian Stage (= Middle Volgian Substage), widely distributed in European Russia (Sokolov 1912; Jirmunski 1918; Sokolov 1921, etc.).

P.A. Gerasimov (1955) described the species *I. pseudoretrorsus* on the basis of material from sections of the Kostroma and Samara regions, noting that it occasionally co-occurred with *I. retrorsus.* Gerasimov provided only a brief description and figured only a single valve, later re-figured (Gerasimov et al. 1995). After Gerasimov's studies, the species was never redescribed and was figured only once, in a recent publication (Ippolitov et al. 2023). Today, it is clear that the generic affiliation of this species should be reconsidered and the species needs revision.

We collected a representative number of specimens of this species, and also studied material stored in the Central Scientific Research Geological Exploration Museum named after Academician F. N. Chernyshev (CNIGR Museum, St. Petersburg), V.I. Vernadsky State Geological Mu-

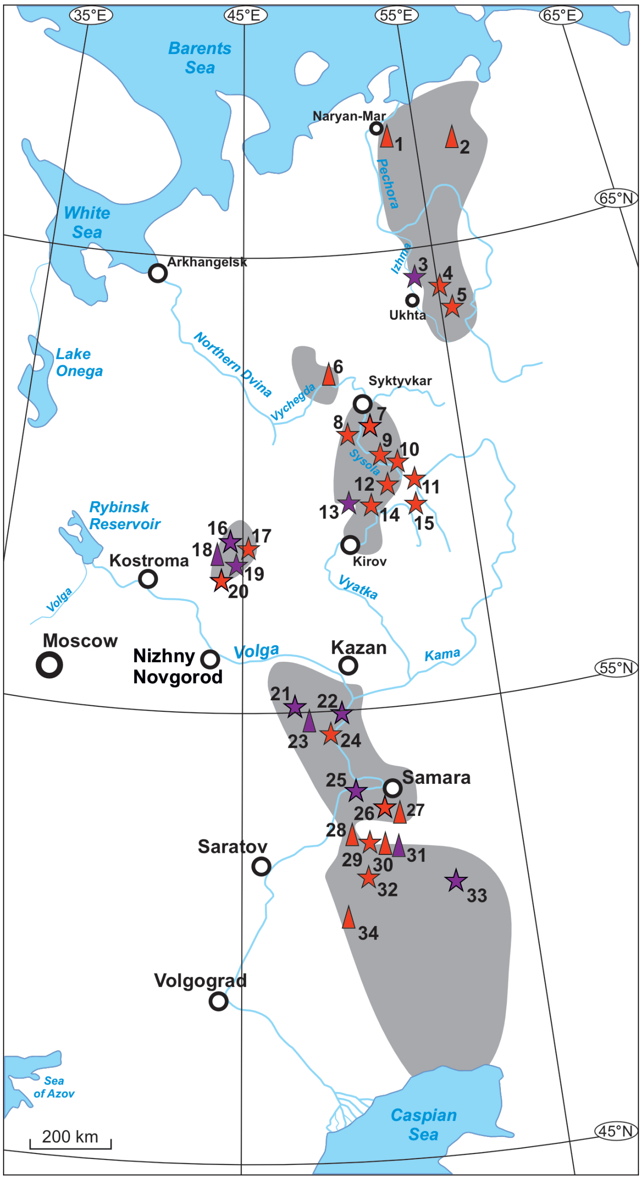

Fig. 1 - Location of the sections from which the material originates: 1) Naryan-Mar borehole 3; 2) Borehole Kharyaginskaya 260; 3) Izhma river; 4) Ayuva river, Ayuva-7 section; 5) Vonyu river; 6) Chim-Loptyuga field, boreholes 338 and 353; 7) Sysola river, Yb section; 8) Vizinga river; 9) Koygorodok; 10) Sysola river, Kazhimsky factory; 11) Loyno; 12) Sinegor'ye; 13) Letka river; 14) Kobra river; 15) Vyatka river; 16) Neya river; 17) Ivkino; 18) boreholes 1 and 52; 19) Unzha river, near the village of Ugory; 20) Gorka; 21) Bula river; 22) Sviyaga and Kilna rivers; 23) borehole 1; 24) Gorodischi; 25) Kashpir; 26) Yablonovy ravine, burnt shales quarry; 27) borehole 559; 28) borehole 120; 29) Ivanikha; 30) borehole 121; 31) borehole 1038; 32) Ozinsky shale mine; 33) near the city of Uralsk; 34) borehole Aleksandrovogayskaya-1. The distribution of the Panderi Zone shales is shown in gray (Lyurov, 1996). Stars are natural outcrops, triangles are boreholes. Purple color indicates localities known from the literature; red symbols indicate localities from which the material has been studied by the authors.

seum of the Russian Academy of Sciences (GGM RAS, Moscow), and Paleontological Institute, Russian Academy of Sciences (PIN RAS, Moscow).

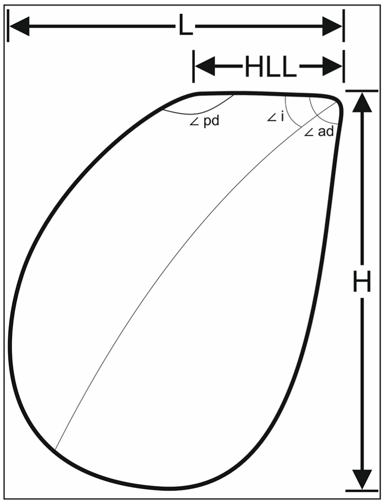

Fig. 2 - Right valve of '*Parainoceramya*' *pseudoretrorsa* (Gerasimov, 1955), showing the measurements used in the description: H – height, L – length, HLL – hinge line length, pd – posterodorsal angle, ad – anterodorsal angle, i – angle of inclination.

This made it possible to redescribe the species '*P.*' *pseudoretrorsa* and clarify its geographic and stratigraphic distribution.

Material

The material for the present work comprises specimens collected by the authors since 2002 in sections of the Volga region and the Komi Republic (Russia). In addition, we have samples from well cores from the Saratov Volga region. All these samples are usually accompanied by ammonite finds and are reliably dated. We also studied specimens from the collections of P.A. Gerasimov (including paratypes of '*P.*' *pseudoretrorsa*), L.I. Lutugin, N.G. Kassin, and I.E. Khudyaev. Individual specimens were provided by A.A. Mironenko, E.V. Shchepetova (GIN RAS), and I.A. Meleshin (K.A. Timiryazev Biological Museum); materials from well cores were provided by I.N. Burtsev (IG Komi Scientific Center of the Ural RAS), V.A. Musatov (GIN RAS), and E.Y. Baraboshkin (Lomonosov Moscow State University). A sample from a borehole core recovered near Naryan-Mar (Nenets Autonomous Okrug, Russia) was found in the collection of V.S. Kravets stored in the Aprelevka Branch of All-Russian Research Geological Oil Institute (VNIGNI), Russia.

We compiled a list of all localities with '*Parainoceramya*' *pseudoretrorsa*, their age, and their facies (Table 1). To date, '*P.*' *pseudoretrorsa* is known from 34 localities in European Russia and Kazakhstan (Fig. 1). Material from 21 localities was studied by us, and information on the remaining localities was obtained from the literature. Information on eight localities is published for the first time.

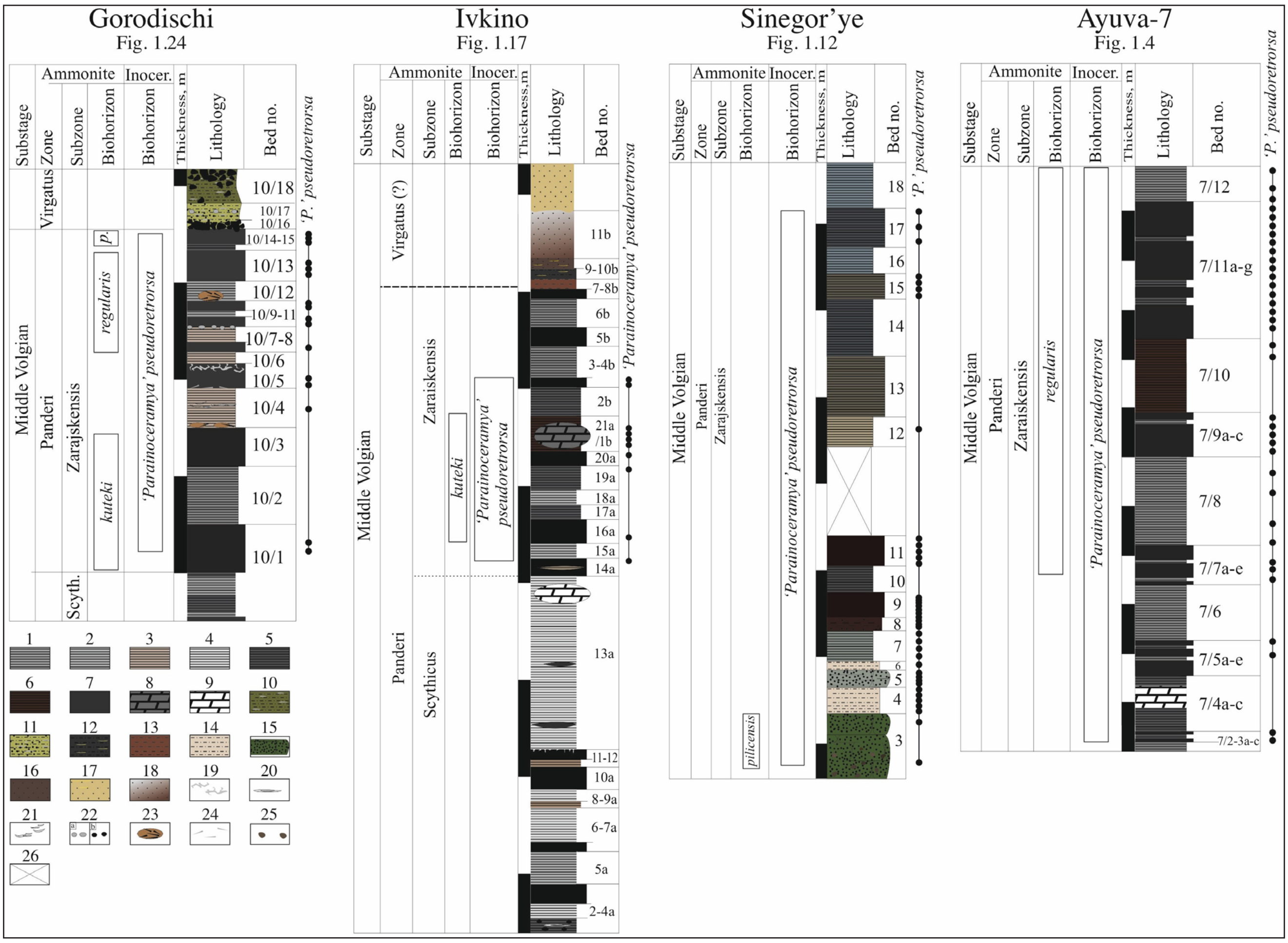

Fig. 3 - Stratigraphic range of *'Parainoceramya' pseudoretrorsa* (Gerasimov, 1955) in four Middle Volgian sections of the European Russia. Colors in the figure represent actual rock color: (1) gray clay, (2) silty clay, (3) gray-beige clay, (4) light-gray clay, (5) dark-gray clay, (6) dark-brown clay, (7) argillaceous black shale, (8) bituminous marl, (9) marl, (10) dark-green sandy silt, (11) greenish-yellow sandy silts with lenses of beige silt, (12) argillaceous silt, black with yellow spots, (13) brown silt, (14) light beige silt, (15) green glauconitic sandstone, (16) dark gray-brown sand, (17) yellow sand, (18) brown-gray sand gradually brightening upward, (19) burrows of Thalassinoides, (20) crushed shells of large ammonites, (21) shell beds, (22) phosphorite concretions (a – beige, b – black), (23) concretions with belemnites, (24) accumulations of belemnite rostra, (25) siderite pebbles, (26) interval not studied.

All material comes from the Panderi Zone of the Middle Volgian Substage. The specimens collected by us were dated based on the infrazonal ammonite scale (Rogov 2013, 2021a, b; Rogov & Kiselev 2024). This allowed us to accurately date most of the studied finds.

All specimens, the stratigraphic position of which was established with high precision, are restricted to the Zarajskensis ammonite Subzone excluding the upper *zarajskensis* biohorizon. The earliest occurrence of the species is in the *kuteki* biohorizon and was recorded in the Yablonovoe pit, the Alexandrovogayskaya-1 and 559 boreholes, and the Ivkino and Gorodischi sections; the latest finds come from the *pilicensis* biohorizon of the Gorodischi section and of borehole 559. '*P.' pseudoretrorsa* is most widespread in the *regularis* biohorizon, occurring in the Gorka, Ayuva-7, Vonyu and Gorodischi sections, and the 559 and Alexandrovogayskaya-1 boreholes.

The overwhelming majority of finds (Figs. 5-8) are confined to alternations of clayey and black shale deposits, where *'P.' pseudoretrorsa* occurs en masse in association with bivalves of the genus *Buchia*, with *'Parainoceramya'* more frequently occurring in black shales and *Buchia* distinctly predominating in clays. Such a situation, with high abundance and low biodiversity of benthic organisms, is characteristic of oxygen-depleted environments, including the sediments of the Panderi Zone, which formed under dysoxic-anoxic conditions (Rogov et al. 2020).

Of particular interest are the assemblages from the Vyatka, Kobra, and Sysola river basins (Fig. 8a-e). These finds partly come from sandy marls,

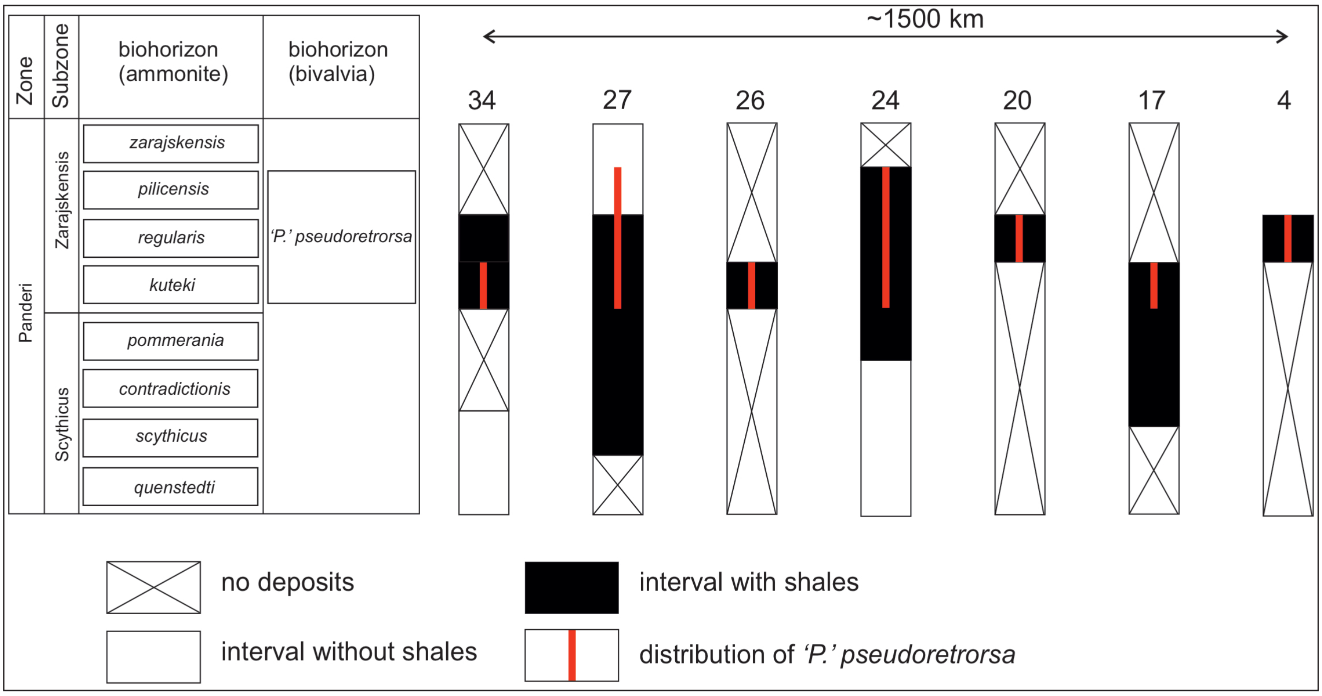

Fig. 4 - Distribution of '*Parainoceramya*' *pseudoretrorsa* (Gerasimov, 1955) in the Dorsoplanites panderi Zone. Section numbers according to Fig. 1

where bivalve moulds are undeformed, in contrast to specimens from shale and clay deposits. In some cases, '*Parainoceramya*' in these localities occurs in sands and sandstones.

The specimens were imaged using low-angle light with a Fujifilm GFX 50R digital mirrorless medium-format camera with a Fujinon GF 120 mm f/4.0 R LM OIS macro lens in the Geological Institute of the Russian Academy of Sciences, Moscow (GIN RAS). To enhance the contrast in photographs, the fossils were whitened with ammonium chloride. The ligament area was studied on a VEGA3 TESCAN scanning electron microscope at the Paleontological Institute of the Russian Academy of Sciences (PIN RAS, Moscow).

The studied collection includes more than 50 specimens, most of which are represented by single valves, but there are also articulated specimens. It includes both juvenile (20 mm) (Fig. 6h-j) and adult, occasionally very large (up to 200 mm) shells (Fig. 7a).

The described and figured material is stored in the Aprelevka branch of VNIGNI, collection No. RMA-48. Additional specimens come from the collection of P.A. Gerasimov (No. 5670) (PIN RAS), as well as from the collections of Kassin (No. 873) and L.I. Lutugin (No. 214) stored in the Academician F.N. Chernyshev Central Scientific Research Geological Exploration Museum (CNIGR Museum).

The following abbreviations are used in the descriptions (Fig. 2): RV - right valve, LV - left valve, H – height, L – length, HLL – hinge line length, VC - valve convexity, pd – posterodorsal angle, ad – anterodorsal angle, i – angle of inclination.

Biostratigraphy

In the Late Jurassic-Early Cretaceous inoceramoids were less consistently retrieved than Buchiidae in the Northern Hemisphere. Consequently, bivalve stratigraphy of Upper Jurassic deposits in the Panboreal Superrealm has usually relied on the genus *Buchia* (Zakharov 1981). The *Buchia* zonal scale for the Upper Bathonian - Hauterivian, first proposed in the late 19th century (Lahusen 1888), is widely used in the Northern Hemisphere (Zakharov & Rogov 2020), and is one of the most important tools for dating sections (Vyachkileva et al. 1990). An undoubted advantage of this scheme is the high potential of *Buchia* zones for correlating sediments of different regions (Rogov et al. 2024b). The distribution of *Buchia* was practically independent of facies, so the same species are known not only from the Panboreal Superrealm, but also from lower latitudes (Yanin 1970; Tovbina 1988; Zakharov & Rogov 2020; Zakharov 2022).

In certain regions, inoceramids may provide an additional biostratigraphic tool for Upper Jurassic successions. A continuous Upper Jurassic Inoceramoidea zonal scheme is unlikely at present because the record is uneven. Nevertheless, mass occurrences in narrow intervals can form useful marker horizons (Panchenko et al. 2015; Shilekhin & Rogov 2024; Rogov et al. 2025), which may qualify as biohorizons, i.e. infrazonal stratigraphic units commonly applied by ammonite researchers for Jurassic and Cretaceous strata (Callomon 1985; Page 1995; Rogov et al. 2012). The use of these markers requires detailed taxonomic revision, as well as documentation of their geographic and stratigraphic distributions. The present work is a first step in this direction.

'P.' pseudoretrorsa is widely distributed in the Middle Volgian of European Russia, from the coast of the Barents Sea in the north to the Saratov Volga region and northern Kazakhstan in the south. The stratigraphic distribution of the species corresponds to a major part of the Zarajskensis ammonite Subzone (excluding its upper biohorizon), and thus the presently known range of this species is considerably narrower than that of any species of the genus *Buchia* and is comparable to those of the most rapidly evolving ammonoid species. This species reached high population densities in black shales. Apparently, *'P.' pseudoretrorsa* may have occupied relatively oxygen-depleted biotopes.

The narrow stratigraphic distribution and mass occurrence of this species in black shales of the Panderi Zone allow *'P.' pseudoretrorsa* to be used as a biohorizon within the Middle Volgian. This biohorizon can refine the age of the Middle Volgian deposits in sections lacking zonal ammonites. This situation is not rare in cored successions. For example, in wells 338 and 353 (Chim-Loptyuga deposit, Yarenga district, Arkhangelsk region), there are no finds of virgatitids, and *Buchia* records from the boreholes only allow us to date the sediments to the Middle Volgian Substage, i.e., much less precisely than *'P.' pseudoretrorsa*.

In this paper, biohorizons are used as minimal biostratigraphic units corresponding to the full stratigraphic range of the index taxon. Such units have long been used in the study of the Mesozoic, primarily by specialists in cephalopod mollusks. Ammonite-based biohorizons have been established in all stages of the Jurassic and part of the Lower Cretaceous (Page 1995; Rogov et al. 2012), and belemnite-based biohorizons have been applied in the Middle Jurassic (Ippolitov 2018a,b). The use of such biostratigraphic units enables much more detailed correlation and subdivision of sections, allowing the establishment of features of geologic history that are not distinguishable at the zonal level (Rogov & Gulyaev 2025). Previously, biohorizons were not recognized on the basis of bivalve records. In contrast to phylozones and other range zones, which are also based on the total range of their index species, biohorizons correspond to the observed range of their index taxon within each studied section (i.e., barren intervals are omitted) and may not be bounded by other biostratigraphic units of the same type above or below.

Description of the '*Parainoceramya*' *pseudoretrorsa* biohorizon

'P.' pseudoretrorsa biohorizon nov.

Index species: '*Parainoceramya*' *pseudoretrorsa* (Gerasimov, 1955) (Figs. 5–8).

Stratotype: Gorodischi section, beds 10/1–10/15 (Fig. 3). Alternation of black shales and clays with a total thickness of ca. 3.5 m.

Paleontological characteristics: '*Parainoceramya' pseudoretrorsa* (Gerasimov, 1955), *Buchia russiensis* (Pavlow, 1907), *B. mosquensis* (Buch, 1844). Among ammonites *Zaraiskites* (*Z. kuteki* Rogov, 2013, *Z. regularis* Kutek, 1994, *Z. densicostatus* Rogov, 2014, *Z. pilicensis* (Michalsky, 1890)) are especially numerous, while *Acuticostites* spp., *Dorsoplanites panderi* (Eichwald, 1840), *Pavlovia pavlovi* (Michalsky, 1890), and *Haploceras* sp. indet. are not so common (Rogov 2013). In the northern part of European Russia dorsoplanitid ammonites are numerous, while virgatitids are rare.

Comments. The distinguished biohorizon corresponds to a part of the *Buchia russensis* Zone and the *Zaraiskites zarajskensis* ammonite Subzone without its upper horizon (*kuteki*, *regularis*, and *pilicensis* biohorizons). The *'P.' pseudoretrorsa* biohorizon is fully recorded in the Volga and Trans-Volga regions. In sections of the Kostroma region, *Zaraiskites* is rare, and the *pilicensis* biohorizon is not established. In the Timan-Pechora region, *'P.' pseudoretrorsa* is only recorded from the *regularis* ammonite biohorizon; in this region, virgatitids are unknown in other intervals of the Panderi zone. The *zarajskensis* biohorizon is apparently characte-

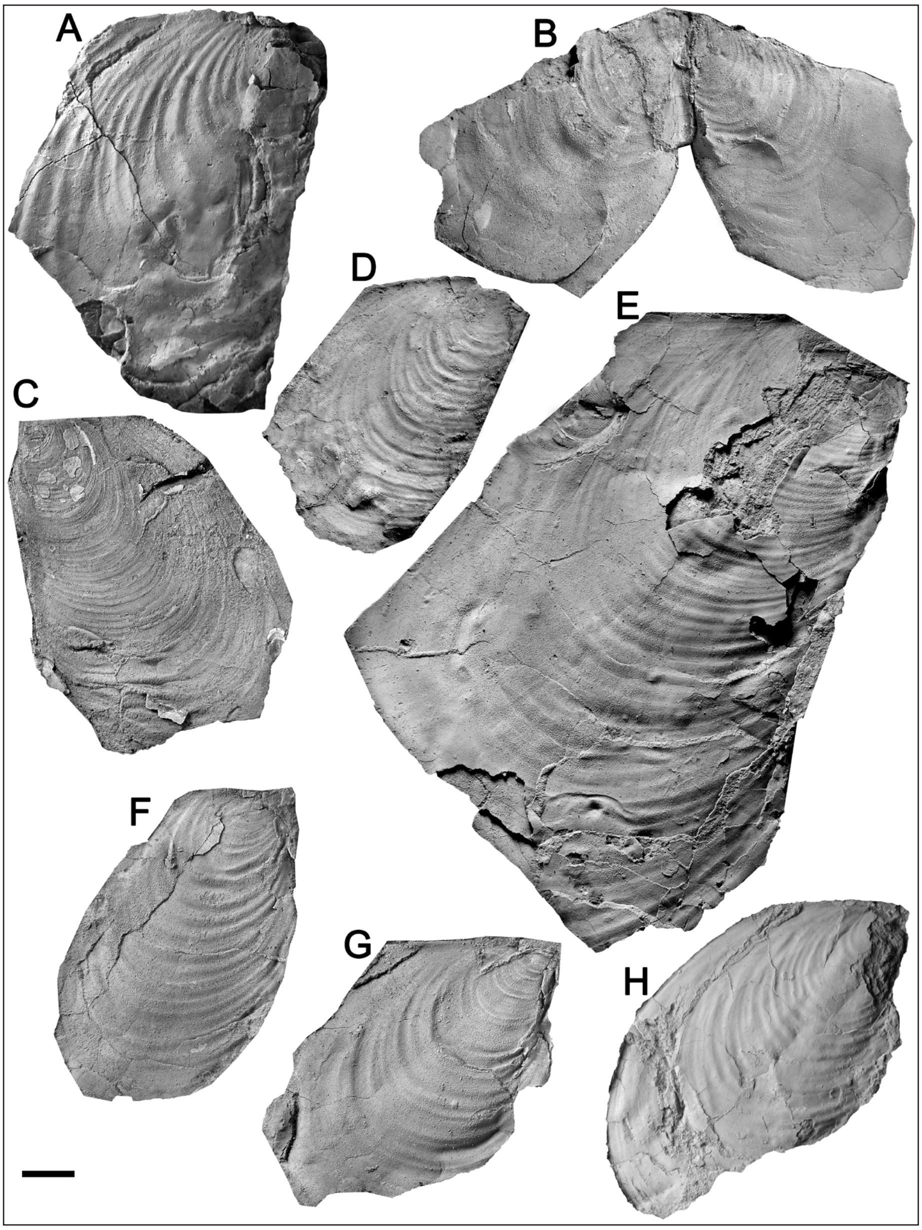

Fig. 5 – *'Parainoceramya' pseudoretrorsa* (Gerasimov, 1955), Middle Volgian, Dorsoplanites panderi Zone. Scale bar: 1 cm.
A-G – Ayuva-7 section, Komi Republic; Zarajskensis Subzone, *regularis* biohorizon: A) right valve, specimen RMA-48/1; B) articulated valves, specimen RMA-48/2, 0.85-0.9 m above base of bed 11; C) left valve, specimen RMA-48/3, 0.15 m above base of bed 7; D) right valve, specimen RMA-48/4, bed 7c; E) right valve, specimen RMA-48/5, 0.7 m above base of bed 7; F) right valve, specimen RMA-48/6, 0.35 m above base of bed 7; G) right valve, specimen RMA-48/7, 0.85-0.9 m above base of bed 11; H) right valve, specimen RMA-48/8, Ozinsky shale mine, Saratov region.

rized by the presence of another species of inoceramids, '*P.' jurensis*.

Geographic distribution (Fig. 1): Russian Platform, Timan-Pechora plate.

Localities (Fig. 4): Gorodischi, Gorka, Ivkino, Ayuva-7, Yablonovy ravine, Vonyu river, Koygorodok, Loyno, Sinegor'ye, Ozinsky shale mine, Aleksandrovogayskaya-1, 3, 120, 121, 338, 553, and 559 boreholes.

Systematic paleontology

Suprageneric systematic arrangement follows Carter et al. (2011).

Order **Myalinida** Paul, 1939
Superfamily Inoceramoidea Giebel, 1852
Family Inoceramidae Giebel, 1852
Genus *Parainoceramya* Ros-Franch, Damborenea, Márquez-Aliaga et Manceñido, 2015

Note. The quotation marks used below indicate a provisional generic assignment; the observed hinge and ligament characters suggest that the species is related to, but not congeneric with, *Parainoceramya* sensu stricto.

'Parainoceramya' pseudoretrorsa (Gerasimov, 1955)

Figs. 5–8

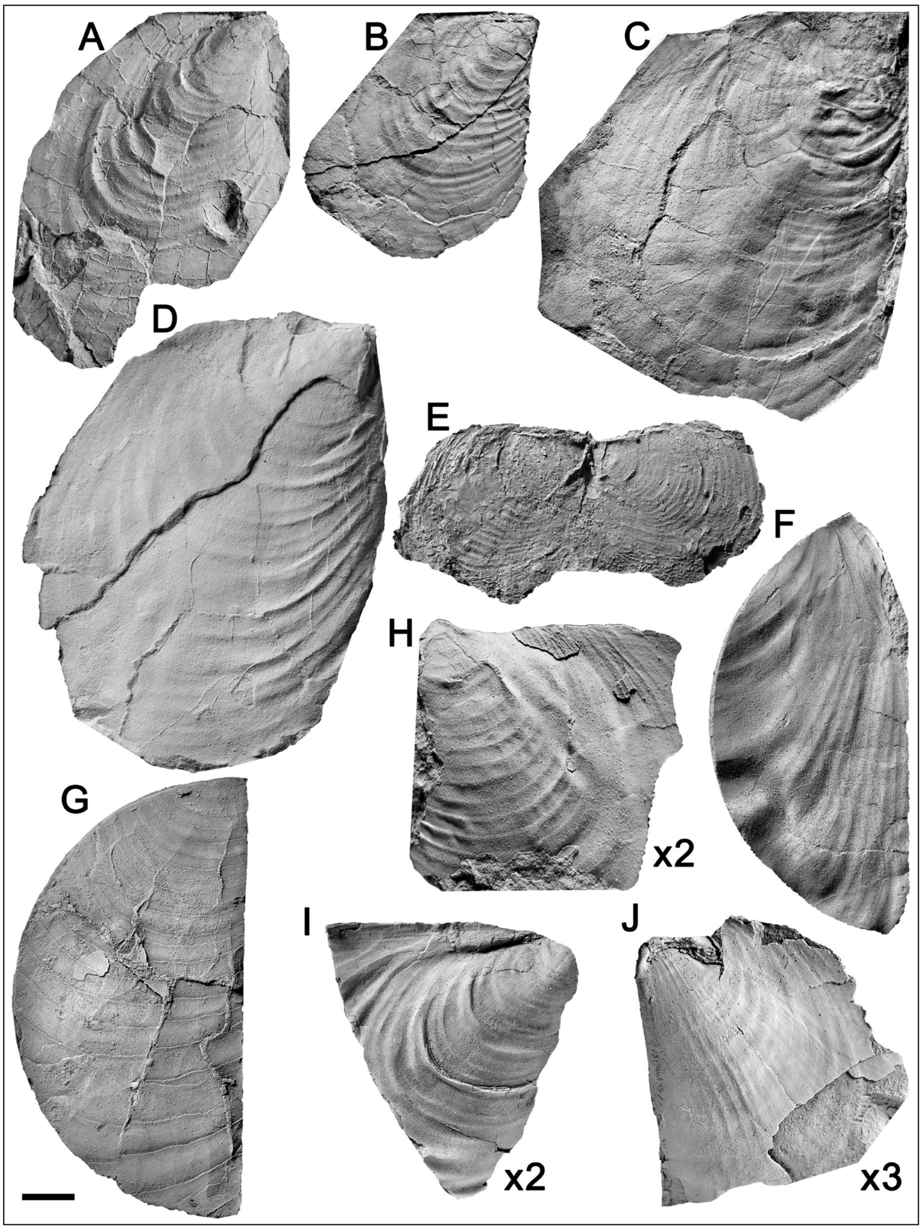

Fig. 6 – *'Parainoceramya' pseudoretrorsa* (Gerasimov, 1955), Middle Volgian, Dorsoplanites panderi Zone, Zaraiskites zarajskensis Subzone. Scale bar: 1 cm.
A-B, D-E – Ivkino, Kostroma region, *kuteki* biohorizon: A) right valve, specimen RMA-48/9; B) right valve, specimen RMA-48/10; C) right valve, specimen RMA-48/11, Gorka, Kostroma region; *regularis* biohorizon; D) right valve, holotype № 1083 (GGM RAS, Moscow); E) articulated valves, paratype №5670/1, from the collection of P.A. Gerasimov (PIN RAS, collection No. 5670); F-H – borehole 559 (depth 63.9-121.1 m), Samara region: F) shell fragment, specimen RMA-48/12, depth 63.9 m, *pilicensis* biohorizon; G) shell fragment, specimen RMA-48/13, depth 72.9 m, *regularis* biohorizon; H) left valve, specimen RMA-48/14, depth 64.2 m; I-J – borehole Aleksandrovogayskaya-1 (depth 2050-2055 m), Saratov region, *regularis* biohorizon: I) right valve, specimen RMA-48/15; J) left valve, specimen RMA-48/16.

1886 *Inoceramus retrorsus* – Nikitin, p. 409-410.
1887 *Inoceramus retrorsus* – Krotov, p. 22, 28.
1918 *Inoceramus retrorsus* – Jirmunski, p. 13, 35.
1921 *Inoceramus retrorsus* – Sokolov, p. 9.
1927 *Inoceramus retrorsus* – Kazakov, p. 155.
1927 *Inoceramus* sp. – Kazakov, p. 155.
v1927 *Inoceramus retrorsus* – Khudyaev, p. 500-501.
v1928 *Inoceramus retrorsus* – Kassin, p. 113, 121.
1929 *Inoceramus* cf. *retrorsus* – Sokolov, p. 9.
1933 *Inoceramus* sp. – Krom, p. 10, 21.
1939 *Inoceramus retrorsus* – Gerasimov & Kazakov, p. 66.
1939 *Inoceramus* cf. *retrorsus* – Zonov, p. 190.
1939 *Inoceramus* ex gr. *retrorsus* – Zonov, p. 159.
1939 *Inoceramus* aff. *retrorsus* – Zonov, p. 192.
v1941 *Inoceramus retrorsus* – Kassin, p. 66.
v1955 *Inoceramus pseudoretrorsus* – Gerasimov, p. 317, pl. 21, fig. 7.
v1964 *Inoceramus* cf. *retrorsus* – Firer & Chernyavsky, p. 158.
1976 *Inoceramus* sp. – Saks, p. 19.
1983 *Inoceramus pseudoretrorsus* – Zhmur et al., p. 28.
1985 *Inoceramus* cf. *retrorsus* – Bukina et al., p. 55.
1985 *Inoceramus pseudoretrorsus* – Bukina et al., p. 25, 28, 36-37, 41, 54, 64, 66.
1986 *Inoceramus pseudoretrorsus* – Mitta, p. 52-53.
1988 *Inoceramus pseudoretrorsus* – Kuleva & Baryshnikova, p. 127.
v1995 *Inoceramus pseudoretrorsus* – Gerasimov et al., 1995, p. 80, pl. 14, fig. 9.
2004 *Inoceramus* sp. – Kuleva et al., p. 19, 21.
2004 *Inoceramus pseudoretrorsus* – Kuleva et al., p. 29-31, 33-34.
v2004 *Retroceramus pseudoretrosus* – Molostovsky et al., p. 159.
2006 *Inoceramus* sp. – Repin et al., p. 15.
2007 *Inoceramus pseudoretrorsus* – Zorina., p. 37.
v2021a *Parainoceramya pseudoretrorsus* – Rogov, p. 35 (supplement).
v2021b *Parainoceramya pseudoretrorsus* – Rogov, p. 201.
v2023 *Inoceramus pseudoretrorsus* – Ippolitov et al., p. 87, pl. 14, figs. 6, 7, 10.

Note on synonymy. Records preceded by "v" were checked by the authors directly or are based on figured material; unmarked records are retained as literature occurrences from the Panderi Zone and should be treated as unverified where no specimen number or illustration was provided in the original source.

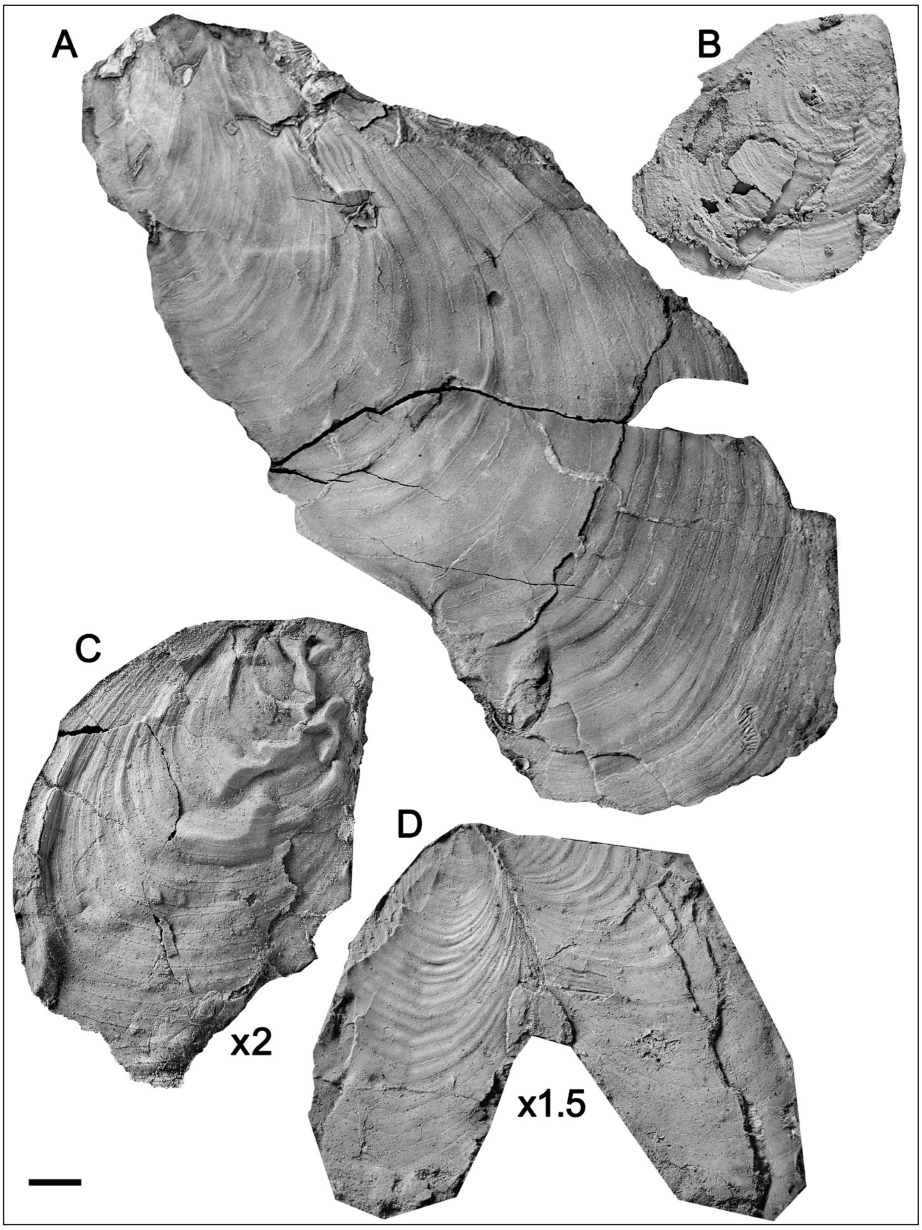

Fig. 7 – *'Parainoceramya' pseudoretrorsa* (Gerasimov, 1955), Middle Volgian, Dorsoplanites panderi Zone. Scale bar 1 cm.
A) specimen 92/214, Vizinga river, Komi Republic; B) right valve, specimen RMA-48/19, Yablonovy ravine, burnt shales quarry, Samara region; C-D – Gorodischi, Ulyanovsk region, Zaraiskites zarajskensis Subzone: C) right valve, specimen RMA-48/17, *pilicensis* biohorizon, bed 10/15; D) articulated valves, specimen RMA-48/18, *regularis* biohorizon.

Type material. Holotype, specimen no. 1083 (Fig. 6d), housed in SGM RAS, Moscow; ravine near village Ivkino (Kostroma region); Upper Jurassic, Middle Volgian, Dorsoplanites panderi Zone, Zaraiskites zarajskensis Subzone, *kuteki* biohorizon.

Additional material. Over 50 specimens, most of which are represented by flattened molds and imprints.

Description. Shell medium-sized to large, equivalve, subrectangular or suboval, slightly higher than long or with length approximately equal to height (L:H = 0.77-0.96), moderately oblique (i = 45°-60°). Hinge margin relatively long, approximately equal to or greater than half of shell length (HLL:L = 0.44-0.69), nearly straight, meeting the posterior margin at an obtuse angle (pd = 120°-140°). Posterodorsal margin evenly rounded and not developed into a distinct posterior wing. Ventral margin relatively short, rounded. Anterior margin long, almost straight, forming acute angle with the hinge margin (ad = 70°-80°). Shell moderately convex (VC:H = 0.34), point of maximum convexity being located in the middle of valve. Beaks low, broad, not or only slightly extending above the hinge margin, usually blunt, less often pointed, prosogyrate. Sculpture represented by commarginal growth lines and low, broad commarginal plicae; true radial costae are not observed . Shell thin, outer layer composed of prismatic calcite, thickening near hinge margin, forming narrow, up to 2 mm wide, ligament area. Ligament is multivincular with at least four resilifers, twice the width of the ridges

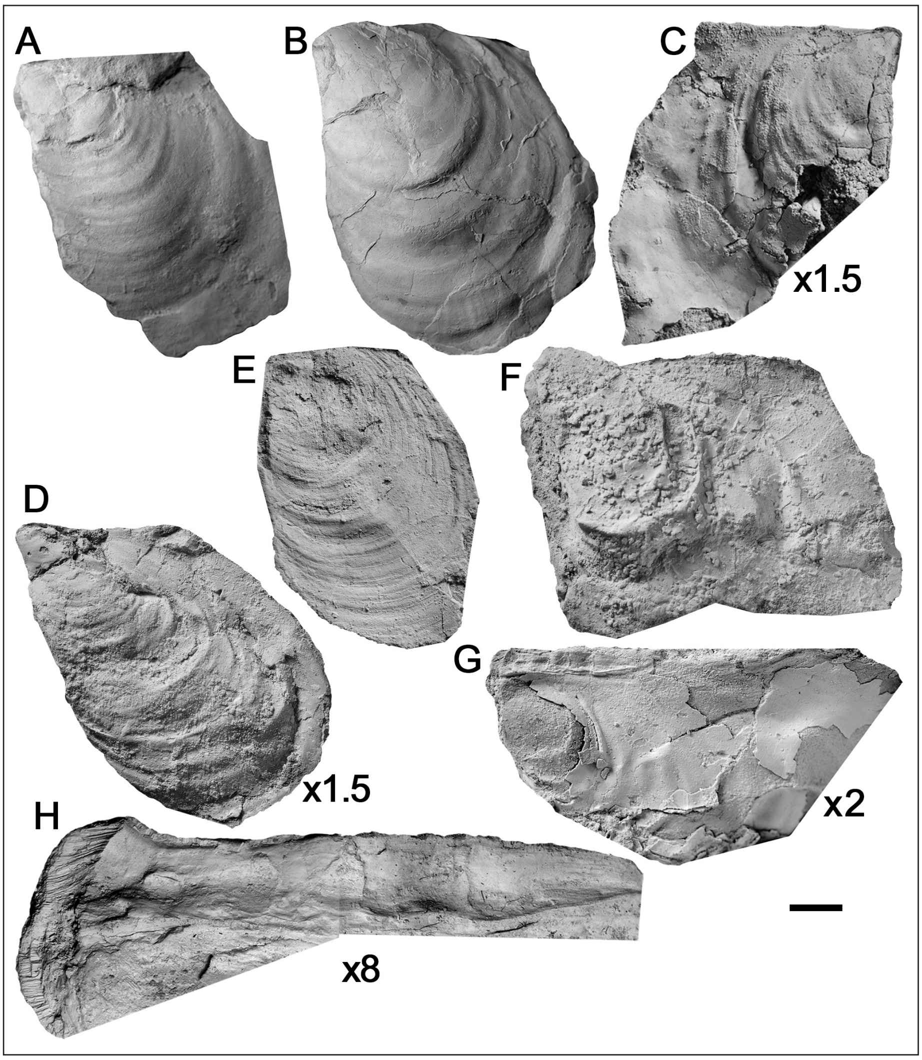

Fig. 8 - *'Parainoceramya' pseudoretrorsa* (Gerasimov, 1955), Middle Volgian, Dorsoplanites panderi Zone. Scale bar 1 cm.
A-B – specimens from the collection of N.G. Kassin (CNIGR Museum, collection No. 873): A) left valve, specimen 299/873, Kobra river, Kirov region; B) left valve, specimen 300/873, Kobra river, Kirov region; C) right valve, specimen RMA-48/21, Loyno, Kirov region, Zaraiskites zarajskensis Subzone; D-F – Sinegor'ye, Kirov region, Zaraiskites zarajskensis Subzone: D) left valve, specimen RMA-48/22, bed 4; E) left valve, specimen RMA-48/23, bed 9; F) right valve, specimen RMA-48/24, bed 4; G-H – part of the left valve, specimen RMA-48/20, borehole 3, district of Naryan-Mar, Nenets region: G) general view; H) SEM of ligament area.

separating them (= resilia; Fig. 8h). No traces of muscle attachment or mantle line were observed.

Variability. Intraspecific variability is rather high, manifested primarily in size, beak termination, shell obliquity (i = 45°-60°) and width of the posterior dorsal angle (pd = 120°-140°).

Measurements.

Specimen no.	Valve	H	L	HLL	VC	L:H	HLL:L	VC:H	pd, °	ad, °	i, °
RMA-48/1	RV	80	63	41	-	0.79	0.65	-	120	75	55
RMA-48/3	LV	67	56	25	-	0.84	0.45	-	125	75	50
RMA-48/4	RV	55	53	30	-	0.96	0.57	-	135	70	50
RMA-48/5	RV	>126	>112	>48	-	-	-	-	-	70	45
RMA-48/6	RV	62	48	24	-	0.77	0.5	-	125	80	50
RMA-48/8	RV	63	60	27	-	0.95	0.45	-	140	80	50
RMA-48/9	RV	70	55	24	-	0.79	0.44	-	135	-	50
RMA-48/10	RV	49	47	24	-	0.96	0.51	-	130	75	50
RMA-48/11	RV	81	73	47	-	0.9	0.64	-	130	-	55
1083 (H)	RV	70	56	28	-	0.8	0.5	-	125	80	55
CNIGR 92/214	-	>158	>149	-	-	-	-	-	-	-	-
RMA-48/17	RV	46	35	18	-	0.76	0.51	-	140	80	50
CNIGR 300/873	LV	66	56	38	-	0.85	0.69	-	120	80	55
CNIGR 301/873	LV	83	70	41	28	0.84	0.59	0.34	140	75	60

Comparison. The sculpture of *'Parainoceramya' jurensis* (Gerasimov, 1955), originally assigned to the genus *Dreissena*, from the Middle Volgian Virgatites virgatus ammonite Zone of the Russian Platform resembles that of the present species. *'P.' pseudoretrorsa* is distinguished by the subrectangular or suboval shape of the shell (wedge-shaped in *'P.' jurensis*), lower and blunt beaks, lower shell obliquity, and greater anterodorsal angle. It differs from *'Parainoceramya' cramei* (Clausen et Wignall, 1990) from the Upper Kimmeridgian - lower Middle Volgian of England by a coarser commarginal sculpture, larger size, and broader beaks. From *'Parainoceramya' vereshagini* (Pochialaynen, 1969) from the Upper Volgian-Valanginian of Siberia, Northeast Russia, and the Far East, the studied species differs by its larger shell and straight anterior margin. *'Parainoceramya' golberti* (Zakharov & Turbina, 1979) from the Upper Volgian of England (Kelly 1984) and the Ryazanian of Siberia (Zakharov & Turbina

1979) differs from '*Parainoceramya' pseudoretrorsa* by its much longer hinge margin and almost straight anterior margin.

Remarks. We studied the collections of P.A. Gerasimov in GGM (coll. no. GGM-1898) and in PIN RAS (coll. no. 5670), including the type material of *Inoceramus pseudoretrorsus*. We figure the holotype (Fig. 6d), present photographs of a previously unfigured paratype from his collections (Fig. 6e), and illustrate new specimens from the type locality (Fig. 6a, b). The main difficulty in the study of the species lies in the deformation of most specimens, which are usually strongly flattened laterally. Such preservation does not allow to properly assess the convexity of the valves and the morphology of the beaks. We were able to study these features in several undeformed specimens collected from sandy marl (Fig. 8a-c, d, f).

The most probable ancestor of '*P.' pseudoretrorsa* is '*P.' cramei* (Clausen et Wignall 1990) from the Upper Kimmeridgian to the lower Middle Volgian of England. The English species is likewise characterized by the development of a hinge plate on a prismatic layer and is associated with black shales, i.e., it existed under oxygen-depleted conditions (Clausen & Wignall 1990). In addition, the last occurrence of this species in the middle part of the Fittoni Zone is approximately coeval with the first occurrence of '*P.' pseudoretrorsa* in the middle part of the Panderi Zone. It is possible that *'P.' cramei* is ancestral to '*P.' pseudoretrorsa* and migrated into the Middle Russian Sea via the Polish Sea; however, inoceramids are not known from the Upper Jurassic of Poland.

A second, closely related species to '*P.' pseudoretrorsa* is '*P.' jurensis* (Gerasimov, 1955), originally described from the Middle Volgian Virgatites virgatus ammonite Zone of the Moscow region and recently also reported from the Izhma River in the Komi Republic (Ippolitov et al. 2023, p. 87, pl. 14, fig. 9). The potential phyletic lineage linking '*P.' pseudoretrorsa* and '*P.' jurensis* is of particular interest, as it is documented both on the Russian Platform and in the Timan–Pechora region, despite differences in the ammonite successions of these areas (Rogov 2021a). In this case, given the close stratigraphic proximity of the two species and the overlap in their geographic distribution, there is little doubt that '*P.' jurensis* is a descendant of '*P.' pseudoretrorsa*.

The Middle Volgian inoceramids of Western Siberia are traditionally referred to '*I.' vereshagini* Pochialaynen, 1969, described on the basis of material from the Valanginian. Some of these bivalves resemble '*P.' pseudoretrorsa* and come from a similar stratigraphic interval - the lower Middle Volgian (Vyachkileva et al. 1990, pl. 34, fig. 8). Also interesting is the closely similar facies distribution of '*I.' vereshagini* from Western Siberia and '*P.' pseudoretrorsa*: these are black shales of the Bazhenov Formation and black shales of the Panderi Zone, respectively. However, due to the poor preservation and limited material, it cannot be stated today that the West Siberian finds belong to '*P.' pseudoretrorsa*.

The assignment of Upper Jurassic inoceramids to the genus *Parainoceramya* is provisional. It appears that a phyletic sequence can be recognised linking '*P.' cramei*, '*P.' pseudoretrorsa*, and '*P.' jurensis*. With the acquisition of new evidence on the structure of the hinge plate in these species, the establishment of a new genus may become possible. However, despite the large number of specimens studied for '*P.' pseudoretrorsa*, the ligament has been observed in only a single specimen (Fig. 8h).

The available material allows us to confirm Knight & Morris' (2009) observation that the mineralogy of the hinge plate in Inoceramoidea changed from aragonitic to calcitic during the Late Jurassic, as evidenced by '*P.' cramei* and '*P.' pseudoretrorsa*. The mineralogy of the hinge plate is a key character for family-level classification within Inoceramoidea (Pokhialainen 1972). We found that in '*P.' pseudoretrorsa* the ligament area is developed on a thickened prismatic layer. This allows us to attribute the species to the family Inoceramidae and not to the family Retroceramidae, as the latter is characterized by a ligament area developed on the lamellar layer. Previously, this had not been confirmed and '*P.' pseudoretrorsa* was occasionally referred to the genus *Retroceramus* (Molostovsky et al. 2004, p. 159). Coeval Tithonian inoceramoids of the Southern Hemisphere are traditionally referred to the family Retroceramidae (Crame 1982), but their ligament area is insufficiently studied.

Geological age and geographic distribution. Upper Jurassic, Middle Volgian, Dorsoplanites panderi Zone, Zaraiskites zarajskensis Subzone, *kuteki*, *regularis* and *pilicensis* ammonite biohorizons of the Russian Platform and the Timan-Pechora region.

Author contributions: Lev E. Shilekhin: Writing – review & editing, Writing – original draft, Visualization, Conceptualization, Fieldwork. Mikhail A. Rogov: Writing – review & editing, Writing – original draft, Conceptualization, Fieldwork.

Data Availability Statement. The data supporting the results of this research are available upon request. Interested resear-chers may contact the corresponding author to obtain access

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