ISSN 0031-0301, Paleontological Journal, 2017, Vol. 51, No. 11, pp. 1167–1248. © Pleiades Publishing, Ltd., 2017.

Revision of the Cambrian Agnostina (Trilobita?) from Russia

E. B. Naimark[a], * and T. V. Pegel[b], **

[a]*Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117467 Russia*
[b]*Siberian Research Institute of Geology, Geophysics, and Mineral Resources (SNIIGiMS), Krasnyi pr. 67, Novosibirsk, 630091 Russia*
**e-mail: naimark@paleo.ru*
***e-mail: pegel@mail.ru*

Received November 11, 2016

Abstract—Cambrian genera and species of Agnostina (?Trilobita) found in Russia are revised. Agnostid trilobite species are used as index taxa in chronostratigraphic subdivisions of the traditional Middle and Upper Cambrian in both regional and global stratigraphic scales. The correlation of the regional and international stratigraphic schemes largely depends on the state of knowledge of the regional agnostid fauna. Therefore, an up-to-date revision of this group based on the Russian collections taking into account their global diversity is very timely. For this study we reexamined the type collections of agnostids, including the holotypes of species described by Russian authors. This paper contains new photographic images of the holotypes housed in Russian museums. The compiled data offered solutions for some difficult taxonomic problems of the families Agnostidae, Ptychagnostidae, Peronopsidae, and some genera of Pseudagnostidae, Diplagnostidae. Apart from listing the diversity, this paper serves as the basis for studying the biogeography and evolution of this interesting arthropod group.

Keywords: Agnostina, revision, Cambrian, Russia

DOI: 10.1134/S0031030117110016

CONTENTS

INTRODUCTION

This study summarizes the data on the diversity of agnostids found in Russia. Agnostids are in many ways an enigmatic group of marine invertebrates, inhabitants of open marine environments, which appeared at the beginning of the Middle Cambrian (according to the current stratigraphic nomenclature this is the still–unnamed Series 3) and became extinct at the end of the Ordovician. They were most diverse in the Middle and Upper Cambrian (Furongian). In modern taxonomy (Shergold and Laurie, 1997), this group is considered as a suborder; along with the suborder Eodiscina, they are united in the order Agnostida. The phylogenetic affinity of these suborders is questioned (Müller and Walossek, 1987) and their kinship as well as the assignment of Agnostina to the class Trilobita are provisionally accepted. Further on the study will be dealing only with Agnostina, but they will be referred to as "agnostids," which is customary among specialists on this group. To avoid confusion, the family Agnostidae will only be referred to by its Latin name.

Agnostids are abundant and diverse in the Middle and Upper Cambrian beds (traditional subdivision) and include readily recognizable cosmopolitan taxa. Species and genera of this group had short geochronological ranges, hence, it is not surprising that agnostids are successfully used for Middle and Upper Cambrian biostratigraphy and correlation. Many species are used as zonal index species for the two upper Cambrian series. Hence, the taxonomic revisions of this group become of stratigraphic value. Presently, the stratigraphic scale of the Cambrian is revised to conform to the new standards and rules of stratigraphic nomenclature. This revision encounters, apart from the usual, tasks, with subjective problems of identification of index species. Such subjective obstacles include the difficulty in obtaining original descriptions, poor–quality images, incomplete species descriptions, absence of formal indications to holotypes or other name–bearer specimens, exceedingly terse descriptions, and absence of the generic diagnoses. The latter is a consequence of the incomplete understanding of the genus and species concepts in this group. All these limitations are totally applicable to the species and genera, which were described by the Russian authors in the mid–20th century, i.e., at the time of the most intense study of agnostids in Russia. With time, these drawbacks became particularly clear when the known diversity of agnostids considerably increased. New species and genera continue to be described from all over the world. Their identification and correlation with the published Russian materials are not always adequate. It should be considered that not only the global geochronological scale of the upper series of the Cambrian, but also stratigraphic scales of the Middle and Upper Cambrian of Russia, including the reference sections on the Siberian Platform, are based, along with the polymere trilobites, on the succession of agnostid index species. Because of the work on the refinements of the global stratigraphic scale of the Cambrian and the need in correlation of the regional stratigraphic scale, it is pertinent to update and streamline the taxonomy of this stratigraphically important group.

The solution of theoretical questions related to the evolution of the biosphere is largely based on the information on fossil diversity. Evidently, the more precise are these data, the more reliable are the conclusions. Agnostids are a model group for various evolutionary interpretations; this is a compact group with a very limited range of morphological variations. Therefore, the taxonomic diversity of agnostids reflects various combinations of homologous characters. It is difficult to find a more appropriate group to study the nature of homologous variations, appearance of homologous series, mosaic evolution, i.e., the most urgent concepts that are currently in focus of evolutionary biologists. So far, there is no satisfactory or at least universally accepted explanation of this commonplace evolutionary phenomenon. It interpretation requires using reassessed data on suitable fossil groups, and agnostids are one of such groups. In this sense, the most urgent task of the refinement on the basis of revised data brings other, perhaps less practical, but equally interesting problems, connected with the nature of parallel evolution.

The purpose of this study is a revision of agnostids housed in Russian museums. A similar review was written on trilobites of China (Zhou and Zhen, 2008). The experience shows that such reviews are exceptionally convenient and required for various studies and as the reference material. We reexamined and made new photographs of such type specimens that could be found in Russian collections. Some type materials are lost, which is indicated in the relevant sections of the catalogue.

A revision of all collections allowed the reinterpretation of the taxonomy of some families and genera of agnostids and even recognition of new species. This resulted in the new generic diagnoses. As the study did not aim at the taxonomic description of families, genera, and species, this paper contains brief diagnoses of the taxa with a list of recognized species and detailed data of their occurrences in Russia. The formal taxonomic revision was published separately, in a series of papers (Naimark, 2012, 2014, 2016).

The systematic review follows the order of description, most suitable for inventory of taxonomic diversity. The name of the family is followed by its diagnosis, then, by remarks, then, by a list of species assigned to this family. After that, genera of this family found in Russian localities are listed in the alphabetical order. The entry of each genus contains it diagnosis, remarks on species diversity, a list of species identified from Russian localities, with their synonyms and relevant references. Remarks on each genus focus on problems

on identification and comparison of species primarily from Russian localities and some closely similar taxa from other regions of the world. The catalogue contains photographs of the holotypes and some type specimens housed in Russian collections. The remarks in the family entries focus on the major problems of taxonomy and comparison of all genera of the family, rather than only those identified from Russian sections. Therefore, sections on the families have a more general character than remarks on the genera. The section on each family is completed with the scheme of stratigraphic distribution of its species and genera. These schemes are based on the Russian Stratigraphic Scale of the Cambrian System adopted by the Interdepartmental Stratigraphic Commission of the Russian Federation (Sukhov et al., 2016). This scheme retains the classical tripartite subdivision of the Cambrian. Its correlation with the global chronostratigraphic scale is given in the subsequent sections, which also have summaries of correlation of the scales of the regions known to contain agnostid occurrences.

HISTORICAL OVERVIEW

The systematic study of Cambrian agnostids in Russia began in the 20th century, shortly before the Second World War and was connected with the name of Ekaterina Vladimirovna Lermonotova. However, A. Chekanowski first discovered a few agnostid imprints as early as the end of the 19th century in Yakutia, in the deposits on the Olenek River. Schmidt (1885) described these imprints as *Agnostus czekanowskii*. Later, Kobayashi (1939) assigned this species to the genus *Clavagnostus*. In the early 1920s, E.V. Toll during an expedition to Bennett Island (New Siberian Archipelago) collected agnostids later studied by Westergård (Holm and Westergård, 1930). Of this collection, Westergård for the first time described *Agnostus pisiformis pater, A. nudus hyperboreus, A. latirhachis, A. arcticus, A. repandus,* and the previously known species *Agnostus glandiformis* Angelin and *A. bituberculatus* Angelin.

In the 1920s–1930s, E.V. Lermontova, who worked in St. Petersburg (then Leningrad) in the Russian Geological Research Institute (VSEGEI) was the main expert on the Cambrian trilobites in Russia. She received extensive material collected during geological mapping and exploration. Based on the study of fossil trilobite faunas, she compiled the first correlation schemes of Cambrian deposits in Russia and correlated them to then accepted Scandinavian scale, which was based on the succession of agnostid species. She summarized all these data in the *Atlas of Index Taxa of Fossil Faunas of the USSR* (Lermontova, 1940), which included a small collection of agnostids found in Siberia, Bennett Island, and Kyrgyzstan. This Atlas is still in wide use. It contains the first descriptions of the genus *Pseudorhaptagnostus* with the species *P. punctatus*, genus *Euplethagnostus* with the species *E. subangulatus,* genus *Cyclagnostus* with the species *Cyclagnostus elegans,* genus *Pentagnostus* with the species *Pentagnostus anabarensis,* the species *Peronopsis crassa, Pseudagnostus rotundatus, P. impressus, P.* cf. *obsoletus, Enetagnostus tricuspis, Hypagnostus latirhachis, Cotalagnostus globiceps, Grandagnostus longifrons, Homagnostus paraobesus,* and *H. ultraobesus.*

E.V. Lermontova did not survive the siege of Leningrad; she died in 1942, leaving behind collections and unfinished manuscripts. After the war, Nina Evgenievna Chernysheva prepared these manuscripts for publications. Therefore, three papers authored by Lermontova were published many years after her death (Lermontova, 1951a, 1951b, 1951c).

The prewar geological prospecting work produced evidence that the Cambrian series host hydrocarbon–bearing beds; hence, their study became an important strategic task for the country. In addition, geological mapping at various scales conducted at that time required reliable chronostratigraphy. Therefore, in the mid–20th century, paleontological studies, including the study of agnostids, were very essential.

The second large work after *Atlas* of 1940 concerning the diversity of agnostids was published by Pokrovskaya (1958). She pointed to the shortcomings of the *Atlas*, including exceedingly brief descriptions of species and genera, sometimes unjustified generic assignments of species, ignoring the synonyms proposed at that time, absence of figures of Siberian representatives of common species, often substituted by Swedish specimens. Pokrovskaya compiled new more formalized descriptions of agnostid species and genera from Yakutia and accompanied them by photographs of Siberian specimens. Here, she described two new genera (*Dolichagnostus* and *Pseudophalacroma*), to which later other species were assigned in other regions, and several new species of previously known genera, *Tomagnostus deformis, Phoidagnostus angustiformis, Phalacroma maja, Ph. antiqua, Ph. laevis, Ph. calva, Goniagnostus longispinus,* and *G. longispinus* var. *latirhachis.*

The 1950s–1980s marked a period of the most intense Cambrian trilobite studies (including agnostids) in Russia.

The studies of stratigraphy and paleobiogeography of Cambrian in Siberia led to the recognition of facies zones in the Siberian Platform (Balashova, 1963; Egorova and Savitzkiy, 1969; Savitzkiy et al., 1972; Egorova and Pegel, 1979, Rosova, 1979; *Resheniya Vsesoyuznogo* ..., 1983; Astashkin et al., 1991). These are relatively shallow water facies of the western Siberian Platform (Turukhansk–Irkutsk–Oliokma area), reef facies of its central region (Anabar–Sinsk area), and open sea deposits of the eastern Siberian Platform (Yudoma–Olenek area) (Fig. 1).

The first detailed descriptions of agnostids from different facies regions of the Siberian Platform were published by L.I. Egorova, N.P. Lazarenko, and

Global scale			Russian scale			Regional trilobite biostratigraphy of the Siberian Platform			Regional trilobite biostratigraphy and Horizons of the Altai–Sayany Folded Belt	
System	Series	Stage	System	Series	Stage	Inner shelf (Turukhansk–Irkutsk–Oliokma facies region)	Outer shelf (Anabar–Sinsk facies region)	Open basin (Yudoma–Olenek facies region)		
						Trilobite zones	Trilobite zones and beds	Trilobite zones and beds	Trilobite zones	Horizons
Cambrian	Furongian	Stage 10	Ordovician			*Eoapatokephalus nyaicus*	?	?	not determined	Dobrinsky
			Cambrian	Upper	Batyrbayan	*Loparella loparica—Plethopeltides magnus*				
						Dolgeuloma—Kaninia — *Dolgeuloma* subzone		*Lotagnostus americanus* — Beds with *Parabolinites levis*		Zolotokitatsky
						Kaninia subzone				
		Jiangshanian ·?			Aksayan	*Kujandaspis*		*Parabolinites rectus*		
						Amorphella—Yurakia		*Plicatolina perlata*		
								Maladioidella abdita		
					Sakian	*Kuraspis* — *Pesaiella—Parakoldinia* subzone	*Faciura—Garbiella*	*Agnostotes orientalis—Irvingella*		Shorsky
		Paibian					*Maspakites—Idahoia—Raashellina*	*Eugonocare (Pseudeugonocare) borealis*		Khristinovsky
										Arininsky
								Glyptagnostus reticulatus		Ust'-Kul'bichsky
	Series 3	Guzhangian		Middle	Ayusokkanian	*Kuraspis* — *Letniites jakuticus* subzone	*Pedinocephalina—Toxotis*	*Glyptagnostus stolidotus*		
						Kuraspoides planus subzone		*Clavagnostus spinosus*		
					Mayan	Beds with *Markhaspis*	Beds with *Ritella elgensis*	*Proagnostus bulbus*	*Lejopyge laevigata*	Elandinsky
						?	?	*Lejopyge laevigata*		
		Drumian					Beds with *Urjungaspis*	*Anomocarioides*	*Goniagnostus nathorsti*	Altyrgainsky
							Proasaphiscus privus	*Corynexochus perforatus—Anopolenus henrici*	*Centropleura oriens*	Arajgol'sky
						?	*Corynexochus perforatus—Hatangia*			
							Solenopleura patula	*Tomagnostus fissus—Acadoparadoxides sacheri*	*Pseudanomocarina*	El'dakhsky
		Stage 5			Amgan		Unnamed zone	*Triplagnostus gibbus*	not determined	Mundybashsky
							Kounamkites	*Kounamkites*		
	·?	·?				Beds with *Proasaphiscus—Deltocephalus*	*Enixus (=Schistocephalus)*	*Ovatoryctocara*		Agatinsky
	Series 2	Stage 4		Lower	Toyonian	*Namanoia*	*Anabaraspis splendens*	*Anabaraspis*	*Kooteniella—Edelsteinaspis*	Obruchevsky
						Parapoliella—Pseudoeteraspis	*Lermontovia grandis*	*Paramicmacca petropavlovskii—Lermontovia*		
							Bergeroniellus ketemensis		*Parapoliella—Onchocephalina*	

Fig. 1. Global and Russian Cambrian series and stage nomenclature and current biostratigraphic subdivisions of the Siberian Platform and Altai-Sayany Folded Belt (on trilobites) (Astashkin et al., 1991; 1995; Sukhov et al., 2016).

A.V. Rosova. Rosova and Lazarenko synchronously studied the trilobite fauna from the Cambrian sections of the Igarka and Norilsk areas in the northwestern Siberian Platform (Lazarenko, 1960; Rosova, 1963, 1964, 1968, 1977; Datsenko et al., 1968; Lazarenko and Nikiforov, 1968). A section on the Kulyumbe River in the Igarka Region was proposed as the type section of the carbonate shelf (*Resheniya Vsesoyuznogo* ..., 1983). Abundant and diverse faunal assemblages characterizing these deposits are to a large extent represented by endemic taxa of polymere trilobites and relatively rare agnostids. Several new agnostid species are described from these assemblages (*Phalagnostus cuneatus* Rosova, 1964, "*Agnostus" simplexiformis* Rosova, 1964, *Pseudagnostus nganasanicus* Rosova, 1964, and *Skryjagnostus implicatus* Lazarenko, 1968).

One of these species (*nganasanicus)* was later designated the type species of the genus *Nahannagnostus* Pratt, 1992. In the Norilsk Region, a section on the Chopko River is very important for correlation of the Upper Cambrian shelf and open sea deposits. The lower part of this section is composed of the rocks of the Chopko Formation formed in the slope environment in a basin with wide biogeographic connections, whereas the upper part (Tukalanda Formation) was deposited in the conditions of an inner shelf inhabited predominantly by geographically restricted trilobite taxa, many of which are found in the sections of the Kulyumbe Formation on the Kulyumbe River. Faunas from the Chopko River Basin are also important for understanding the biostratigraphy of this region. Their study took place in the second half of the 20th century (Lazarenko, 1960, 1968; Rosova, 1964, 1968, 1977; Lazarenko and Nikiforov, 1968). In this period, only separate species were described from these sections. Therefore, the intention to resume the paleontological studies in this region seemed natural. Paleontological research in the northwestern Siberian Platform was continued by the studies of A.V. Rosova and her students A.I. Varlamov, K.L. Pack, and A.L. Makarova at the beginning of the 21st century. New paleontological material with numerous agnostids was collected, regional biostratigraphy and correlations were updated, and the diversity of agnostids in the reference sections was reevaluated (Varlamov et al., 2005, Varlamov and Rosova, 2009). A new genus, *Norilagnostus* Pack, 2005, and new species (*Pseudagnostus intermedius* Pack, 2005, *P. cryptus* Pack, 2005) were established and several new taxa were figured, but not described (*Sulcatagnostus antecedens* Rosova et Makarova, 2009, *Formosagnostus primus* Rosova et Makarova, 2009, *Acmarhachis apicula* Rosova et Makarova, 2009, *Quadrahomagnostus norilica* Rosova et Makarova, 2009, *Q. parallelus* Rosova et Makarova, 2009) (Varlamov and Rosova, 2009). The section on the Chopko River was proposed as the possible Russian stratotype for the subdivisions of the Upper Cambrian (Varlamov and Rosova, 2009).

From the end of the 1950s, agnostids have been studied from the Cambrian of the northern and eastern regions of the Siberian Platform. The results of the study of Cambrian agnostids from the western Anabar Region in the north of the Siberian Platform were published by Egorova and Savitzkiy (1969). That work included a description of *Triplagnostus remotus* Pokrovskaya et Egorova, 1969.

A monograph of Chernysheva (1961) dealt with the study of the stratotype of the Amgan Stage of the Middle Cambrian in the southeast of the Siberian Platform. The stage was established in the reef formations of the Amga Formation, the faunal assemblages of which are mainly composed of polymere trilobites with rare agnostids. In that paper, Chernysheva described only three agnostid species: *Triplagnostus praecurrens* (Westergård), *Peronopsis fallax* (Linnarsson), and *Peronopsis scutalis* (Salter in Hicks). This list was supplemented by *Triplagnostus gibbus* (Linnarsson) and *T. pictinatus* Pokrovskaya et Egorova included in the monograph by Egorova et al. (1976).

Most sections of open sea deposits are located in the east of the Siberian Platform. For this paleogeographic region, agnostids are the main zonal indices of the two upper Cambrian series. In this paleogeographic region, agnostids serve as the main zonal indices of the two upper Cambrian series. Monographs of Savitzkiy et al. (1972) and Egorova et al. (1976) summarized the diversity of Amgan agnostids represented by the Kuonamka Formation in this region and contained about 20 species of agnostids.

The Middle Cambrian section of the Kuonamka Formation on the Molodo River (southeastern slope of the Olenek Uplift) containing agnostid trilobites was compiled by Shabanov et al. (2008a, 2008b) and proposed as a Global Standard Stratotype Section and Point (GSSP) of a potential global stratotype between Cambrian Series 3 and 4.

Egorova et al. (1982) summarized data on the taxonomic diversity of agnostids in the stratotype region of the Mayan Stage (Middle Cambrian) in the southeast of the Siberian Platform and described over 50 agnostid species.

The section of the Ogon'or Formation on the Khos-Nelege River in the Chekurovka Anticline of the Kharaulakh Mountains on the northeastern margin of the Siberian Platform is the type open sea Upper Cambrian section for this region (*Resheniya Vsesoyuznogo ...*, 1983). It contained abundant agnostids of over 60 species—group taxa and was proposed as the global stratotype for the bases of two Furongian stages defined by the first appearance datum of the agnostids *Agnostotes orientalis* and *Lotagnostus americanus* (Lazarenko et al., 2008a, 2008b; Lazarenko et al., 2011).

Important paleontological summaries were published from the drilling cores of the inaccessible territories of the Siberian Platform (Shabanov et al., 1987; Ogienko and Garina, 2001; Pegel et al., 2016). The drilling core material allowed the refinement and correlation of the Cambrian deposits of this region, thereby determining the stratigraphic positions and facies affinities of trilobite assemblages that include more than 20 agnostid species.

These studies have expanded information on the diversity of agnostids, reevaluated the taxonomic significance of their morphological characters and, correspondingly, stratigraphic ranges of species and genera. Based on the material from this region, the following species have been established: *Cyclopagnostus orientalis* Lazarenko, 1966, *C. asper* Lazarenko, 1966, *Agnostus captiosus* Lazarenko, 1966, *Pseudagnostus quadratus* Lazarenko, 1966, *Condylopyge carinata vicina* Egorova, 1972 (=*C. eli* Geyer, 1998), *Tomagnostus sibiricus* Pokrovskaya et Egorova, 1972, *T. clarus* Pokrovskaya et Egorova, 1982, *Triplagnostus ademptus* Pokrovskaya et Egorova, 1972, *T. contortus* Pokrovskaya et Egorova, 1972, *T. arctus* Pokrovskaya et Egorova, 1976, *T. pictinatus* Pokrovskaya et Egorova,

1976, *Peronopsis lata* Shabanov, 1972, *P. recta* Pokrovskaya et Egorova, 1972, *P. bulkurensis* Pokrovskaya et Pegel, 1982, *Linguagnostus sibiricus* Pokrovskaya et Egorova, 1982, *Dolichagnostus levis* Pegel, 1978, *Hypagnostus facetus* Pokrovskaya et Egorova, 1982, *Innitagnostus angustus* Pokrovskaya et Pegel, 1997, *Pentagnostus proanabrensis* Fedoseev, 1999, and *Skryjagnostus usitatus* Salikhova, 2016. The genus *Glyptagnostotes* with the species *G. elegans* established by Lazarenko (1966) were later assigned to the genus *Agnostotes* and species *Agnostotes orientalis* (Kobayashi, 1935). Rosova (Lisogor et al., 1988), based on the material from the Cambrian sections in South Kazakhstan and southeastern Siberian Platform, established the genus *Lisogoragnostus,* which was later found out to have a global distribution. The representatives of the genera *Eurudagnostus* and *Pseudorhaptagnostus* and the species *Pseudagnostus obsoletus* occurring in Siberia were for the first time described by Lermontova (1951a) from the Cambrian deposits of Kazakhstan (Boshche–Kul borehole).

The Cambrian trilobites and agnostids from the Arctic regions of Russia (Taimyr Peninsula, Severnaya Zemlya Archipelago) were mainly studied by N.P. Lazarenko, I.I. Koptev and A.K. Semashko also collected and identified this Taimyr fauna. The results of these studies are published in the framework of the presently adopted regional stratigraphic schemes (*Resheniya Vsesoyuznogo* ..., 1983) and those by Sobolevskaya and Kabankov (2014) on Taimyr do not contain taxonomic descriptions and only give lists of species in the sections.

After Lermontova (1940), agnostids of the Altai-Sayany Folded Region, including Altai, Salair, and Kuznetsky Alatau, were studied by N.K. Ivshin, N.V. Pokrovskaya, O.K. Poletaeva, A.V. Rosova, M.F. and E.V. Romanenko (Egorova et al., 1960; Romanenko and Romanenko, 1967; Poletaeva and Romanenko, 1970; Rosova, 1977; Egorova and Romanenko, 1982; Romanenko, 1985, 1988) and also Bognibova (1965), Bognibova et al. (1971), E.S. Fedjanina in Rosova (1977), and Petrunina and Gabova (2008). Many endemic agnostid taxa are established in this region, although some cosmopolitan taxa are also found. The latter include the genera *Glaberagnostus* E. Romanenko, 1985 with the type species *G. altaicus* E. Romanenko, *Kormagnostella* E. Romanenko, 1967 with the type species *K. glabrata* E. Romanenko, 1967 (Romanenko and Romanenko, 1967), *Barrandagnostus* Ivshin, 1960 with the type species *B. barrandei* Ivshin, 1960, and *Salagnostus* Gabova, 2008 with the type species *S. gorskinus* Gabova, 2008. Thirty–two agnostid species are established based on the material from the Altai-Sayany Region.

In the West Siberian Plate, the first trilobite occurrences were recorded on the left bank of the Yenisei River in a drill core. N.E. Chernysheva for the first time identified from the Elogui reference borehole representatives of the agnostid genus *Peronopsis* (Dragunov et al., 1967). Later, the study of the core of borehole Vostok-1 situated in the northeastern Tomsk Region revealed several agnostid species previously revealed in the Middle Cambrian of an open marine basin on the West Siberian Platform (Korovnikov et al., 2010).

More than 100 years of studies by three generations of paleontologists allowed a new interpretation of the agnostid diversity in Russia. A total of 70 genera and about 210 species have been described from this vast region. Of these, 14 genera and 62 species are established by Russian authors. At present, this diversity needs to be in a meaningful way compared with the global diversity of agnostids. This is the basis for biostratigraphic correlation of the deposits, correct interpretation of the paleobiogeography of Cambrian seas, and evolutionary reconstructions of this enigmatic animal group.

MAJOR CAMBRIAN DEPOSITIONAL ENVIRONMENTS IN THE SIBERIAN PLATFORM AND ALTAI-SAYANY FOLDED BELT

Cambrian deposits in Russia are most common in the Siberian Platform and Altai-Sayany Folded Belt.

In Cambrian, the Siberian Platform was a marine basin with clear differentiation of depositional settings (Fig. 2). The central, southwestern, and northern parts of the platform were occupied by mainly inner (isolated) *shallow shelf (carbonate platform)*, with deposition of hypersaline and sulfatized dolomitic and, less commonly, calcareous mudstone. In the east, northeast, and northwest of the Siberian Platform, there were deepwater normal marine *open basins* separated from the inner shelf by a narrow band of bioclastic carbonate rocks, usually with reef limestones forming on the margin of a carbonate platform (*outer shelf)*. In the regional scheme of the Cambrian of the Siberian Platform, these sedimentary regions include *Turukhansk–Irkutsk–Oliokma facies region* (inner shelf); *Anabar–Sinsk facies region* (outer shelf); *Yudoma–Olenek facies region* (open basin) (Savitzkiy et al., 1972, *Resheniya Vsesoyuznogo* ..., 1983; Sukhov, 1997; Pegel, Sukhov, 2013; Sukhov et al., 2016).

Each of these large landscape zones (inner shelf, outer shelf, and open sea) showed a pronounced disparity in taxonomic diversity of biological communities, including that of trilobites, throughout the entire history of evolution of the Cambrian basin on the Siberian Platform (Rosova, 1979; Repina, 1983, 1987; Pegel, 2000; Sukhov et al., 2016). This required new biostratigraphic scales for each facies region of the Siberian Platform (*Resheniya Vsesoyuznogo* ..., 1983; Fig. 1). Agnostids are characteristic of open marine basins and continental slope facies, but are also present in other facies. With their wide geographic ranges, agnostids allow correlation of beds from widely separated areas of the Siberian Platform and adjacent regions. This is the main biostratigraphic significance of agnostids.

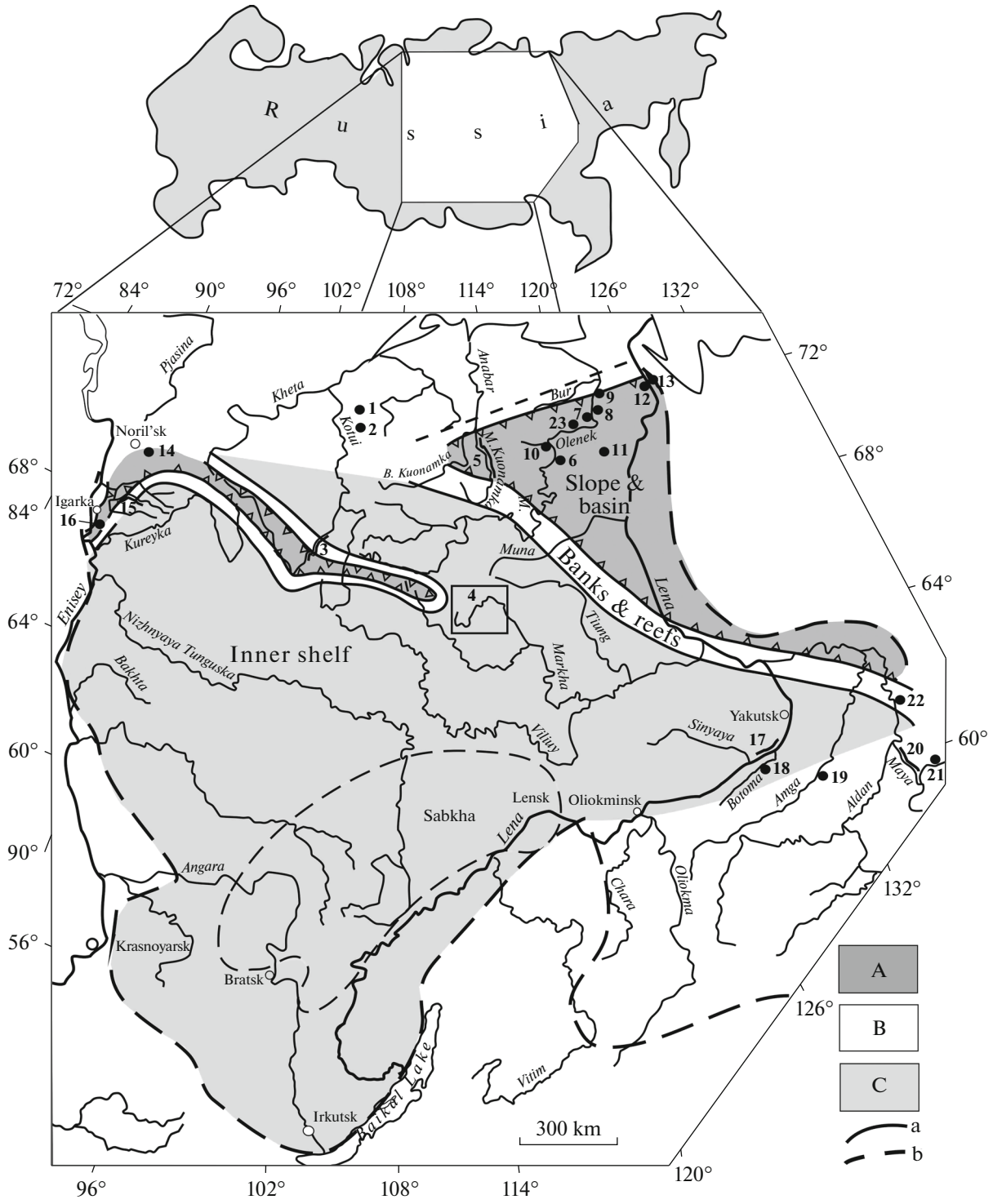


Fig. 2. Paleogeographical scheme of the Siberian Platform with location of the key sections. Uppermost Guzhangian Stage–Furongian Series (after Sukhov, 1997, modified). **Anabar Region:** (1) Yurung–Tas–Suluda River, (2) Buom–Pastakh River, (3) Kotuy River (middle reaches), (4) Daldyn–Alakit Region, (5) Malaya Kuonamka River. **Sukhana trough:** (6) Amyday River, (10) Nekekit River. **Olenek Uplift:** (7) Boroluolakh River, (8) Torkukuy River, (9)Khorbusuonka River, (11) Molodo River. **Kjutjungde trough:** (23) Khoyguollakh Spring. **Kharaulakh Mountains:** (12) village of Chekurovka , (13) Khos-Nelege River. **Northwest Siberian Platform:** (14) Chopko River, (15) Kulyumbe River, (16) Igarka region, well 141. **Southeast Siberian Platform:** (17) Lena River (middle reaches), (18) Botoma River, (19) Amga River, (20) Maya and Chabda rivers, (21) Yudoma River, (22) Aldan River and Kerbi River mouth; (A) deep water open basins and slopes, (B) banks and reefal zones, (C) inner shallow water shelf, (a) boundaries of the facial zones, (b) boundaries of the Siberian Platform.

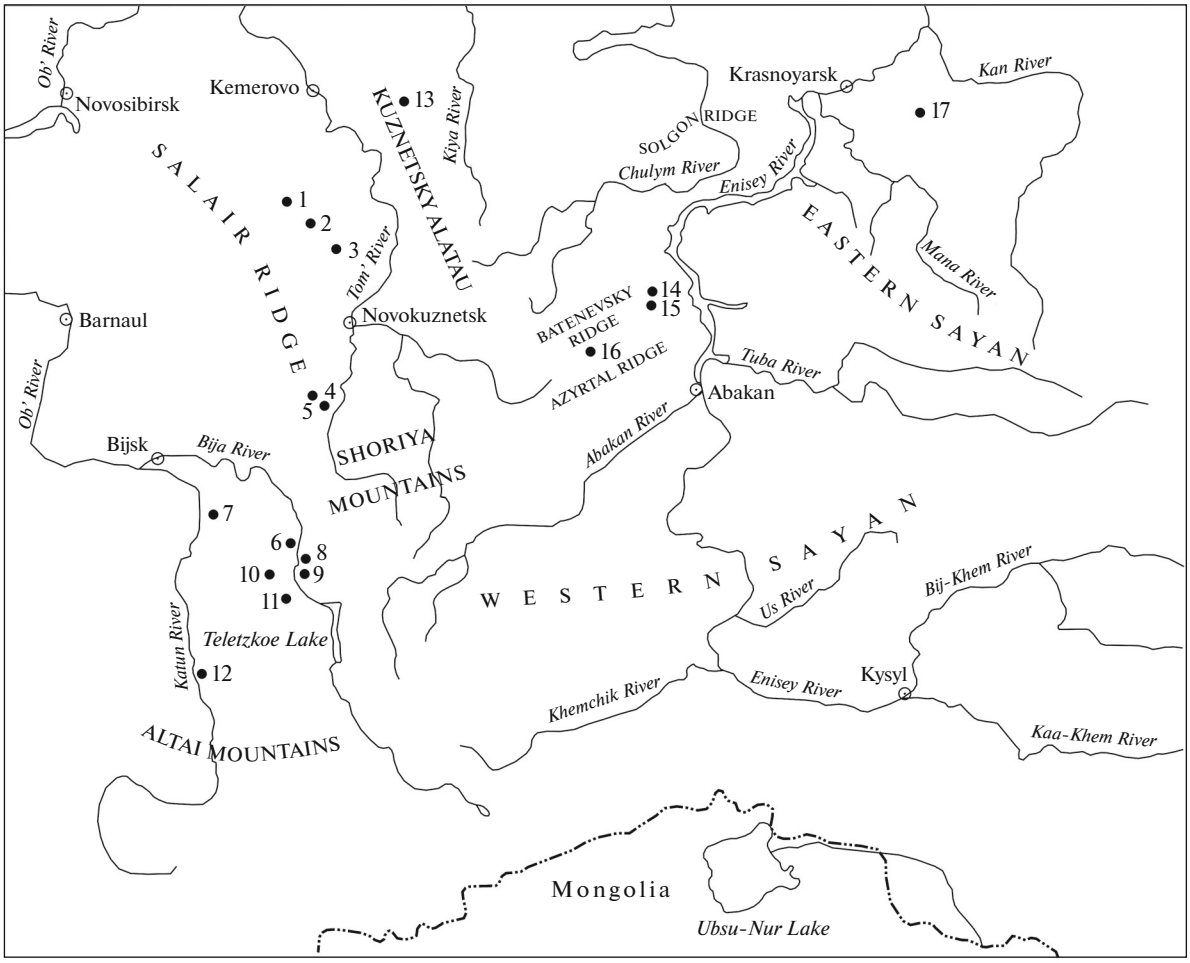


Fig. 3. Location of key sections of the Altai-Sayany Folded Belt. **Northeastern Salair Ridge:** (1) village of Arinichevo, (2) village of Gorskino, (3) Orlinaya Mountain. **Southern Salair Ridge**: (4) Chumysh River, (5) Anyshtaikha River. **Altai Mountains:** (6) Bol'shaya Isha River, (7) Isha River; (8) Tandoshka and Tagaza rivers, (9) Ishpa River; (10) Verkhnyaya Yinirga River, (11) Kul'bich Spring, (12) Verkhnyaya Elanda River. **Kuznetsky Alatau**: (13) Kazennaya Vasil'evka River, (14) Batenevsky Ridge, Sladkie Koren'ya Mountain, (15) Batenevsky Ridge, Doldiy Mys Mountain, (16) Azyrtal Ridge. **Eastern Sayan:** (17) village of Shakhmatovo.

Deposits of the Altai-Sayany Folded Belt containing Cambrian agnostids occur in Salair, Gornyi Altai, Kuznetsky Alatau, and East Sayan (Fig. 3). The tectonic activity of this region in the Cambrian determined its blocky structure, widely present volcanism, numerous disruptions, variety of facies, and differences in completeness of geological sections in different tectonic zones. In the northeastern part of the Altai-Sayany Folded Belt, in the sections of the Batenevsky and Azyrtal Ridges of Kuznetsky Alatau and in the northeast of the East Sayan contain Amgan deposits (first half of the Middle Cambrian), mainly carbonate in composition with numerous fossils. The western and southern parts of the region are dominated by siliciclastic and volcanic rocks. The deposits of the Mayan and Ayusokkanian stages of the second half of the Middle Cambrian with agnostids are known from Salair (Orlinaya Mountain) and Gornyi Altai (sections on the Bol'shaya Isha, Tandoshka, Tagaza, Verkhnyaya Elanda, and Verkhnyaya Ynyrga rivers). In Gornyi Altai, at the end of the Amgan (Middle Cambrian) in some tectonic zones, sections show a considerable gap in sedimentation synchronous with the period of strong volcanism. A westward sea transgression in the Mayan facilitated the restoration of biotic connections with the Siberian Platform and Kazakhstan. By the end of this time, a considerable part of the paleobasin of Gornyi Altai represented a semi-isolated shallow sea with siliciclastic, less commonly, carbonate–siliciclastic sedimentation (Romanenko and Romanenko, 1967).

The Upper Cambrian deposits with fossils occur in the western part of the Altai-Sayany Folded Belt. Here, a number of tectonic provinces are established based on the characters of the sections reflecting differences in the geological history and sedimentary set-

tings in the Late Cambrian (Astashkin et al., 1995). Agnostids of the lower part of the Upper Cambrian are found in the following localities:

• in siliciclastics of the Zolotokitatsky Province in the northwest of Kuznetsky Alatau (Kazennaya Vasil'evka River); in the Berdsk–Eltsovka Province which includes the northeastern and southern regions of Salair with sections of volcanic–siliciclastic–carbonate deposits (Orlinaya Mountain, Chumysh and Anyshtaikha Rivers, vicinity of the villages of Arinichevo and Gorskino);

• in siliciclastic–carbonate deposits of the Biya–Katun Province (sections on the Isha and Bol'shaya Isha rivers) and Uimen–Lebed Province (Tandoshka, Tagaza, Ishpa rivers and Kul'bich Spring) in the northeastern part of Gornyi Altai.

The biostratigraphic zonal scale in the Altai-Sayany Folded Belt is poorly developed for the Middle Cambrian and absent in the Upper Cambrian. Their subdivision and correlation on the regional scale are based on the regional stages ("horizons"), uniting synchronous deposits formed in different depositional settings (Fig. 1).

CORRELATION OF THE REGIONAL AND GLOBAL SCALES

The correlation of the Middle and Upper Cambrian biostratigraphic units in the Altai-Sayany and Siberian Platform has a varying degree of reliability (Fig. 1).

In the Middle Cambrian Amgan Stage, the most reliable correlations include those on the basis of the *Kounamkites* Zone of the Siberian Platform and Mundybashsky Horizon of the Altai-Sayany Folded Belt, and also the base of the Amgan Stage, corresponding to the base of the Agatinsky Regional Stage corresponding the base of the *Ovatoryctocara* Zone on the Siberian Platform and the base of the Agatinsky Horizon of the Altai-Sayany Folded Belt. The correlation of the lower boundary of the El'dakhsky Horizon of the Altai-Sayany Folded Belt is less certain. It is possible that it correlates with a certain level within the *Triplagnostus gibbus* Zone of the Siberian Platform.

In the Mayan Stage of the Middle Cambrian, the most reliable is the correlation of the ranges of agnostids of the genus *Lejopyge* (*Anopolenus henrici* and *Proagnostus bulbus* zones of the Siberian Platform and the *Anopolenus henrici* Zone of the Elandinsky Horizon of the Altai-Sayany Region). The deposits of the *Anomocarioides* Zone of the Mayan Stage of the Siberian Platform and the *Goniagnostus nathorsti* Zone of the Altyrgainsky Horizon of the Altai-Sayany Region and also the *Corynexochus perforatus–Anopolenus henrici* Zone of the Mayan Stage of the Siberian Platform and Araigol'sky Horizon of the Altai-Sayany Region are reasonably reliably correlated based on the fossil assemblages and on the position in the section of the zone.

The deposits of the lower part of the Ust'-Kulbichsky Regional Stage belong to the Ayusokkanian Stage (upper Middle Cambrian) in the Altai-Sayany Region. The upper part of this regional stage contains fossil assemblages, including the agnostids *Glyptagnostus reticulatus,* allowing the host rocks to be assigned to the lower part of the Upper Cambrian Sakian Stage. Thus, the deposits of the Ust'-Kulbichsky Horizon in the Altai-Sayany Region correspond to the deposits of the *Clavagnostus spinosus*, *Glyptagnostus stolidotus*, and *Glyptagnostus reticulatus* zones of the Siberian Platform.

In the scheme of the Upper Cambrian of the Altai-Sayany Region (*Resheniya Vsesoyuznogo* ..., 1983; Astashkin et al., 1995), the Ust'-Kul'bichsky Horizon composed of siliciclastics is overlain by the Arininsky Horizon, with a limestone lense containing trilobites similar in their taxonomic composition to the assemblages of the *Pedinocephalina–Toxotis* Zone of the Ayusokkan Stage of the Siberian Platform. Thus, it is possible that the Arininsky Horizon is partly a facies equivalent of the Ust'-Kul'bichsky Horizon. However, this hypothesis needs to be confirmed.

The correlation of the total stratigraphic range of the Khristinovsky and Shorian regional stages of the Altai-Sayany Region to the zonal subdivisions of the Sakian Stage of the Siberian Platform is more evident. The Khristinovsky Horizon contains taxa from the *Eugonocare* (*Pseudeugonocare*) *borealis* and *Maspakites–Idahoia–Raashellina* zones of the Siberian Platform, while the Shorsky Horizon encloses those of the *Agnostotes orientalis–Irvingella* and *Maladioidella abdita* zones. The Zolotokitatsky Horizon of the Altai-Sayany Region with certainty correlates with the Aksayan Stage of the Siberian Platform represented by the open sea facies.

The lower boundaries of the officially adopted Cambrian stages of the global stratigraphic scale are readily correlated to the boundaries of the biostratigraphic scale of the open sea facies on the Siberian Platform (Fig. 1): the base of the Drumian Stage corresponds to the base of the *Tomagnostus fissus–Acadoparadoxides sacheri* Zone; that of the Guzhangian Stage, to the base of the *Anopolenus henrici* Zone; that of the Paibian Stage, to the base of the *Glyptagnostus reticulatus* Zone; and that of the Zhangshanian Stage, to the base of the *Agnostotes orientalis–Irvingella* Zone.

Of the zonal subdivision of the Middle and Upper Cambrian of the Altai-Sayany Region, only the base of the *Anopolenus henrici* Zone of the Mayan Stage with certainty correlates with the base of the Guzhangian Stage of the global scale. The correlation with the boundaries of other subdivisions of the global scale is indirect and to a large extent tentative, through the correlation with the units of the Siberian Platform.

SYSTEMATIC PALEONTOLOGY

Superfamily Condylopygoidea Raymond, 1913

Family Condylopygidae Raymond, 1913

Diagnosis. Cephalon with laterally expanded anteroglabella; cheeks usually subdivided by furrow in front of expanded anteroglabella; glabellar rear angulated. Pygidial axis with triannulated anteroaxis.

Genus *Condylopyge* Hawle et Corda, 1847

Plate 2, figs. 1 and 2

Paragnostus: Jaekel, 1909, p. 396.

Fallagnostus: Howell, 1935, p. 230; Moore, 1959, p. O173.

Condylopyge: Moore, 1959, p. O174; Rushton, 1966, p. 29; 1979, p. 46; Shergold et al., 1990, p. 57; Shergold and Laurie, 1997, p. 383; Fletcher et al., 2005, p. 317; Rushton, Weidner, 2007, p. 394.

Type species. *Battus rex* Barrande, 1846.

Diagnosis. En grande tenue; cephalon and pygidium with strongly deliquiate border furrows; anteroglabella very large, approximately semicircular; posterior lobe cylindrical, with retral axial node; pygidial axis bearing elongate keel formed by fusion of axial nodes anteriorly; spines, where developed, short; prosopon smooth.

Remarks. Two specimens (cephalon and pygidium) were originally indicated as the "holotype" for *C. carinata* subsp. *vicina* (Egorova and Savitzkiy, 1972, pl. 3, figs. 6, 8). These two parts do not represent a single organism; thus, only one of them must be the holotype (*International Code* ..., 1999, Art. 73.1.5). We refer the holotype of this species to the cephalon (Egorova et al., 1972, pl. 3, fig. 6).

Species occurring in Russia. *C. carinata vicina* Egorova, 1972—Siberian Platform: Nekekit River, *Ovatoryctocara* and *Kounamkites* zones; Yudoma River, *Tomagnostus fissus–Paradoxides hicksi* Zone (Savitzkiy et al., 1972; Egorova et al., 1976; Egorova et al., 1982); Amyday River, *Kounamkites* Zone (Savitzkiy et al., 1972); Molodo River, *Ovatoryctocara* Zone (Shabanov et al., 2008).

C. eli Geyer, 1998—Siberian Platform, Nekekit River, *Kounamkites* Zone (Egorova et al., 1976, pl. 50, fig. 12 as *Condylopyge carinata vicina*).

Condylopyge sp.—Siberian Platform, Lena River (middle reaches), *Anopolenus henrici* Zone (Egorova et al., 1982).

Family Ptychagnostidae Kobayashi, 1939

Diagnosis. En grande tenue; cephalon and pygidium with narrow border structures; cephalon with median preglabellar furrow. Basal lobes with tendency to elongate, but usually elongate, and never large. Pygidium with F1 and F2 well developed, posteroaxis moderately wide and high. Postaxial furrow well developed, at least in juveniles.

Remarks on generic composition: *Triplagnostus, Acidusus, Ptychagnostus* (subgenera *Ptychagnostus and Zeteagnostus*), *Aotagnostus* (subgenera *Aotagnostus* and *Myrmecomimus*), *Onymagnostus, Goniagnostus* (subgenera *Goniagnostus, Allobodochus, Criotypus*), *Tomagnostus, Lejopyge*, and *Pseudophalacroma*.

Kobayashi establishing the subfamily Ptychagnostinae, including two genera, *Ptychagnostus* and *Goniagnostus*; Triplagnostinae was reserved for *Triplagnostus* and Tomagnostinae, for *Tomagnostus*. Later, these genera were shuffled and transferred to different families using selected sets of traits (Rusconi, 1951; Moore, 1959). Öpik (1979) reconsidered the concept of Ptychagnostidae, reserved it for species with narrow border structures, tapering glabellar front, well–developed transaxial furrows, and with median preglabellar furrow developed or with median notch in the anteroglabella. Such a revision allowed 15 genera and subgenera to be combined under the Ptychagnostidae. After the revision, the list of genera included previously known furrowed genera *Ptychagnostus* with the subgenera *P. (Ptychagnostus*), *P. (Acidusus); Goniagnostus* with the subgenera *G. (Goniagnostus), G. (Allobodochus*), and *G. (Criotypus); Pentagnostus, Tomagnostus; Triplagnostus* with the subgenera *T. (Triplagnostus), T. (Aristarius*); and effaced genera *Lejopyge* and *Pseudophalacroma*. In addition, Öpik described three new genera: *Onymagnostus, Zeteagnostus,* and *Aotagnostus*.

Robison (1984) placed *Triplagnostus, Zeteagnostus, Aotagnostus*, and *Pentagnostus* in synonymy to *Ptychagnostus* as he thought their diagnostic characters unreliable and insufficient. He characterized the expanded genus by elongated basal lobes and necessary presence of a postaxial furrow. In addition, he inferred that all these forms are combined by common origin; therefore, the group is monophyletic. Species with short basal lobes and a postaxial furrow, Robison assigned to *Lejopyge* and species with short basal lobes and undivided postaxial space he referred to *Onymagnostus*. Therefore, *Agnostus lundgreni* Tullberg, 1880 and *Lejopyge rigbyi* Robison, 1984, which possesses all characters of *Ptychagnostus* except elongated basal lobes, were assigned to *Lejopyge*. The genus (or subgenus) *Acidusus* he also considered within *Ptychagnostus*. Robison indicated that the only diagnostic feature mentioned by Öpik was the terminal node on the posteroaxis, and it seemed to be inadequate to diagnose a genus.

Robison's concept of *Ptychagnostidae* taxonomy was not accepted unconditionally by other authors. Laurie (1988, 1989) reinstated the generic status of *Triplagnostus, Zeteagnostus,* and *Acidusus* and subgeneric status of *Aotagnostus*. But, according to Robison's criticism, Laurie emended the generic diagnoses. He considered the shifted rearward median glabellar node and large axial node to be the main

Table 1. Distribution of the generic diagnostic characters of Ptychagnostidae

Cephalon pygidium	Basal lobes with tendency to elongate			Basal lobes short	
	Glabella expanded rearward and upward	Glabella expanded by sides	Glabellar F1, F2 well developed	Glabella expanded rearward and upward	Glabella expanded by sides
F1, F2 equally developed	*Triplagnostus* *Acidusus*	*Ptychagnostus* *Zeteagnostus*	*Goniagnostus*		
F1 deeper than F2, large axial node		*Aotagnostus* *Myrmecomimus*		*Lejopyge*	*Onymagnostus*

diagnostic characters for *Acidusus*, while the terminal axial node was excluded from the diagnosis. *Aotagnostus* was defined by the posterior glabellar lobe expanded rearward and upward and expanded posteroaxis, and, in addition, by a large axial node. Thus, Laurie differentiated *Acidusus* and *Aotagnostus* by the shape of the posteroglabella: in the latter genus, the posteroglabella was expanded laterally, while in the former, it expanded rearward and upward; the pygidia are similar in both genera. *Zeteagnostus* was restored as a distinct phylogenetic lineage for the forms with an expanded posteroglabella, but with a small axial node. This taxonomic view on Ptychagnostidae was incorporated in the last edition of *Treatise* (Shergold and Laurie, 1997). Table 1 summarizes the mosaic distribution of the generic diagnostic characters.

Table 1 shows that Robison's *Ptychagnostus* in fact combined five genera from the two left columns, while *Myrmecomimus* is a separate genus showing a strong tendency to expand the posteroaxis and posteroglabella. At the same time, *Lejopyge* lost its status as an effaced ptychagnostid genus, as it is only distinguished from *Onymagnostus* by its glabellar shape and from other ptychagnostid genera, by the short basal lobes. Lauries' taxonomy provided generic status for the two names in the first left cell, but the cells of the second column acquired a subgeneric status and the whole column became the genus *Ptychagnostus*. Therefore, this taxonomy seems to be subjective, as all morphological characters defined in the cells were selected as taxonomically equal. This means that the taxonomic status for each cell should be equal, and *Triplagnostus, Ptychagnostus,* and *Aotagnostus* were given the generic rank, and each contains two subgenera. Thus, we distinguish *Triplagnostus (Triplagnostus), Triplagnostus (Acidusus), P. (Ptychagnostus), P. (Zeteagnostus), A. (Aotagnostus),* and *A. (Myrmecomimus)* according to the formal logic. The two closely related species *Agnostus lundgreni* and *Lejopyge rigbyi* are suggested to be included in *Aotagnostus,* although they possess short basal lobes. Actually, the basal lobes may shorten when the posterior part of the glabella strongly expanded at the rear. Also noteworthy that distinguishing *Onymagnostus* and *Lejopyge* by the presence of a postaxial furrow seems to be unreliable, as a postaxial furrow is present in all ptychagnostids, at least in the meraspid stages and frequently became effaced in adults. However, in any case, these genera are characterized by another set of characters. Other genera of Ptychagnostidae were defined by more reliable diagnostic sets of traits. The preglabellar furrow, being a diagnostic feature for Ptychagnostidae yet is absent in *Tomagnostus* and *Pentagnostus*. *Tomagnostus* has a median notch in the anteroglabella instead of preglabellar furrow; representatives of *Pentagnostus* bear an incipient preglabellar furrow or it is completely absent. The median notch was formed in parallel in Diplagnostidae (in *Diplagnostus*) and in Agnostidae (*Barrandagnostus* Ivshin, 1960). However, other characters in *Tomagnostus* are similar to those in ptychagnostids. Such a feature probably forms in every agnostid lineage and may be considered as a good example of parallel evolution. *Pentagnostus* seemed to be transitional between Peronopsidae and Ptychagnostidae and here is referred to as a member of Peronopsidae.

The effaced ptychagnostids *Lejopyge* and *Pseudophalacroma* are very similar and sometimes synonymized (Shergold and Laurie, 1997), but yet are introduced here as separate genera (Robison, 1994; Peng and Robison, 2000). This similarity seems superficial and provided by the effacement of the majority of the structures. Robison and his colleagues suggested that these genera originated from different ancestral groups; from their point of view, *Lejopyge* originated from *Onymagnostus seminula* and *Agnostus lundgreni* became a predecessor of *Pseudophalacroma*. Robison based his taxonomic decision on the shape of the border structures, which persistently differ in *Lejopyge* and *Pseudophalacroma*. Our analysis of Peronopsidae has shown that border structures are rather conservative and should indicate superspecies taxonomic rank (Naimark, 2012). Therefore, irrespectively of their evolutionary history, these two genera should be considered as separate.

The taxonomic system reflected in the table above is applied in this work: each cell contains one genus and groups within one cell are referred to as subgenera. The ptychagnostid genera do not represent separate phyletic lineages, but rather introductions of morphological possibilities within the ptychagnostid habitus. These genera are more probably polyphyletic.

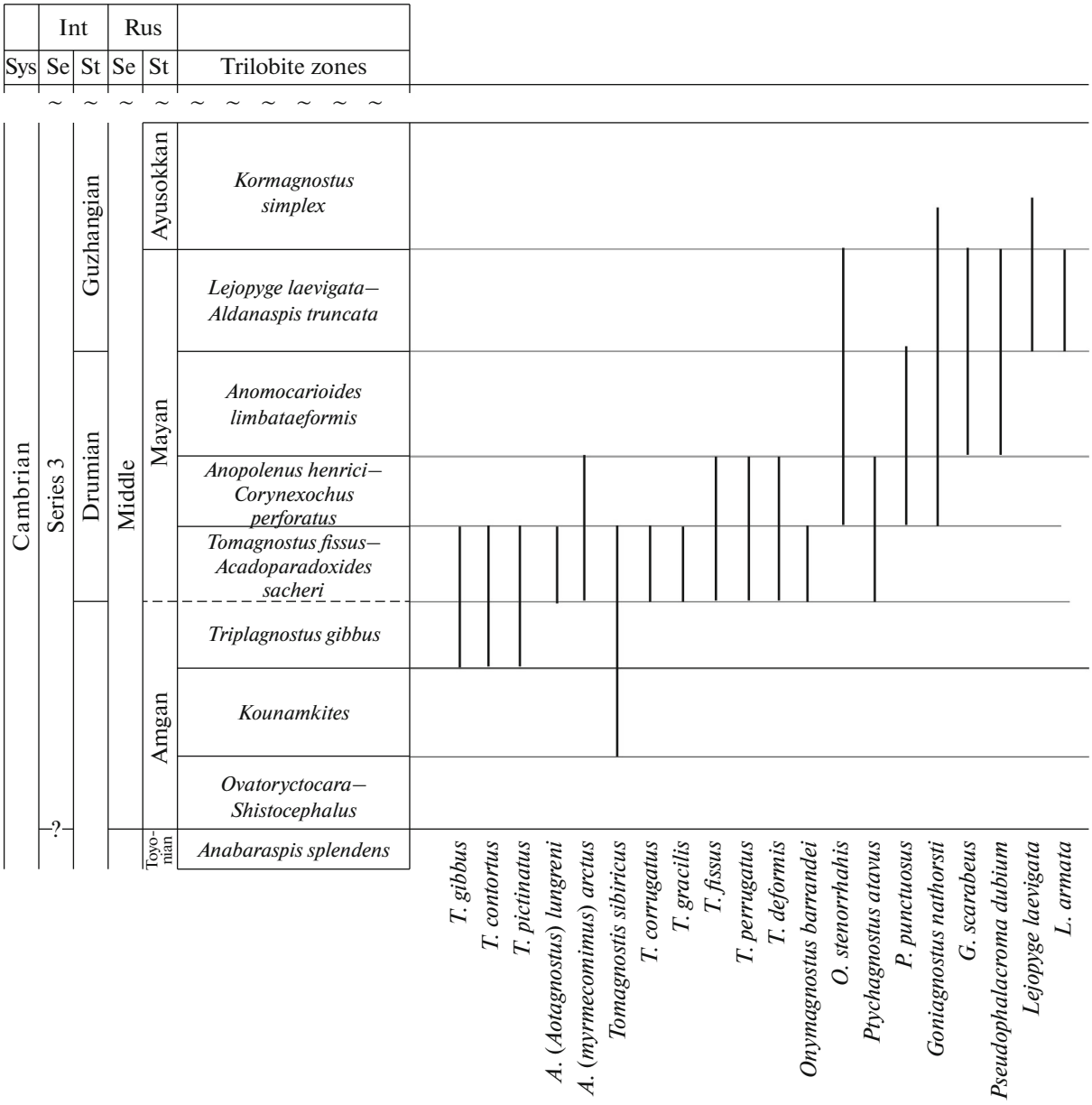


Fig. 4. Stratigraphic distribution of Ptychagnostidae species known from Russia.

The summary of stratigraphic distribution for Ptychagnostidae from Russia is shown in Fig. 4.

Genus *Triplagnostus* Howell, 1935

Plate 1, figs. 1, 2, 5–7

Triplagnostus: Howell, 1935b, p. 14; Moore, 1959, p. O179; Öpik, 1979, p. 114.

Triplagnostus (Triplagnostus): Laurie, 1988, p. 193; Shergold and Laurie, 1997, p. 354

Ptychagnostus (Triplagnostus): Westergård, 1946, p. 67.

Solenagnostus: Whitehouse, 1936, p. 86.

Type species. *Agnostus gibbus* Linnarsson, 1869.

Diagnosis. Cephalon with median preglabellar furrow. Glabellar M1 and M2 of equal width (not widened across M1 or M2); M1 inflated; F2 developed. Basal lobes with tendency to elongate, but usually oval. Pygidium with F1 and F2 equally developed; posteroaxis of moderate width and height. Posteroaxial furrow well developed. Prosopon usually smooth.

Species occurring in Russia. *Triplagnostus gibbus* (Linnarsson, 1869)—Siberian Platform: Boroluolakh, Amyday, and Amga rivers, *Pseudanomocarina* Zone (Egorova et al., 1976); Buom–Pastakh River, *Pseudanomocarina aojiformis* Zone (Egorova and Savitzkiy, 1969); Igarka District, well 141, *Triplagnostus gibbus* Zone (Sukhov et al., 2016); Amyday

River, *Triplagnostus gibbus* and *Tomagnostus fissus* zones (Fedoseev, 1999); Khorbusuonka, Nekekit, Boroluolakh, Olenek, Malaya Kuonamka, and Torkukuy rivers, *Triplagnostus gibbus* and *Pseudanomocarina* zones (Savitzkiy et al., 1972); Maya River, *Tomagnostus fissus* Zone (Pokrovskaya, 1960).

T. contortus Pokrovskaya et Egorova, 1972—Siberian Platform: Boroluolakh, Amyday, Malaya Kuonamka rivers, *Pseudanomocarina* Zone (Egorova et al., 1976); Amyday River, *Tomagnostus fissus–Ptychagnostus atavus* Zone (Fedoseev, 1999).

T. pictinatus Pokrovskaya et Egorova, 1976 (=*Triplagnostus fretus* Öpik, 1979)—Siberian Platform: Khorbusuonka River, Amgan Stage, Lena River (middle reaches), *Tomagnostus fissus* Zone; Malaya Kuonamka River, *Pseudanomocarina* Zone; Amga River, Amgan Stage (Egorova et al., 1976); Amyday River, *Tomagnostus fissus–Ptychagnostus atavus* Zone (Fedoseev, 1999). Western Siberia, Tomsk Region, Vostok-1 well, Upper Amgan (Korovnikov et al., 2010).

Genus *Aotagnostus* Öpik, 1979

Aotagnostus: Öpik, 1979, p. 133.

Triplagnostus (Aotagnostus): Laurie, 1988, p. 200; Shergold and Laurie, 1997, p. 354

Type species. *Aotagnostus culminosus* Öpik, 1979.

Diagnosis. Cephalon with median preglabellar furrow. Posterior glabellar lobe inflated and widened across M1 (approximately at the middle of M1). Basal lobes elongated. Pygidium with narrow border, spines small or absent. Axis with equally developed F1 and F2 or F2 weak; large median node strongly deflecting F2; F1 bent forwards; posteroaxis and M2 inflated. Postaxial furrow well developed in adults.

Subgenus *Aotagnostus* s. str.

Type species. *Aotagnostus culminosus* Öpik, 1979, p. 133.

Diagnosis. Anterior glabellar lobe, preglabellar and postaxial furrows well developed; posteroglabella, pygidial lobe M2, and posteroaxis moderately inflated.

Species found in Russia. *A. lundgreni* (Tullberg, 1880)—Siberian Platform: Lena and Amyday rivers, *Tomagnostus fissus* Zone (*T. arctus* Subzone) (Egorova et al., 1982; Fedoseev, 1999 as *Triplagnostus* sp.).

Subgenus *A. (Myrmecomimus)* Öpik, 1979

Plate 1, fig. 8

Myrmecomimus: Öpik, 1979, p. 136; Shergold and Laurie, 1997, p. 352.

Type species. *Myrmecomimus tribulis* Öpik, 1979, p. 136.

Diagnosis. Anterior glabellar lobe, preglabellar and postaxial furrows with tendency to efface; posteroglabella, pygidial lobe M2, and posteroaxis strongly inflated.

Species found in Russia. *A. (Myrmecomimus) arctus* (Egorova et al., 1976)—Siberian Platform: Amyday and Malaya Kuonamka rivers, *Pseudanomocarina* Zone (Egorova et al., 1976 as *Triplagnostus arctus*), Amyday River, *Tomagnostus fissus* Zone (*T. arctus* Subzone) (Fedoseev, 1999 as *Triplagnostus arctus*), Maya River, *Anomocarioides limbataeformis* Zone (Egorova et al., 1982 as *Triplagnostus convexus* Westergård, 1946).

Genus *Tomagnostus* Howell, 1935

Plate 1, figs. 3 and 4

Tomagnostus: Howell, 1935b, p. 15; Whitehouse, 1936, p. 90; Harrington, 1938, pp. 149, 154; Kobayashi, 1939, p. 149; Westergård, 1946, p. 31; Moore, 1959, p. O175; Pokrovskaya, 1960, p. 20; Ruston, 1979, p. 54; Shergold et al., 1990, p. 41; Robison, 1994, p. 57; Shergold and Laurie, 1997, p. 354; Weidner and Nielson, 2015, p. 10.

Ptychagnostus (Ptychagnostus): Westrop et al., 1996, pp. 814, 819.

Explanation of Plate 1

Ptychagnostidae

Figs. 1 and 2. *Triplagnostus contortus* Pokrovskaya et Egorova, 1972: (1) holotype TsNIGR, no. 66/10606, dorsal shield, 7.3 mm long (Savitzkiy et al., 1972, pl. 6, fig. 7); (2) pygidium from the same slab, 2.5 mm long; Siberian Platform; Khorbusuonka River, loc. 23/1d.

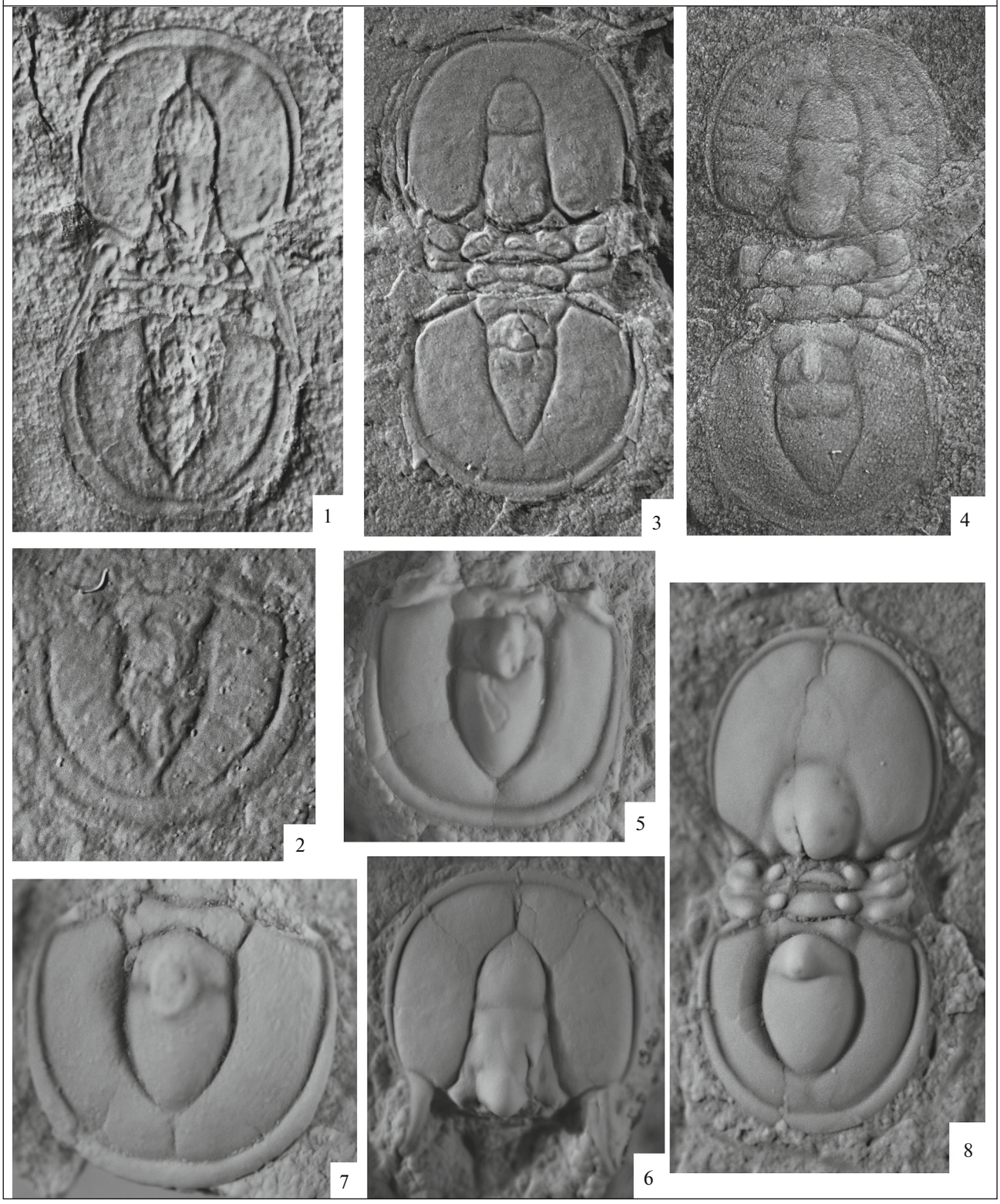
Fig. 3. *Tomagnostus sibiricus* Pokrovskaya et Egorova, 1972, holotype TsNIGR, no. 40/10606, dorsal shield, 12.1 mm long (Savitzkiy et al., 1972, pl. 4, fig. 1); Siberian Platform, Khorbusuonka River, loc. 23/1d.

Fig. 4. *Tomagnostus deformis* Pokrovskaya, 1958, TsNIGR, no. 80/10112, dorsal shield, 2.4 mm long (Egorova et al., 1982, pl. 5, fig. 5). Siberian Platform, Maya River, loc. EB–35/I–3a.

Figs. 5–7. *Triplagnostus pictinatus* Pokrovskaya et Egorova, 1976. (5) TsNIGR, no. 137/11262, pygidium from the type coll., 2.9 mm long (Egorova et al., 1976, pl. 55, fig. 2); (6) holotype TsNIGR, no. 136/11262, cephalon, loc. 22/2b, 4.9 mm long (Egorova et al., 1976, pl. 55, fig. 1); Siberian Platform, Malaya Kuonamka River; (7) TsNIGR, no. 133/11262, pygidium, 3.4 mm long (Egorova et al., 1976, pl. 38, fig. 4); Siberian Platform, Lena River (middle reaches).

Fig. 8. *Aotagnostus (Myrmecomimus) arctus* (Pokrovskaya et Egorova, 1972), holotype TsNIGR, no. 126/11262, dorsal shield, 4.9 mm long (Egorova et al., 1976, pl. 55, fig. 3); Siberian Platform, Malaya Kuonamka River, loc. 22/2b.

Plate 1



Type species. *Agnostus fissus* Lundgren in Linnarsson, 1879; neotype in Westergård, 1946, pl. 7, fig. 22.

Diagnosis. En grande tenue; cephalon and pygidium with moderate borders; median preglabellar furrow commonly weakly developed; anterior glabellar lobe subquadrate or semiovate, with short sulcus in front. Posterior glabellar lobe with well-developed F2 furrows; basal lobes simple, commonly indistinct anteriorly. Pygidial axis with well-developed F1 and F2 furrows; posteroaxis with transverse depression; postaxial furrow rarely present. Pygidial spines absent or very small; surface usually scrobiculate.

Remarks. The holotype of *T. deformis* was lost as well as the entire collection of Pokrovskaya for the manuscript of 1958, but the images show the morphology more or less clearly. Robison (1994) included *T. deformis* into synonymy list of *T. corrugatus* (Illing, 1916), but did not explain this synonymy. This decision seems to be erroneous due to the difference in the pygidial morphology of these two species. They differ in the presence of posterolateral spines in the former (absent in the latter) (Pl. 1, fig. 4). But some samples illustrated in Egorova et al. (1982 pl. 8, fig. 9) for *deformis* certainly belong to *corrugatus*, which probably governed Robison's (1994) decision.

Species found in Russia. *T. fissus* (Lundgren, 1879)—Siberian Platform: Lena (middle reaches in Chernysheva, 1960; Egorova et al., 1976, 1982), Nekekit and Boroluolakh rivers, *Pseudanomocarina* Zone (Egorova et al., 1976, 1982), Yudoma River, *Tomagnostus fissus* Zone, Maya River, *Anopolenus henrici* Zone (Egorova et al., 1982; Pegel, 2000), Maya River, *Tomagnostus fissus–Paradoxides hicksi* Zone (Pokrovskaya, 1958), Amyday River, *Tomagnostus fissus–Ptychagnostus atavus* Zone (Fedoseev, 1999).

T. sibiricus Pokrovskaya et Egorova, 1972—Siberian Platform: Lena River, *Tomagnostus fissus* Zone, Nekekit River, *Kounamkites* Zone, Boroluolakh River, *Pseudanomocarina* Zone (Egorova et al., 1976), Khorbusuonka, Nekekit, and Olenek rivers, *Maspakites* key horizon, *Pseudanomocarina* Zone (Savitzkiy et al., 1972), Western Siberia, Tomsk Region, Vostok-1 well, Upper Amgan Stage (Korovnikov et al., 2010).

T. perrugatus (Grönwall, 1902)—Siberian Platform: Maya River, *Anopolenus henrici* Zone, Lena River (middle reaches), Khorbusuonka River, *Tomagnostus fissus* Zone (Egorova et al., 1982), Khorbusuonka River, *Pseudanomocarina* Zone (Savitzkiy et al., 1972).

T. deformis Pokrovskaya, 1958—Siberian Platform: Yudoma River, *Tomagnostus fissus* Zone (Egorova et al., 1982), Maya River, *Anopolenus henrici* Zone (Egorova et al., 1982), uppermost *Tomagnostus fissus–Paradoxides hicksi* Zone, *Anopolenus henrici* Zone (Pokrovskaya, 1958).

T. corrugatus (Illing, 1916)—Siberian Platform: Yudoma River, Maya River, Lena River (middle reaches), *Paradoxides hicksi–Tomagnostus fissus* Zone (Pokrovskaya, 1958; Egorova et al., 1982, pl. 8, fig. 9, as *T. deformis*).

T. gracilis (Illing, 1916)—Siberian Platform: Maya River, *Paradoxides hicksi–Tomagnostus fissus* Zone (Pokrovskaya, 1958).

Genus *Onymagnostus* Öpik, 1979

Onymagnostus: Öpik, 1979, p. 107; Robison, 1984, p. 50; Laurie, 1988, p. 187; Shergold and Laurie, 1997, p. 352.

Type species. *Agnostus gibbus* var. *hybridus* Brögger, 1878.

Diagnosis. Cephalon with median preglabellar furrow. Posterior glabellar lobe widened at mid-M1. Basal lobes small. Pygidial border nonspinose or with very small spines. Axis with weak F2; relatively small median node deflecting F2, F1 bent gently forwards. Postaxial furrow developed in meraspids.

Species found in Russia. *O. stenorrhachis* (Brögger, 1878)—Siberian Platform: Maya River, *Anomocarioides limbataeformis* Zone (Egorova et al., 1982 as *Triplagnostus stenorrhachis*; Pegel, 2000 as *Ptychagnostus hybridus*), Maya River, *Anopolenus henrici* Zone, Lena River (middle reaches), *Liostracus allachjunensis* Zone (*A. henrici* Subzone) (Lermontova, 1940, pl. 35, fig. 12, as *Triplagnostus atavus;* Egorova et al., 1982).

O. barrandei (Hicks, 1872)—Siberian Platform: Maya River, *Tomagnostus fissus–Paradoxides hicksi* Zone (Egorova et al., 1982 as *Cotalagnostus* aff. *altus*).

Genus *Goniagnostus* Howell, 1935

Goniagnostus: Moore, 1959, p. O178; Öpik, 1979, p. 143; Laurie, 1989, p. 175; Shergold et al., 1990, p. 40; Shergold and Laurie, 1997, p. 350; Peng and Robison, 2000, pp. 71, 72; Ergaliev and Ergaliev, 2008, p. 107.

Ptychagnostus (Goniagnostus): Westergård, 1946, p. 80; Öpik, 1961a, p. 84; Öpik, 1967, p. 90; Westrop et al., 1996, p. 808.

Type species. *Agnostus nathorsti* Brögger, 1878.

Diagnosis. Cephalon scrobiculate, with or without cephalic spines; anteroglabella with low relief, while posteroglabella very convex in posterior part; F2 well developed, axial glabellar node behind F1; basal lobes elongate, their anterior extremities indistinct, associated with well-developed apodemal pits. Pygidium bispinose, axial node as large tubercle strongly deflecting F2; posteroaxis with secondary node located on transverse depression; postaxial furrow always well developed.

Remarks. *G. nathorsti* from the Gornyi Altai Region (Fedjanina, 1977, pl. 19, figs. 5, 6) differs from typical representatives in the relatively short pygidial axis. The preservation of the specimens from Altai did not allow accurate specific identification; thus, we left it with a question mark. The specimens from Altai resemble a specimen published from Kazakhstan

(Ergaliev and Ergaliev, 2008, p. 110, pl. 12, fig. 13); the latter also bears a short axis and was left by its authors in open nomenclature as *Goniagnostus* sp. I.

Pokrovskaya's (1958) collection has been lost, including the type series and the holotype of *G. longispinus* Pokrovskaya, 1958. The differential characters of this species included a spiny pygidium (with long posterolateral spines), a narrow axis on both the cephalon and pygidium. The width of glabella and rachis was not measured and, thus, the variability of these characteristics was not indicated in the original publication; also, the width of rachis and glabella did not differ superficially from *G. scarabeus* Whitehouse, 1939 (Laurie, 1989). Specimens from Siberia which were assigned to *G. longispinus* (Egorova et al., 1982; here Pl. 2, fig. 8) did not display long spines, the only distinguishing element; at least they did not differ in length from *G. scarabeus*. Therefore, we only refer to *G. longispinus* the specimens described by Pokrovskaya (1958) in the original publication until additional material will appear.

Species found in Russia. *G. nathorsti* (Brögger, 1878)—Siberian Platform: Maya River, *Anomocarioides limbataeformis* Zone (Pokrovskaya, 1960; Egorova et al., 1982; Pegel, 2000); Maya River, *Anopolenus henrici* and *Anopolenus henrici–Aldanaspis truncata* zones; Chabda River, *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982); Maya and Lena rivers, *Anomocarioides limbataeformis* and *Centropleura oriens* zones (Pokrovskaya, 1958); Kharaulakh Mountains, Khos-Nelege River, *Anopolenus henrici* Zone (Lazarenko et al., 2008b); Altai-Sayany Folded Belt: Altai Mountains, Bol'shaya Isha River, uppermost Middle Cambrian, *Goniagnostus nathorsti* Zone (Egorova et al., 1960; Astashkin et al., 1995); Salair Ridge, Orlinaya Mountain, uppermost Middle Cambrian (Fedjanina, 1977).

G. longispinus Pokrovskaya, 1958 – Siberian Platform: Maya River, *Prohedinia–Anomocarioides limbataeformis* Zone (Pokrovskaya, 1958).

G. scarabeus Whitehouse, 1939—Siberian Platform: Maya River, Lena River (middle reaches), *Anomocarioides limbataeformis* Zone (Pokrovskaya, 1958 as *G. longispinus* except the holotype, including *G. longispinus* var. *latirhachis*; Egorova et al., 1982 as *G. longispinus*); Chabda River, *Anomocarioides limbataeformis*, *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982).

Genus *Ptychagnostus* Jaekel, 1909

Ptychagnostus: Jaekel, 1909, pp. 400–401; Kobayashi, 1939, p. 152; Shimer and Shrock, 1944, p. 600; Howell, 1935b; Westergård, 1946, p. 67; Palmer, 1954, p. 60;1968, p. B28, p. 35; Snajdr, 1958, p. 70; Moore, 1959, p. O178; Pokrovskaya, 1960, p. 58; Robison, 1964, p. 522; 1978, p. 2; 1982, p. 145; 1994, p. 55; Lu et al., 1965, p. 37; Rushton, 1966, p. 35; Öpik, 1967, p. 90; Jago, 1976, p. 150; Rushton 1978, p. 261; 1979, p. 53; Öpik, 1979, p. 88; Laurie, 1988, p. 171; Westrop et al., 1996, p. 816; Shergold and Laurie, 1997, p. 200; Peng and Robison, 2000, p. 67; Peng et al., 2009, p. 22.

Ptychagnostus (Ptychagnostus): Öpik, 1961a, p. 76.

Solenagnostus: Whitehouse, 1936, p. 86.

Huarpagnostus: Rusconi, 1950, p. 92.

Canotagnostus: Rusconi, 1951, p. 13.

Acidusus: Öpik, 1979, p. 100.

Aristarius: Öpik, 1979, p. 125.

Zeteagnostus: Öpik, 1979, p. 105.

Type species. *Ptychagnostus punctuosus* Angelin, 1851.

Diagnosis. Cephalon with median preglabellar furrow. Anteroglabella semiovate, posterior glabellar lobe evenly convex; F2 well developed; basal lobes elongated, sometimes subdivided. Acrolobes scrobiculate. Pygidial border nonspinose or with very small spines. Axis with F1 and F2 evenly developed; relatively small median node deflecting F2, F1 bent angularly forwards. Postaxial furrow variably developed in adults.

Species found in Russia. *P. atavus* (Tullberg, 1880)—Siberian Platform: Maya River, *Anopolenus henrici* Zone (Pokrovskaya, 1960; Egorova et al., 1982; Pegel, 2000), *Paradoxides forchhammeri* Zone (Lermontova, 1940 as *Triplagnostus atavus*, not pl. 35, fig. 12); Lena River (middle reaches), *Tomagnostus fissus* Zone, *Liostracus allachjunensis* Zone (*Triplagnostus lundgreni* Subzone); Yudoma and Maya rivers, *Tomagnostus fissus–Paradoxides hicksi* Zone (Egorova et al., 1982); Amyday River, *Tomagnostus fissus* Zone (*T. arctus* Subzone) (Fedoseev, 1999).

P. punctuosus (Angelin, 1851)—Siberian Platform: Maya River, *Anopolenus henrici* Zone (Egorova et al., 1982).

Genus *Lejopyge* Hawle et Corda, 1847

Lejopyge: Hawle and Corda, 1847, p. 51; Kobayashi, 1939; p. 131; Moore, 1959, p. O178; Pokrovskaya, 1960, p. 60; Öpik, 1961a, p. 85; Robison, 1964, p. 521; 1984, p. 36; 1988, p. 48; 1994, p. 48; Öpik, 1967, p. 92; 1979, p. 157; Palmer, 1968, p. 27; Daily and Jago, 1975, p. 12; Robison and Laurie, 1989, p. 186; Shergold et al., 1990, p. 40; Pratt, 1992, p. 40; Shergold and Laurie, 1997, p. 352; Peng and Robison, 2000, p. 76; Peng et al., 2009, p. 23; Ergaliev and Ergaliev, 2008, p. 111.

Miagnostus: Jaekel, 1909, p. 401.

Type species. *Battus laevigatus* Dalman, 1828.

Diagnosis. Cephalon with very narrow border structures; glabella of moderate height or expanded at M1; axial furrows effaced, except part outlining M1 and basal lobes; median node very small if present, located at level of F1; pygidium with high acrolobe, with convex or slightly flattened border of moderate width, and narrow border furrow; axis outlined around M1, sometimes with vestiges of M2 and M3; axial node very small; postaxial furrow sometimes discernible in juveniles and aberrant adults.

Species found in Russia. *L. laevigata* (Dalman, 1828)—Siberian Platform: Maya River, *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982; Pegel, 2000); Chabda River, *Anopole-*

nus henrici–Aldanaspis truncata zones (Egorova et al., 1982); Olenek and Maya rivers, from the *Prohedinia–Forchhammeria–Anomocarioides limbataeformis* to *Lejopyge armata–Acrocephalites mirabilis* zones (Pokrovskaya, 1958), *Anopolenus henrici* Zone (Pokrovskaya, 1960 as *Cyclagnostus elegans* Lermontova, 1940); Kharaulakh Mountains, Khos-Nelege River, *Anopolenus henrici* and *Proagnostus bulbus* zones (Lazarenko et al., 2008a); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010, 2014).

L. armata (Linnarsson, 1869) – Siberian Platform: Kharaulakh Mountains, *Anopolenus henrici* Zone (Lermontova, 1940), Khos-Nelege River, *Anopolenus henrici* and *Proagnostus bulbus* zones (Lazarenko et al., 2008b); Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River, uppermost Middle Cambrian (Egorova et al., 1960 as *Lejopyge laevigata* (Dalman); Astashkin et al., 1995).

Genus *Pseudophalacroma* Pokrovskaya, 1958

Pseudophalacroma: Peng and Robison, 2000, p. 79 (see synonymy list); Ergaliev and Ergaliev, 2008, p. 113; Peng et al., 2009, p. 23.

Type species. *Pseudophalacroma crebra* Pokrovskaya, 1958 *(=?Phalacroma dubium* Whitehouse, 1936).

Diagnosis. Cephalon with very narrow border structures, glabella moderately high; axial furrows effaced, except part outlining basal lobes; median node usually absent. Pygidium with high acrolobe, with convex or slightly flattened border, widened at rear, nonspinose, border furrow deliquiate and moderately wide; axis outlined at M1, sometimes with vestiges of M2 and M3; axial node very small.

Species found in Russia. *P. dubium* (Whitehouse, 1936) – southeast Siberian Platform: Maya River, *Anomocarioides limbataeformis* and *Centopleura oriens* zones; Yudoma River, *Anomocarioides limbataeformis* Zone (Pokrovskaya, 1958); Maya River, *Anopolenus henrici* and *Anomocarioides limbataeformis* zones (Egorova et al., 1982 as *Pseudophalacroma crebra*); northwest Siberian Platform, Kulyumbe River, Selkupian Horizon (Rosova, 1964, pl. 2, figs. 16–21 as *Phalagnostus glandiformis*).

Pseudophalacroma sp.—Siberian Platform, Maya River, *Anopolenus henrici* and *Anomocarioides limbataeformis* zones (Egorova et al., 1982).

Family Peronopsidae Westergård, 1936

Diagnosis. *En grande tenue* or anteroglabella partly effaced; preglabellar furrow absent or partly developed in front of anteroglabella; pygidium tending to elongate, transaxial furrows F1 and F2 rarely present; pygidial border without zonation.

Remarks. The taxonomy of this family was revised recently (Naimark, 2012); the revision was based on the ontogenetic sequence of the pygidial characteristics. The ontogenetic order appeared to be more or less comparable to stratigraphic levels, in which species with the certain characters had originated. Peronopsidae included some transient genera, which bear characters of both peronopsids and other families. Such genera are *Pentagnostus* (descendants are Prychagnostidae), *Baltagnostus, Acadagnostus* (descendants are Diplagnostidae), *Redeagnostus* (possible descendants are Ammagnostidae, Agnostidae), *Itagnostus* (descendants are Doryagnostidae). The integration of such genera with other peronopsids makes the familial diagnosis rather obscure. If detached, the diagnoses of other families would become unclear. Anyway, the assignment of these transient genera to Peronopsidae seems to reflect subjective point of view. Other genera mentioned among Peronopsidae, that is, *Reslagnostus* Hinz–Schallreuter et Buchholz, 2004a and *Oleagnostus* Hinz–Schallreuter et Buchholz, 2004a, are based on agnostid meraspids degree 0 unidentifiable at the generic level.

A summary of stratigraphic distribution for Peronopsidae from Russia is shown in Fig. 5.

Genus *Archaeagnostus* Kobayashi, 1939

Arhaeagnostus: Kobayashi, 1939, p. 112; Moore, 1959, p. O184; Shergold et al., 1990, p. 55; Shergold and Laurie, 1997, p. 377; Naimark, 2012, p. 995.

Peronopsis (in part)*:* Robison, 1994, p. 42.

Peronopsis (Eoagnostus): Blaker and Peel, 1997, pp. 26–27; Fletcher, 2003, p. 85.

Eoagnostus: Resser and Howell, 1938, p. 216; Moore, 1959, p. O184; Rasetti and Theokritoff, 1967, p. 193.

Type species. *Archaeagnostus primigeneus* Kobayashi, 1939.

Diagnosis. Cephalon semiovate, border furrow narrow and deliquate, border convex and moderately wide; glabella with parallel sides, F1 and F2 absent; M1 large or medium-sized; glabellar node absent or very small; basal lobes small. Preglabellar furrow absent. Pygidium semiovate, border furrow moderate and deliquate, border convex and moderately wide; spines absent; axis triangular or semiovate; F1, F2, and postaxial furrow absent and postaxial space rather wide; axial node small or absent.

Species found in Russia. *Archaeagnostus primigeneus* Kobayashi, 1939—Siberian Platform: Molodo River, lowermost Amgan Stage, *Ovatoryctocara* Zone (Shabanov et al., 2008 as *Peronopsis crassa*; Korovnikov and Shabanov, 2008 as *Peronopsis* aff. *inarmata*); Nekekit River, Amgan Stage, *Ovatoryctocara* and *Kounamkites* zones (Savitzkiy et al., 1972 as *Peronopsis* aff. *inarmata*; Egorova et al., 1976 as *Peronopsis* aff. *integra* in pl. 44, fig. 23).

A. evansi (Rasetti et Theokritoff, 1967)—Siberian Platform: Molodo River, Amgan Stage, *Ovatoryctо-*

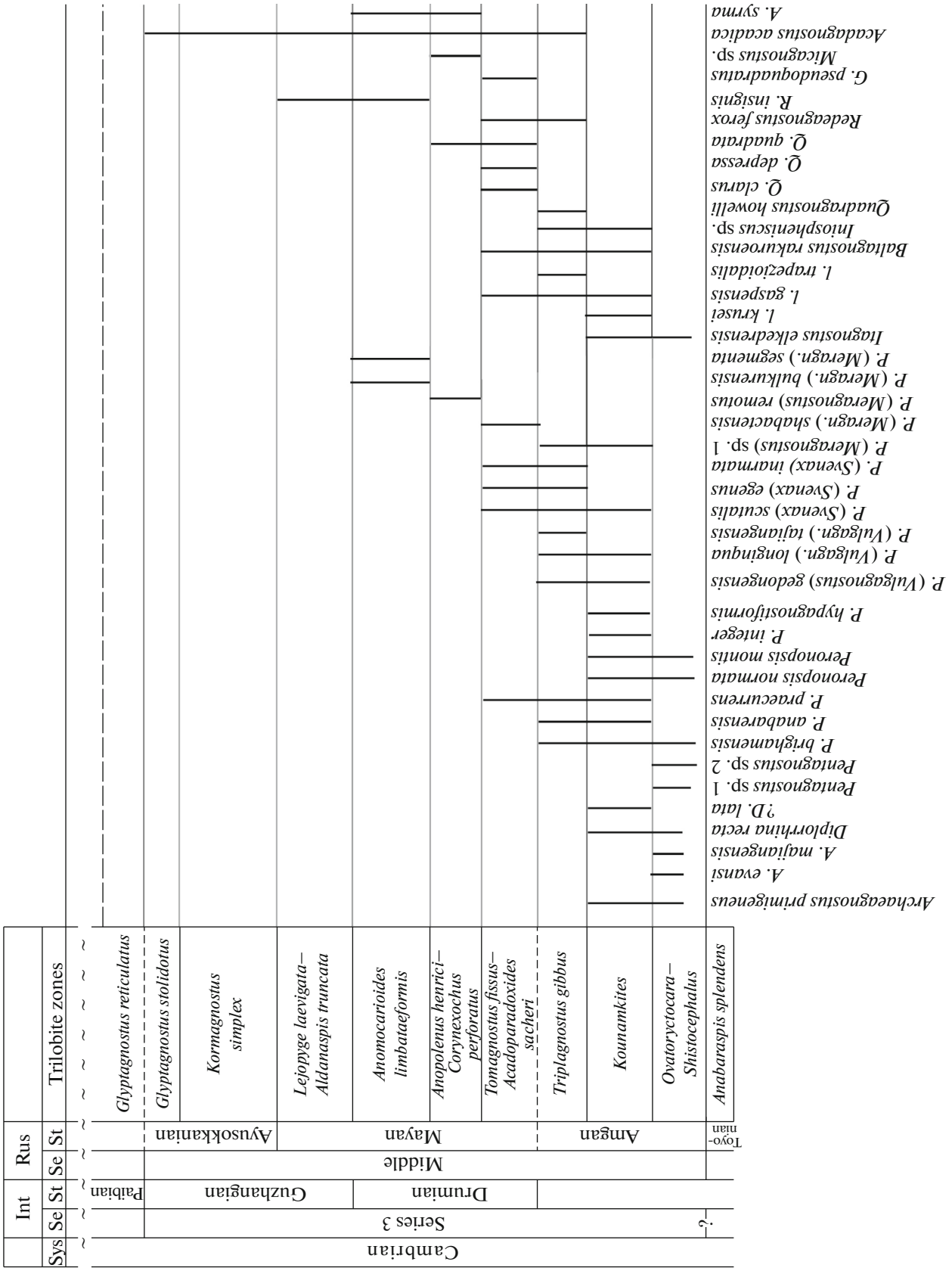


Fig. 5. Stratigraphic distribution of Peronopsidae species known from Russia.

cara Zone (Shabanov et al., 2008 as *Peronopsis crassa* in pl. 8, figs. 4, 6; Naimark, 2012).

A. majiangensis (Lu, 1967)—Siberian Platform: Molodo River, Amgan Stage, *Ovatoryctocara* Zone (Naimark, 2012).

Genus *Pentagnostus* Lermontova, 1940

Type species. *Pentagnostus anabarensis* Lermontova, 1940.

Diagnosis. En grande tenue, borders on cephalon and pygidium narrow; median preglabellar furrow partly developed at glabellar front or as median depression in front of glabella; pygidial border nonspinose or with spines, F1 and F2 well developed; posteroaxis without transverse depression.

Subgenus *Pentagnostus* sensu stricto

Plate 2, fig. 7, plate 3, figs. 1–4

Pentagnostus: Lermontova, 1940, p. 127; Moore, 1959, p. O185; Öpik, 1979, p. 139; Laurie, 1988, p. 192; Shergold et al., 1990, p. 41; Shergold and Laurie, 1997, p. 354; Laurie, 2004, p. 228; Ergaliev and Ergaliev, 2008, p. 121.

Pentagnostus (Pentagnostus): Naimark, 2012, p. 1006.

Type species. *Pentagnostus anabarensis* Lermontova, 1940, p. 127, pl. 35, fig. 10.

Diagnosis. Pygidial spines absent or minutely small, narrow border furrows both on cephalon and pygidium; postaxial furrow partly developed or absent.

Remarks. *Pentagnostus praecurrens* Westergård, 1936 shows significant variability in the preglabellar furrow from the complete absence to a more or less expressed furrow. But in the majority of specimens, the preglabellar furrow is expressed only in front of the glabella or effaced. Therefore, this species is considered to belong to *Pentagnostus*. This species is very similar to *P. anabarensis*, but differs from it in the pentagonal shape of the pygidial shield and in the slightly more expanded posteroaxis. Their cephala are indistinguishable.

Triplagnostus ademptus Pokrovskaya et Egorova, 1972 bears all generic characters of *Pentagnostus*, that is, a ptychagnostoid pygidium with cephalon lacking a full preglabellar furrow. Moreover, it resembles *Pentagnostus praecurrens* and *P. brighamensis* in both cephalic and pygidial characters. The original description of *T. ademptus* notes a comparatively wide cephalic border furrow, deep pygidial border furrow, and a comparatively wide flat pygidial border. Reinvestigation of the type material showed a narrow cephalic border, and comparatively narrow pygidial border structures (see here Pl. 3, figs. 1, 2). This species differs from *P. praecurrens* in the narrower and less triangular pygidial axis and in the narrower glabella with smaller basal lobes. The distinguishing characters from *P. brighamensis* are much less obvious; we can point the slightly narrower pygidial border in the latter, but in our view, in this range of width, the border may vary and, thus, the difference is not very reliable. Therefore, *T. ademptus* is reassigned here to *P. brighamensis*.

We inclined to refer *Agnostus czekanovskii* Schmidt, 1886 to *Pentagnostus* at least the illustrated cephalon (Schmidt, 1886, pl. 1, fig. 4), rather than to *Clavagnostus* as it possesses all diagnostic characters of *Pentagnostus*. The illustrated pygidium (Schmidt, 1886, pl. 1, fig. 5) may belong to a meraspid as it bears a possible incipient trunk segment.

Species found in Russia. *P. praecurrens* (Westergård, 1936)—Siberian Platform: Lena River (middle reaches), Amgan Stage, *Kounamkites* Zone, lowermost Mayan Stage, *Tomagnostus fissus* Zone and Nekekit River, *Kounamkites* Zone (Egorova et al., 1976 as *Triplagnostus praecurrens*), Daldyn–Alakit Region, Amgan Stage, *Chondranomocare–Kounamkites* Zone, lowermost Mayan Stage, *Pseudanomocarina aojiformis*

Explanation of Plate 2

Condylopyge, *Itagnostus*, *Peronopsis*, *Goniagnostus*

Figs. 1 and 2. *Condylopyge carinata vicina* Egorova, 1972: (1) holotype TsNIGR, no. 35/10606, cephalon, 9.1 mm long (Savitzkiy et al., 1972, pl. 3, fig. 6); (2) paratype TsNIGR, no. 37/10606, pygidium, 7.1 mm long (Savitzkiy et al., 1972, pl. 3, fig. 8); Siberian Platform, Nekekit River, loc. 15.

Fig. 3. *Peronopsis (Peronopsis) batenica* Bognibova, 1971; holotype TsNIGR, no. 24/11648, cephalon, 1.5 mm long (Bognibova et al., 1971, pl. 2, fig. 19); Altai-Sayany Folded Belt, Batenevsky Ridge, loc. R-1344.

Fig. 4. *Peronopsis (Peronopsis) hypagnostiformis* Bognibova, 1971; holotype TsNIGR, no. 26/11648, pygidium, 1.7 mm long (originally was defined as the holotype cephalon (Bognibova et al., 1971, pl. 2, fig. 15)); Altai-Sayany Folded Belt, Eastern Sayan, Mansky trough, near the village of Shakhmatovo, loc. Sh-9.

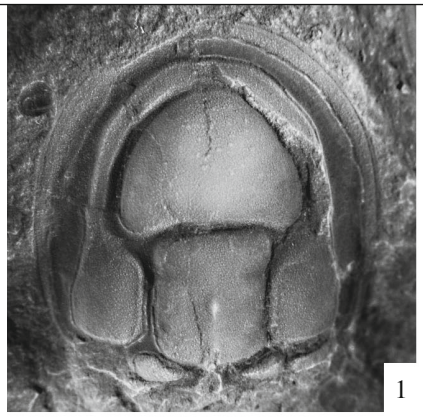
Fig. 5. *?Peronopsis* sp.; TsNIGR, no. 27/11648, pygidium, 1.6 mm long (as ?*Peronopsis hypagnostiformis* in Bognibova et al., 1971, pl. 2, fig. 14); Altai–Sayany Folded Belt, Mansky trough, near the village of Shakhmatovo, loc. Sh–8.

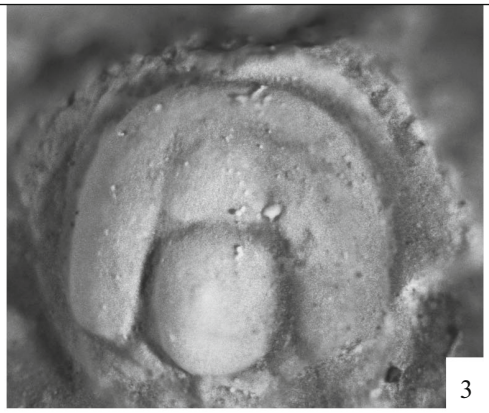
Fig. 6. *?Itagnostus trapezoidalis* (Bognibova, 1965); holotype TsNIGR, no. 15/11648, cephalon, 2.6 mm long (Bognibova, 1965, pl. 1, fig. 17; Bognibova et al., 1971, pl. 2, fig. 6 as *Triplagnostus trapezoidalis*); Altai-Sayany Folded Belt, Batenevsky Ridge, in the vicinity of Dolgii Mys Mountain, loc. R-572.

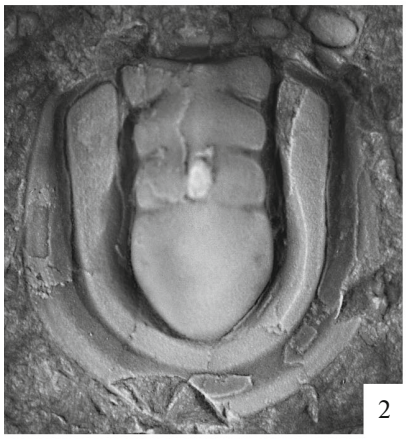
Fig. 7. *Pentagnostus praecurrens* (Westergård, 1936); TsNIGR, no. 15a/11648, cephalon (on the same slab with fig. 6), 3.4 mm long (Bognibova et al., 1971, pl. 2, fig. 3 as *Triplagnostus trapezoidalis*); Altai-Sayany Folded Belt, Batenevsky Ridge, in the vicinity of Dolgii Mys Mountain.

Fig. 8. *Goniagnostus scarabeus* Whitehouse, 1939, TsNIGR, no. 167/10112, pygidium, 2.2 mm long (Egorova et al., 1982, pl. 42, fig. 3 as *Goniagnostus longispinus*); Siberian Platform, Chabda River, loc. C-24.

Plate 2

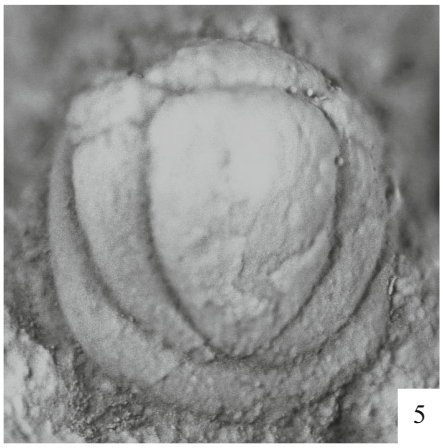

1


3


2


4


6


5


7


8

Zone (Ogienko and Garina, 2001 as *Triplagnostus praecurrens*); Buom–Pastakh River, Amgan Stage, *Kounamkites* Zone (Egorova and Savitzkiy, 1969 as *Triplagnostus praecurrens*); Amyday River, *Kounamkites* Zone (*Pentagnostus praecurrens* Subzone) (Fedoseev, 1999); Altai-Sayany Folded Belt, Kuznetsky Alatau, Batenevsky Ridge, Middle Cambrian (Amgan Stage, Mundybashsky Horizon) (Bognibova, 1965; Bognibova et al., 1971 as *Triplagnostus praecurrens*); Western Siberia, Tomsk Region, Vostok-1 well, Upper Amgan Stage (Korovnikov et al., 2010 as *Triplagnostus praecurrens*).

P. brighamensis (Resser, 1939)—Siberian Platform: Amyday River, Amgan Stage, *Kounamkites* Zone (from the *P. proanabarensis* Subzone) (Fedoseev, 1999 as *P. proanabarensis* Fedoseev, 1999); Nekekit River, *Kounamkites* and *Pseudanomocarina* zones (Savitzkiy et al., 1972; Egorova et al., 1976 both as *Triplagnostus ademptus*). Altai-Sayany Folded Belt, Kuznetsky Alatau, Batenevsky Ridge, Mundybashsky Horizon (Bognibova, 1965 as *Peronopsis* aff. *brighamensis*; Bognibova et al., 1971 as *Peronopsis brighamensis*).

P. anabarensis Lermontova, 1940—Siberian Platform: Anabar Region, Middle Cambrian (Lermontova, 1940 in pl. 35, figs. 10, 10b, 10c, not 10d), Buom–Pastakh River, Amgan Stage, *Kounamkites* Zone (Egorova and Savitzkiy, 1969 as *Triplagnostus* sp.); Nekekit, Amyday, Boroluolakh, Torkukuy, Malaya Kuonamka, and Olenek rivers, Amgan Stage, *Kounamkites* Zone (Savitzkiy et al., 1972 as *Triplagnostus anabarensis*); Altai-Sayany Folded Belt, Kuznetsky Alatau, Batenevsky Ridge, Middle Cambrian (Mundybashsky Horizon) (Bognibova et al., 1971).

Pentagnostus sp. 1—Siberian Platform: Lena River (middle reaches), lowermost Amgan Stage, *Shistocephalus antiquus* Zone (Egorova et al., 1976 as *Triplagnostus* sp.).

Pentagnostus sp. 2—Siberian Platform: Molodo River, lowermost Amgan Stage, *Ovatoryctocara* Zone (Korovnikov and Shabanov, 2008 as *Pentagnostus anabarensis*; Shabanov et al., 2008 as *Pentagnostus anabarensis*).

Subgenus *P. (Meragnostus)* Naimark, 2012

Plate 3, figs. 5–9

Pentagnostus (Meragnostus): Naimark, 2012, p. 1007.

Type species. *Peronopsis bonnerensis* Resser, 1938.

Diagnosis. Cephalon with narrow border, but pygidial border tending to widened, with short spines. Basal lobes medium–sized or large. Pygidial border furrow tending to widened; postaxial furrow usually well-developed, but sometimes short.

Remarks. Two "holotypes" for *P. (Meragnostus) remotus* (Pokrovskaya et Egorova, 1969) were originally designated, i.e., one for a cephalon and another for a pygidium. These specimens do not belong to a single organism. Therefore, here we select the pygidium as the holotype, by excluding the cephalon; the cephalon has the general appearance of *Pentagnostus* species.

A specimen described from the Altai Region as *Peronopsis* aff. *fallax* (Bognibova, 1971, pl. 1, figs. 11, 12) probably belongs to this subgenus. It does not possess the characters of *Acadagnostus acadica* (=*P. fallax*). Instead, it has a specifically shaped pygidium (pentagonal shape, axis narrowing at M2; F1, F2 expressed on sides, short postaxial furrow, border furrow deeply incised). Its cephalon resembles *P. bonnerensis* illustrated by Resser, 1938 as *Agnostus lautus*.

Species found in Russia. *P. (M.) bulkurensis* (Pokrovskaya et Pegel, 1982)—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Liostracus allachjunensis* Zone–*Anopolenus henrici* Subzone (Egorova et al., 1982 as *Peronopsis bulkurensis*).

P. (M.) segmenta (Robison, 1964)—Siberian Platform, Lena River, upper Middle Cambrian (Lermontova, 1940 in pl. 36, fig. 1b as *P. fallax*).

P. (M.) remotus (Pokrovskaya et Jegorova, 1969)—Siberian Platform: Buom–Pastakh River, Amgan

Explanation of Plate 3

Pentagnostus Lermontova, 1940

Figs. 1 and 2. *Pentagnostus brighamensis* (Resser, 1939) (= *Triplagnostus ademptus* Pokrovskaya et Jegorova, 1972): (1a) holotype of *T. ademptus*, TsNIGR, no. 61/10606, dorsal shield, 8.2 mm long (Savitzkiy et al., 1972, pl. 6, fig. 1); (1b) enlarged part of fig. 1 with preglabellar furrow shown; (2) TsNIGR, no. 61b/10606, late meraspis, 2.4 mm long: preglabellar furrow undeveloped, postaxial furrow well developed; Siberian Platform, Nekekit River, loc. 15/V–22a.

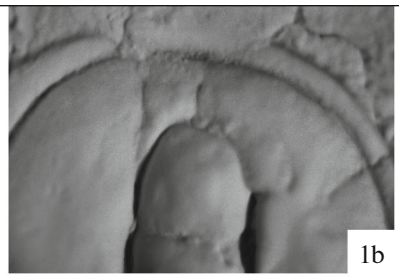
Figs. 3 and 4. *Pentagnostus (Pentagnostus) anabarensis* Lermontova, 1940: (3) lectotype TsNIGR, no. 56/9182, cephalon, 2.9 mm long (Lermontova, 1940, pl. 35, fig. 10c; Laurie, 2004, p. 230); (4) TsNIGR, no. 53/9182, complete shield from the type collection, 5.4 mm long (Lermontova, 1940, pl. 35, fig. 10); Siberian Platform, Anabar Region.

Figs. 6 and 8. *Pentagnostus (Meragnostus) bulkurensis* (Pokrovskaya et Pegel, 1982): (6) TsNIGR, no. 196/10112, pygidium, 2.1 mm long; (8) holotype TsNIGR, no. 3/10112, cephalon, 3.8 mm long (Egorova et al., 1982, pl. 56, figs. 11, 12, respectively); Siberian Platform, Lena River (middle reaches), loc. 6.

Fig. 7. *Pentagnostus (Meragnostus) segmenta* (Robison, 1964), TsNIGR, no. 66/9182f, pygidium, 1.5 mm long; Lena River, Botomsky Region.

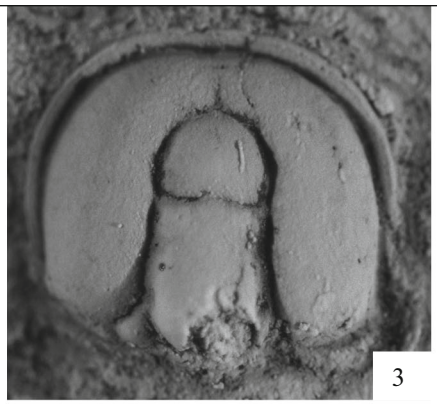
Figs. 5 and 9. *Pentagnostus (Meragnostus) remotus* (Pokrovskaya et Egorova, 1969): (5) TsNIGR, no. 89/8363, cephalon, 3.5 mm long; (9) holotype TsNIGR, no. 90/8363, pygidium, 2.9 mm long (Egorova et Savitzkiy, 1969, pl. 5, figs. 14 and 13, respectively); Siberian Platform, Buom–Pastakh River, loc. 567.

Plate 3

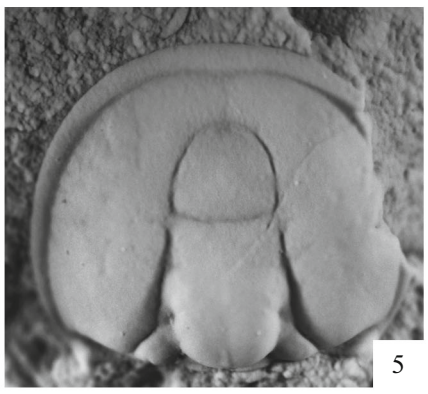

1b

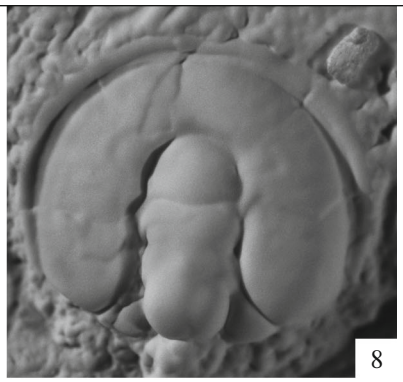

1a

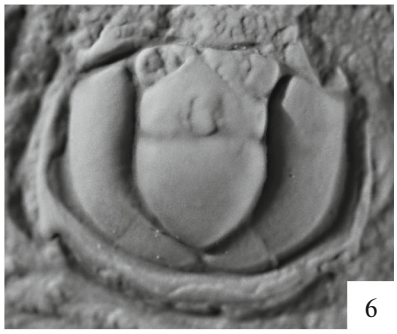

2

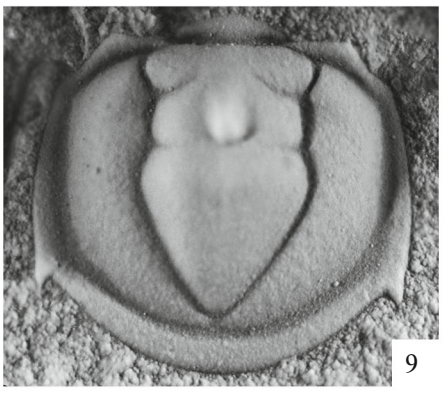

3


4


5


8


6


9

Stage, *Kounamkites* and *Pseudanomocarina aojiformis* zones (Egorova and Savitzkiy, 1969 as *Triplagnostus remotus*, and as *Peronopsis scutalis* in pl. 5, fig. 17).

P. (M.) shabactensis Ergaliev, 2008—Altai-Sayany Folded Belt, Kuznetsky Alatau, Batenevsky Ridge, Dolgii Mys Mountain, Amgan Stage, Mundybashsky Horizon (Bognibova et al., 1971 as *Peronopsis* ex gr. *fallax*).

P. (Meragnostus) sp. 1—Altai-Sayany Folded Belt: Batenevsky Ridge, Amgan Stage, Mundybashsky Horizon (Bognibova, 1965 pl. 1, figa. 11, 12, as *Peronopsis aff. fallax*).

Genus *Peronopsis* Hawle et Corda, 1847

Peronopsis: Hawle and Corda, 1847, p. 115, Howell, 1935c, p. 226; Westergård, 1946, p. 36; Kobayshi, 1939, p. 115; Rasetti, 1951, p. 133, Ivshin, 1953, p. 7; Moore, 1959, p. O186; Palmer, 1954, p. 60, 1968, p. 31; Palmer and Gatehouse, 1972, p. 11; Robison, 1964, p. 529, 1982, p. 150, 1988, p. 47, 1994, p. 42, 1995, p. 302; Pek and Vanek, 1971, p. 269; Öpik, 1979, p. 60; Rushton, 1979, p. 49; Sun, 1989, p. 90; Shergold et al., 1990, p. 45; Huang and Yuan, 1994, pp. 295, 296; Shergold and Laurie, 1997, p. 360; Ergaliev and Ergaliev, 2008, p. 142; Peng et al., 2009, p. 194; Naimark, 2012, p. 996.

Mesospheniscus: Hawle and Corda, 1847, p. 46.

Mesagnostus: Jaekel, 1909, p. 398.

Type species. *Battus integer* Beyrich, 1845.

Diagnosis. Peronopsidae without transverse pygidial depression, without transaxial pygidial furrows, and without traces of preglabellar furrow; with narrow border furrow of cephalon, small basal lobes, moderately wide pygidial border, postaxial space very short or postaxial furrow present. Presence–absence and size of spines on pygidial border varying.

Remarks. A comprehensive revision of the genus was made recently (Naimark, 2012). According to the pygidial morphology and the order of morphogenesis during the ontogeny, it was subdivided into a number of subgenera. The species composition is emended herein.

Subgenus *Peronopsis* sensu stricto

Plate 2, figs. 3–5

Type species. *Battus integer* Beyrich, 1845.

Diagnosis. Glabella bipartite, F3 straight, F2 very weak or absent, cephalic border structures narrow, basal lobes small, stretched more in width than in length. Pygidial border moderately wide, tending to flatten, nonspinose or minutely spinose, border furrow from moderate to narrow; axis almost reaching border furrow leaving very short undivided postaxial space, but sometimes touching border furrow, F1 F2 undeveloped, transaxial depression absent; axis with parallel sides or posteroaxis occasionally slightly expanded, M1 always slightly wider than M2.

Remarks. Two species from the Altai Folded Belt were not discussed in the previous review of *Peronopsis* (Naimark, 2012); they are *Peronopsis batenica* Bogniobova, 1971 and *P.? hypagnostiformis* Bognibova, 1971. The material of these species was transferred to the TsNIGR Museum in St. Petersburg. The revision of *Peronopsis batenica* showed that the species is very close to *P. amplaxis* Robison, 1982. It is only different from *P. amplaxis* in the less expressed axial node on the pygidium. In the original description, Robison did not compare *P. amplaxis* with *P. batenica*; probably, he omitted it. The holotype of the *P. batenica* is a juvenile cephalon with a slightly smoothed axial furrow around anteroglabella (Bognibova et al., 1971, pl. 2, fig. 3). The larger holaspid cephalon does not display such effacement; its anteroglabella is fully outlined (Bognibova et al., 1971, pl. 2, fig. 18). To judge if these two species are synonyms, other cephala of *P. batenica* are needed to see the stability of the anteroglabellar effacement. If it occurs only sporadically, *P. amplaxis* would become a junior synonym of *P. batenica*. *P. amplaxis* occurs in the *T. gibbus* Zone, while *P. batenica* was found in the El'dakhsky Horizon (Upper Amgan).

P.? hypagnostiformis was illustrated by two specimens, one cephalon and one pygidium, with the cephalon being the holotype. The pygidium (Bognibova et al., 1971, pl. 2, fig. 5) appeared to be a meraspid degree 1 of some peronopsid, probably of *P. batenica*. Bognibova (1971) mentioned this similarity comparing her new species with other similar specimens. Meanwhile, the holotype cephalon seemed to be a pygidium upon a closer view (Bognibova et al., 1971, pl. 2, fig. 4; here Pl. 3, fig. 5). Its morphology corresponds to *P. inarmata,* but poor preservation and lack of other material (only two specimens were found in the museum collection) prevent reliable identification.

Species found in Russia: *P. (P.) montis* Hutchinson, 1962—Siberian Platform: Molodo River, Amgan Stage, *Ovatoryctocara* and *Kounamkites* zones (Korovnikov and Shabanov, 2008 and Shabanov et al., 2008 as *P. crassa* in pl. 8, fig. 13, pl. 9, fig. 3); Nekekit River, Amgan Stage, *Kounamkites* Zone (Savitzkiy et al., 1972 as *Peronopsis* aff. *integra* (in part); Egorova et al., 1976 as *P. crassa,* and as *P. fallax* in pl. 30, figs. 10, 11); Lena River (middle reaches), lowermost Amgan Stage, *Shistocephalus antiquus* Zone (Egorova et al., 1976).

P. (P.) integer Beyrich, 1845—Siberian Platform: Daldyn River, *Kounamkites* Zone (Ogienko and Garina, 2001 as *P. fallax* in pl. 2, fig. 11).

P. (P.) batenica Bognibova, 1971—East Sayan, village of Shakhmatovo, Amgan Stage, El'dakhsky Horizon(Bognibova et al., 1971).

P. (P.) hypagnostiformis Bognibova, 1971—East Sayan, village of Shakhmatovo, Amgan Stage, Mundybashsky Horizon (Bognibova et al., 1971).

Subgenus *P. (Vulgagnostus)* Naimark, 2012

Peronopsis (Vulgagnostus): Naimark, 2012, p. 997.

Type species. *Peronopsis longinqua* Öpik, 1979.

Diagnosis. Glabella bipartite, F3 straight or slightly bent backward, F2 undeveloped, border narrow, border furrow from moderate to narrow, basal lobes medium-sized. Pygidial border moderately wide and tending to widen, bispinose, border furrow from moderate to relatively wide; axis reaching border furrow, transaxial F1 and F2 and transaxial depression absent, axis with parallel sides or posteroaxis slightly widened.

Species found in Russia. *P. (V.) ?gedongensis* Huang et Yuan, 1994 —Siberian Platform: Lena River (middle reaches), Amgan Stage, *Kounamkites* Zone (Egorova et al., 1976 as *P. fallax* in pl. 34, fig. 6).

P. (V.) longinqua Öpik, 1979—Siberian Platform: Amga River, Amgan Stage, *Pseudanomocarina* Zone, lower part (Chernysheva, 1961 as *P. fallax* in pl. 1, figs. 15, 17); Nekekit River, Amgan Stage, *Kounamkites* Zone (Savitzkiy et al., 1972 as *P.* aff. *integra* in pl. 7, figs. 1, 2).

P. (V.) tajiangensis Huang et Yuan, 1994—Siberian Platform: Amga River, Amgan Stage, *Pseudanomocarina* Zone, lower part (Chernysheva, 1961 as *P. fallax* in pl. 1, figs. 16, 18).

P. (Vulgagnostus) sp. 1—Siberian Platform: Lena River (middle reaches), Amgan Stage, *Kounamkites* Zone (Egorova et al., 1976, pl. 31, fig. 14 as *P. fallax*).

P. (Vulgagnostus) sp. 2 – Siberian Platform: Anabar Anticline, Daldyn–Alakit Region, lowermost Amgan Stage, *Schistocephalus* Zone (Shabanov et al., 1987 as *P. fallax* in pl. 1, fig. 11).

Subgenus *Peronopsis (Svenax)* Öpik, 1979

Svenax: Öpik, 1979, p. 64; Shergold et al., 1990, p. 44; Shergold and Laurie, 1997, p. 358; Ergaliev and Ergaliev, 2008, p. 136.

Peronopsis (Svenax): Naimark, 2012, p. 998.

Type species. *Agnostus pusillus* Tullberg, 1880.

Diagnosis. Cephalon semiovate, with narrow border structures, glabella with parallel sides, transglabellar F3 straight, F2 absent, basal lobes small. Pygidium semiovate, with narrow border furrow and narrow to moderate border, nonspinose, tending to be convex; postaxial furrow usually present, sometimes as wide postaxial depression; pygidial median node small, elongate, axis parallel-sided, gently narrowing to rear.

Species found in Russia: *P. (S.) scutalis* Hicks, 1871—Siberian Platform: Lena River (middle reaches), lowermost Mayan Stage, *Tomagnostus fissus* Zone; Amga River, *Triplagnostus gibbus* Zone (Egorova et al., 1976); Nekekit, Malaya Kuonamka, Amyday, and Boroluolakh rivers, Amgan Stage, *Kounamkites* Zone (Savitzkiy et al., 1972); Anabar Anticline, Daldyn–Alakit Region, Amgan Stage, *Kounamkites* Zone (Shabanov et al., 1987); Amga River, Amgan Stage, *Pseudanomocarina aojiformis* Zone (Chernysheva, 1961); Altai-Sayany Folded Belt: Kuznetsky Alatau, Batenevsky Ridge (Dolgii Mys Mountain) and Azyrtal Ridge, Amgan Stage, Mundybashsky Horizon (Bognibova et al., 1971).

P. (Svenax) aff. *egenus* (Resser et Endo, 1937)—Siberian Platform: Buom–Pastach River, Amgan Stage, *Pseudanomocarina aojiformis* Zone (Egorova and Savitzkiy, 1969 as *P. scutalis* in pl. 5, fig. 16, 18).

P. (Svenax) inarmata Hutchinson, 1962—Siberian Platform: Nekekit River, uppermost Amgan Stage, *Triplagnostus gibbus* Zone (Naimark, 2008, 2012).

Subgenus *P. (Proacadagnostus)* Naimark, 2012

Peronopsis (Proacadagnostus): Naimark, 2012, p. 998.

Type species. *Diplorrhina normata* Whitehouse, 1936.

Diagnosis. Narrow border structures on both cephalon and pygidium, postaxial furrow very short but present, axial median node small and weak, spines short and wide in shape of angularity in border; axis with parallel sides, F1 sometimes expressed as short notches at sides. Cephalon semiovate, glabella with parallel sides, F3 straight, F2 absent.

Species found in Russia *P. (P.) normata* (Whitehouse, 1936)—Siberian Platform: Nekekit River, Amgan Stage, *Kounamkites* Zone (Egorova et al., 1976 as *P. fallax* in pl. 50, fig. 14, as *Peronopsis* ex gr. *fallax* pl. 51, fig. 1); Molodo River, Amgan Stage, *Ovatoryctocara* and *Kounamkites* zones (Shabanov et al., 2008 as *P.* aff. *inarmata* in pl. 10, figs. 10, 12, as *P. scutalis* in pl. 6, fig. 6; Korovnikov and Shabanov, 2008 as *P. scutalis* in pl. 5, fig. 6).

Genus *Itagnostus* Öpik, 1979

Plate 2, fig. 6

Itagnostus: Öpik, 1979, p. 60; Shergold et al., 1990, p. 45; Shergold and Laurie, 1997, p. 359; Laurie, 2004, p. 237; Naimark, 2012, p. 1000.

Type species. *Agnostus elkedrensis* Etheridge, 1902.

Diagnosis. Cephalon with narrow border structures, glabella bipartite, F3 straight, F2 as short notches on sides, basal lobes small. Pygidial border moderately wide, tending to flatten, with tiny spines, border furrow moderately wide; postaxial furrow present, F1 and F2 as short notches, posteroaxial depression undeveloped, axis constricted across M2, M1 wider than M2, pygidial median node of moderate size.

Remarks. *?Itagnostus trapezoidalis* (Bognibova, 1965) was established based on two cephala. One of them is the holotype (Bognibova, 1965, pl. 2, fig. 17; here Pl. 2, fig. 7) (refigured in Bognibova et al., 1971, pl. 2, figs. 6, 6a). The second is located on the same slab (Bognibova et al., 1971, pl. 2, fig. 3), probably belongs to *P. praecurrens* (here Pl. 2, fig. 7). This species was originally assigned to *Triplagnostus,* but it did

not possess diagnostic characters of *Triplagnostus* (preglabellar furrow, long basal lobes). Instead, it shares the cephalic morphology with species of *Itagnostus*. In addition, it resembles *Rhodotypiscus* with its characteristically expressed preglabellar notch and parallel-sided glabella with slightly enlarged anteroglabella; the only feature which enables to distinguish it from *Rhodotypiscus* is the lack of a glabellar node. To choose between *Itagnostus* and *Rhodotypiscus,* a pygidium is needed, although some specialists bring together these two genera (Laurie, 2004, p. 243).

Species found in Russia. *I. elkedrensis* (Etheridge, 1902)—Siberian Platform: Molodo River, lowermost Amgan Stage, *Ovatoryctocara* Zone (Shabanov et al., 2008 as *P. crassa* pl. 9, fig. 7, 1), Nekekit River, Amgan Stage, *Kounamkites* Zone (Egorova et al., 1976 as *Peronopsis scutalis* in pl. 51, figs. 11, 12, 15, as *Peronopsis* sp. 1 in pl. 51, figs. 13, 14; and *Peronopsis* sp. 2 in pl. 51, fig. 10).

I. gaspensis (Rasetti, 1948)—Siberian Platform: Lena River (middle reaches), lowermost Mayan Stage, *Tomagnostus fissus* Zone (Egorova et al., 1976 as *Peronopsis* ex gr. *fallax* in pl. 36, fig. 3, as *P. fallax* in pl. 37, fig. 7); Daldyn–Alakit Region, Amgan Stage, *Kounamkites* Zone (Ogienko and Garina, 2001 as *P. scutalis* in pl. 2, figs. 12–14).

I. interstricta (White, 1874)—Siberian Platform, Lena River (middle reaches), lowermost Mayan Stage, *Tomagnostus fissus* and *Liostracus allachjunensis* zones (Egorova et al., 1982 as *Peronopsis* ex gr. *scutalis,* as *P.* aff. *gaspensis*).

?I. trapezoidalis (Bognibova, 1965)—Altai-Sayany Folded Belt: Batenevsky Ridge, Dolgii Mys Mountain, Amgan Stage, Mundybashsky Horizon (Bognibova, 1965; Bognibova et al., 1971).

Itagnostus sp. 1—Siberian Platform: Lena River (middle reaches), lowermost Mayan Stage, *Tomagnostus fissus* Zone (Egorova et al., 1976 as *P. fallax* in pl. 36, fig. 18).

Genus *Diplorrhina* Hawle et Corda, 1847

Plate 4, figs. 1–4

Diplorrhina: Hawle, Corda, 1847, p. 46; Whitehouse, 1936, p. 88; Lermontova, 1940, p. 123; Öpik, 1967, p. 75; Pek and Vanek, 1971, p. 271; Šnajdr, 1990 (see synonymy list); Shergold et al., 1990, p. 46; Robison, 1994, p. 37; Shergold and Laurie, 1997, p. 360; Naimark, 2012, p. 1003.

Mesospheniscus: Hawle, Corda, 1847, p. 46.

Type species. *Diplorrhina triplicata* Hawle et Corda, 1847.

Diagnosis. Cephalic border structures narrow to moderate, transglabellar F3 straight or slightly bent backward, F2 as short weak side notches or as gentle relief on glabella. Pygidial border flat and widened, nonspinose or with posterolateral angularity on border; border furrow shallow and widened, axis subdivided by thin transaxial furrows reaching median node but not crossing axis completely; postaxial space short, axis sometimes extending to border furrow, postaxial furrow absent.

Remarks. *?D. lata* Shabanov, 1972 was originally based on two specimens indicated as "holotypes" of a cephalon and pygidium. But these cephalon and pygidium do not represent parts of a single organism; therefore, it cannot be the holotype. We chose the pygidium as the holotype for this species (here Pl. 4, fig. 2, refigured from (Savitzkiy et al., 1972, pl. 7, fig. 14)). The indicated "holotype" cephalon (Savitzkiy et al., 1972, pl. 7, fig. 13) is recorded in the museum CGSM register book no. 80/10606, but we failed to find the illustrated specimen on the slab marked with this number (specimens from this slab (the cephalon and pygidium) are figured here in Pl. 4, figs. 3, 4). These specimens have well preserved unflattened shields. Their morphology closely fits *D. recta*. Other material on *D. lata* is represented by flattened molds. In the original description, there was a comparison with *P. integer* only, but not with *D. recta*. We supposed that *D. lata* may be marginally wide, flattened specimens of *D. recta*.

Species found in Russia. *D. recta* (Pokrovskaya et Egorova, 1972)—Siberian Platform:

Explanation of Plate 4

Peronopsidae

Fig. 1. *Diplorrhina recta* (Pokrovskaya et Egorova, 1972); holotype TsNIGR, no. 82/10606, dorsal shield, 8.5 mm long (Savitzkiy et al., 1972, pl. 7, fig. 9); Siberian Platform, Nekekit River, loc. 128.

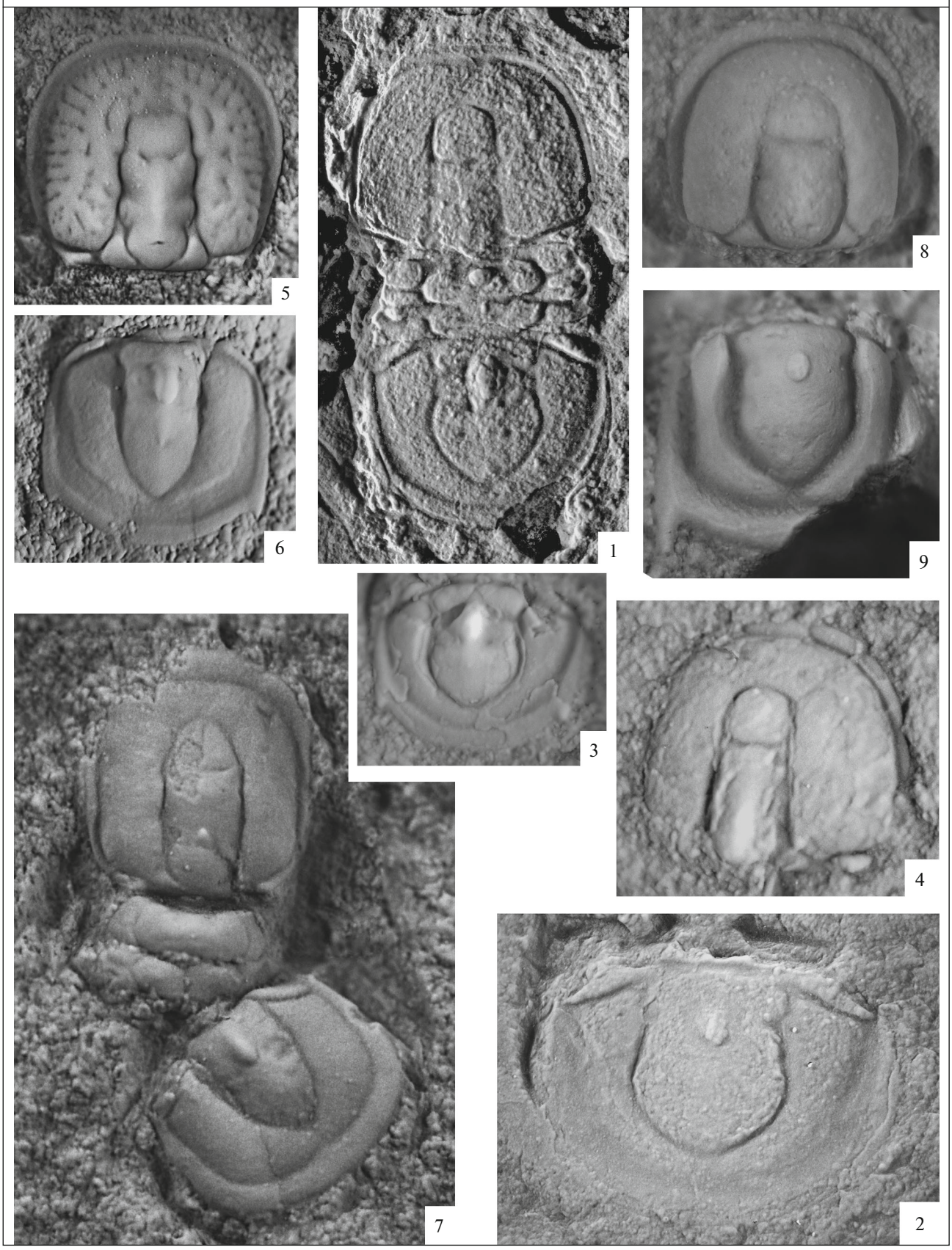
Figs. 2–4. ?*Diplorrhina lata* (Shabanov, 1972): (2) holotype TsNIGR, no. 81/10606, pygidium, 3.5 mm long, loc. 15/10b (in Savitzkiy et al., 1972, pl. 7, fig. 14); (3) TsNIGR, no. 80/10606, pygidium, 2.3 mm long, loc. 15/9a (labeled in the slab as Savitzkiy et al., 1972, pl. 7, fig. 13, but does not match the published image); (4) TsNIGR, no. 80a/10606, cephalon, 2.3 mm long; Siberian Platform, Nekekit River.

Figs. 5 and 6. *Quadragnostus clarus (*Pokrovskaya et Egorova, 1982): (5) TsNIGR, no. 85/10112, cephalon, 3.2 mm long; (6) holotype TsNIGR, no. 1b/10112, pygidium, 2.5 mm long (Egorova et al., 1982, pl. 14, figs. 7, 8, respectively); Siberian Platform, Maya River, loc. C–1.

Fig. 7. *?Quadragnostus howelli* (Hutchinson, 1962), TsNIGR, no. 90/10112, dorsal shield, cephalon 1.7 mm long, pygidium 1.5 mm long (Egorova et al., 1982, pl. 9, fig. 2 as *Diplagnostus* sp. aff. *planicauda*); Siberian Platform, Maya River, loc. Sh-33.

Figs. 8 and 9. *Micagnostus* sp.: (8) TsNIGR, no. 147/11262, cephalon, 3.0 mm long (Egorova et al., 1976, pl. 35, fig. 1), loc. 10a; (9) TsNIGR, no. 148/11262, pygidium, 2.7 mm long (Egorova et al., 1976, pl. 35, fig. 2), loc. 11a; Siberian Platform, Lena River (middle reaches).

Plate 4



Molodo River, Amgan Stage, *Ovatoryctocara* and *Kounamkites* zones (Korovnikov and Shabanov, 2008; Shabanov et al., 2008 in all as *Peronopsis recta*); Nekekit, Amyday, Torkukuy, Malaya Kuonamka rivers, Amgan Stage, *Kounamkites* Zone (Savitzkiy et al., 1972; Egorova et al., 1976; Fedoseev, 1999).

?D. lata (Shabanov, 1972)—Siberian Platform: Nekekit River, *Kounamkites* Zone (Savitzkiy et al., 1972 as *Peronopsis lata*).

Genus *Redeagnostus* Naimark, 2012

Redeagnostus: Naimark, 2012, p. 1002.

Type species. *Agnostus ferox* Tullberg, 1880.

Diagnosis. Cephalon with narrow border structures, anteroglabella rounded in outline, posteroglabella not expanded, with parallel sides, and rounded rear, F2 absent, small median node in front of midlength of posteroglabella, basal lobes of moderate size. Pygidial border narrow to moderately wide, bispinose, border furrow variable in width, axis not reaching border furrow, F1, F2 absent, median node of medium size.

Species found in Russia. *Redeagnostus ferox* (Tullberg, 1880)—Siberian Platform: Yudoma River, lowermost Mayan Stage, *Tomagnostus fissus* Zone (Egorova et al., 1982 as *P. fallax*, pl. 5, fig. 6), Daldyn–Alakit Region, Amgan Stage, *Kounamkites* Zone (Ogienko and Garina, 2001 as *P. fallax* in pl. 2, figs. 9, 10).

R. insignis (Wallerius, 1895)—Siberian Platform: Anabar Anticline, Yurung–Tas–Suluda River, Mayan Stage, *Hatangia* and *Proasaphiscus privus* zones (Egorova and Savitzkiy, 1969 as *P.* ex gr. *fallax* in pl. 6, fig. 1); Sette–Daban Ridge, Kerbi River mouth, Ayusokkanian Stage, *Toxotis venustus* Zone (Gogin and Pegel, 1997); Kulyumbe River, Ayusokkanian Stage, lowermost *Pedinocephalina–Toxotis* Zone (Rosova, 1964; Lazarenko and Nikiforov, 1968); Khos-Nelege River, uppermost Mayan Stage, *Proagnostus bulbus* Zone (Lazarenko et al., 2008a, 2008b); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010, 2014 as *Peronopsis* aff. *insignis*).

Redeagnostus aff. *insignis (Wallerius, 1895)* – Siberian Platform: Maya River, upper Mayan Stage, *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982 as *Peronopsis* ex gr. *fallax* in pl. 36, fig. 2).

Genus *Qudragnostus* Howell, 1935

Plate 4, figs. 5–7

Quadragnostus: Howell, 1935a, p. 219; Moore, 1959, p. O186; Shergold et al., 1990, p. 56; Shergold and Laurie, 1997, p. 380.

Type species. *Quadragnostus solus* Howell, 1935.

Diagnosis. Cephalon subquadrate, border structures narrow to moderate, posteroglabella with parallel sides or slightly expanded at rounded rear, anteroglabella semicircular, transglabellar F3 bent backward. Pygidium subquadrate, border structures narrow to moderate, bispinose, axis narrow, angulated in rear, median node small, posteroaxis with transverse depression, postaxial space very short, variable in having postaxial furrow.

Remarks. *Peronopsis howelli* Hutchinson, 1962 described from northeastern Newfoundland, Trinity Bay, the top of *Paradoxides hicksi* Zone, is based on only two cephala, while the pygidium is unknown. There are two other cephala, which fit the morphology of this species; these specimens were illustrated by Robison as an undetermined genus and species (Robison, 1994, p. 34, text-figs. 9: 2, 3). These two were found in North Greenland, Henson Gletsher Formation, Nyeboe Land, *P. gibbus* and *P. atavus* zones. The complete shield from Eastern Siberia, Maya River (Egorova et al., 1982, pl. 9, fig. 2; here Pl. 4, fig. 7) resembles both the holotype of *P. howelli* and the cephalon in Robison (1994, text-figs. 9: 2a, b). Another cephalon from Greenland bears a short notch on the anteroglabellar front, unlike the first one and the Siberian specimen. Here we assigned all these specimens to the same species. Given the morphology of both pygidium and cephalon, the species was considered to belong to *Quadragnostus*. The characters of *Quadragnostus* are subquadrate cephalon and pygidium with narrow border in the cephalon and flat widened border on the pygidium, narrow border furrows on the cephalon and pygidium; the anteroglabella narrows considerably in its front part, glabellar F3 bent backward; pygidium with small border spines, F1 and F2 weak. But this species has some characters, which separate it from other species of the genus. These are short sulcus at front of anteroglabella and comparatively long postaxial furrow. The difference indicates its affinity with *Diplagnostus*. Thus, we leave the generic assignment of the species with the question as *?Quadragnostus howelli*.

It occurs in Eastern Siberia, *Tomagnostus fissus–Paradoxides hicksi* Zone, and in Greenland and Newfoundland, *Triplagnostus gibbus–Tomagnostus fissus* Zone.

Species found in Russia. *Quadragnostus depressa* (Tullberg, 1880)—Siberian Platform, Lena River (middle reaches), Mayan Stage, *Paradoxides davidis* Zone (Lermontova, 1940, pl. 36, fig. 1a as *P. fallax*).

Quadragnostus quadrata sulcata (Westergård, 1946)—Siberian Platform, Lena River, Mayan Stage, *Liostracus allachjunensis* Zone (Egorova et al., 1982, pl. 60, fig. 8 as *Peronopsis* aff. *quadrata sulcata*).

Q. clarus (Pokrovskaya et Egorova, 1982)—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone (Egorova et al., 1982 as *Tomagnostus clarus*).

?Q. howelli (Hutchinson, 1962)—Siberian Platform: Maya River, lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone (Egorova et al., 1982 as *Diplagnostus* sp. aff. *planicauda*).

Genus *Gratagnostus* Hajrullina, 1975

Gratagnostus: Repina et al., 1975, p. 113; Shergold et al., 1990, p. 46; Shergold and Laurie, 1997, p. 360; Naimark, 2012, p. 1004.

Type species. *Gratagnostus latus* Hajrullina, 1975, p. 113.

Diagnosis. Cephalon subquadrate or subcircular, with convex border, moderate in width, border furrow deliquiate, anteroglabella semicircular, transglabellar F3 straight or bent backward, F2 as deep notches, F1 well developed, directed to front, glabellar rear rounded in outline, narrowed between large basal lobes, median node at level of midlength between F1 and F2. Pygidium subquadrate, with convex narrow border, bispinose, border furrow deliquiate, moderately wide, axis with parallel sides or slightly constricted across M2, F1, F2 well developed, sometimes interrupted at median node, median node elongate, started from M1, posteroaxis gently tapering to rear, transverse depression variable in length from long sulcus to small pit. Postaxial space short, undivided.

Remarks. Compared to the original diagnosis, wide border structures of the cephalon are excluded from the diagnosis. These characters are only observed in the type species. There are some other species, except the type species which should be included in this genus, that is, *G. trilobatus* (Matthew, 1896), *G. abbatiae* (Rushton, 1979), and *G. pseudoquadratus* Naimark, 2012. In general, species of this genus, as other peronopsid genera with a transverse depression on the axis tend to form an undivided postaxial space. The postaxial furrow is not formed in these even in meraspids, in contrast to *Tomagnostus*, a ptychagnostid with transverse depression on the axis and well–defined postaxial furrow in meraspids. *G. pseudoquadratus* is defined by transverse axial furrows well–pronounced (generic feature) elongated transverse depression and by a comparatively wide undivided postaxial furrow, which identify the species.

Species found in Russia. *G. pseudoquadratus* Naimark, 2012 – northeastern Siberian Platform: Khorbusuonka River, lower Mayan Stage, *Pseudanomocarina* Zone (Savitzkiy et al., 1972, pl. 6, figs. 10, 11 as *Peronopsis quadrata*).

Genus *Micagnostus* Hajrullina, 1975

Plate 4, figs. 8 and 9

Micagnostus: Repina et al., 1975, p. 115; Shergold et al., 1990, p. 43; Shergold and Laurie, 1997, p. 356; Naimark, 2012, p. 1000.

Type species. *Micagnostus rectus* Hajrullina, 1975.

Diagnosis. Cephalon subquadrate, border of medium width, convex, border furrow narrow; anteroglabella rounded in outline, partly effaced, posteroglabella with parallel sides, basal lobes small. Pygidium subquadrate to semiovate, border convex, moderately wide, with massive spines, axis reaching narrow border furrow.

Remarks. The genus with its type species was described on the basis of only one cephalon from Middle Asia, Turkestan Ridge. According to partly effaced glabella, this genus was believed to belong to Spinagnostidae (Repina et al., 1975; Shergold et al., 1990; Shergold and Laurie, 1997). A revision of Siberian specimens allows the recognition of representatives of this genus. They include cephala accompanied with pygidia. The combination of cephalic and pygidial characters brings this genus to Peronopsidae: lack of a median preglabellar furrow, axis without F1 and F2, spiny pygidial border. Siberian and Middle Asian specimens come from the same time interval, from the *Pseudanomocarina* Zone.

The morphology of the Siberian and Middle Asia specimens is somewhat different. That is, original cephalon has an anteroglabella effaced in a greater degree, the shape is closer to quadrate. As we do not know if the differences reflect the intraspecific or interspecific variability, we left the Siberian specimens in open nomenclature.

Species found in Russia. *Micagnostus sp.*—Siberian Platform: Lena River, unnamed Zone (Egorova et al., 1976, pl. 35, figs. 1, 2 as *P. fallax*), Middle Cambrian, *Paradoxides davidis* Zone (Lermontova, 1940, pl. 36, fig. 1d as *Peronopsis fallax*).

Genus *Acadagnostus* Kobayashi, 1939

Acadagnostus: Kobayashi, 1939, p. 113; Moore, 1959, p. O184; Hutchinson, 1962, p. 68; Öpik, 1979, p. 62; Shergold et al., 1990, p. 55; Robison, 1995, p. 302; Shergold and Laurie, 1997, p. 362; Laurie, 2004, p. 250.

Axagnostus: Laurie, 1990, p. 318.

Type species. *Agnostus acadicus* Hartt in Dawson, 1868 (=*Peronopsis fallax* Linnarsson, 1869).

Diagnosis. Cephalon circular or subquadrate; border narrow; border furrow from moderate to wide; preglabellar furrow absent or partly developed at glabellar front, glabella with F2 as weak notches or relief on sides of posteroglabella, posteroglabella constricted at F2, F3 straight or bent slightly backward. Pygidium subquadrate, border flattened, moderate to wide, bispinose, border furrow narrow to moderate, axis with M1 wider than M2 and M3, F1 and F2 very weakly expressed or expressed as relief on axis, postaxial furrow present.

Remarks. This genus differs from *Baltagnostus* mainly by postaxial furrow and unexpanded posteroaxis. The former feature, on the one hand, helps to discriminate *Baltagnostus rakuroensis* (Kobayashi, 1935) from *Acadagnostus* and, on th other hand, to

separate species of *Pseudoperonopsis*. The latter feature outlines *Acadagnostus* from species of *Baltagnostus* other than *B. rakuroensis* and from *Iniospheniscus*.

Species found in Russia. *A. acadica* Hartt in Dawson, 1968—Siberian Platform: Yudoma River, lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone, Malokuonamsky Horizon (Egorova et al., 1976); Nekekit River, *Pseudanomocarina* Zone (Egorova et al., 1976, pl. 2, fig. 1 as *Peronopsis fallax*); Sette–Daban Ridge, Aldan River near the Kerbi River mouth, Ayusokkanian Stage, *Toxotis venustus* Zone (Gogin and Pegel, 1997, pl. 22, fig. 11 as *Peronopsis fallax*); Maya River, Middle Cambrian (Pokrovskaya, 1960 as *Peronopsis fallax*).

A. syrma (Öpik, 1979)—Siberian Platform: Maya River, Mayan Stage, Anopolenus *henrici* and *Anomocarioides limbataeformis* zones (Egorova et al., 1982).

Genus *Baltagnostus* Lochman, 1944

Baltagnostus: Peng and Robison, 2000, p. 50 (see synonymy list); Ergaliev and Ergaliev, 2008, p. 158; Peng et al., 2009, p. 19.

Type species. *Proagnostus? centerensis* Resser, 1938.

Diagnosis. Cephalon semiovate; border narrow; border furrow from moderate to wide; preglabellar furrow absent or partly developed at glabellar front; F3 straight or bent slightly backward, median node in midlength of posteroglabella. Pygidium subquadrate; border flattened, moderate to wide, sometimes even widened at rear, bispinose; border furrow moderate to wide, axis unconstricted at M2; M3 usually expanded, F1 and F2 undeveloped, expressed as relief on axis, axis long reaching border furrow.

Species found in Russia. *Baltagnostus rakuroensis* (Kobayashi, 1935)—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Tomagnostus fissus*, *Liostracus allachjunensis,* and *Anomocarioides? curtus* zones (Egorova et al., 1982, pl. 51, figs. 15, 16, pl. 62, fig. 6 as *P. fallax;* pl. 60, fig. 11 as *Peronopsis* sp. 1; and pl. 56, fig. 6 as *Peronopsis* sp. 2); Buom–Pastakh River, *Kounamkites* Zone (Egorova and Savitzkiy, 1969); Amga River, *Pseudanomocarina* Zone (Chernysheva, 1961 as *Peronopsis fallax*).

Genus *Iniospheniscus* Öpik, 1979

Iniospheniscus: Öpik, 1979, p. 50; Shergold et al., 1990, p. 47; Robison, 1994, p. 33; Shergold and Laurie, 1997, p. 364.

Type species. *Iniospheniscus talis* Öpik, 1979.

Diagnosis. Cephalon semiovate; border relatively narrow; border furrow narrow and deliquiate; glabella with F2 weak; glabellar node at about F2. Pygidium with flat border, which may have incipient zonation, short spines present; deliquate border furrow, axis with expanded posteroaxis; F1 and F2 deeply impressed on flanks; axial node large; postaxial space short or absent, postaxial furrow absent.

Remarks. The Siberian form differs from two other species of *Iniospheniscus* (*I. talis* Öpik, 1979 and *I. incanus* Öpik, 1979) in having an undivided postaxial space; both Australian species have an axis reaching the border furrow. Cephalon, which we tentatively assigned to the Siberian species (Egorova and Savitzkiy, 1969, pl. 6, fig. 17), was found together with an *Iniospheniscus*–like pygidium. It fits the generic diagnosis especially in the angular glabellar rear and blunt glabellar front. These two characters are the same as in the type species *I. talis*. But this cephalon differs in having a glabella, which is slightly expanded across M2. The pygidium, expanded in M2 and M3 and displayed both F1 and F2, is specific for the genus. Therefore, we refer this specimen to *Iniospheniscus.*

Species found in Russia. *Iniospheniscus* sp.—Siberian Platform: Buom–Pastakh River, Amgan Stage, *Kounamkites* Zone (Egorova and Savitzkiy, 1969, pl. 6, fig. 17 as *?Peronopsis fallax*, pl. 6, figs. 20–23 as *Peronopsis* aff. *integra*).

Family Diplagnostidae Whitehouse, 1936

Diagnosis. En grande tenue; pygidial border variably zonate, bispinose or trispinose; cephalic and pygidial border furrows deliquiate; basal lobes moderate to large–sized, simple. Pygidial axis with F1 and F2 well developed to effaced, posteroaxis usually with variably shaped transverse depression.

Remarks: There is a transient group of genera, which may be assigned to either Diplagnostidae or Peronopsidae. This group comprises *Acadagnostus, Baltagnostus, Pseudoperonopsis,* and *Iniospheniscus,* and it probably originated from *Peronopsis (Vulgagnostus)* or *Peronopsis (Proacadagnostus)*. These genera are characterized by the lack or incipient zonation on the pygidial border. They differ from Diplagnostidae (*Diplagnostus, Linguagnostus, Dolichagnostus, Oedorhachis, Tasagnostus)* in the condition of the postaxial space and in the development of F1 and F2. In addition, the clearly expressed zonation and narrowing cephalic M1 characterize Diplagnostidae. These genera are probably descendants of the former group, namely, the genus *Baltagnostus*. Here, genus *Pseudoperonopsis* with the pronounced zonation of the pygidial border was placed in the Diplagnostidae, although its early representatives are referred to the first group (Naimark, 2012).

The summary of stratigraphic distribution for Diplagnostidae from Russia is shown in Fig. 6.

Genus *Pseudoperonopsis* Harrington, 1938

Plate 5, fig. 1

Pseudoperonopsis: Harrington, 1938, p. 151; Öpik, 1979, p. 43; Sun, 1989, p. 88; Shergold et al., 1990, p. 45; Shergold and Laurie, 1997, p. 360; Buchholz, 2004a, p. 509; Ergaliev and Ergaliev, 2008, p. 141.

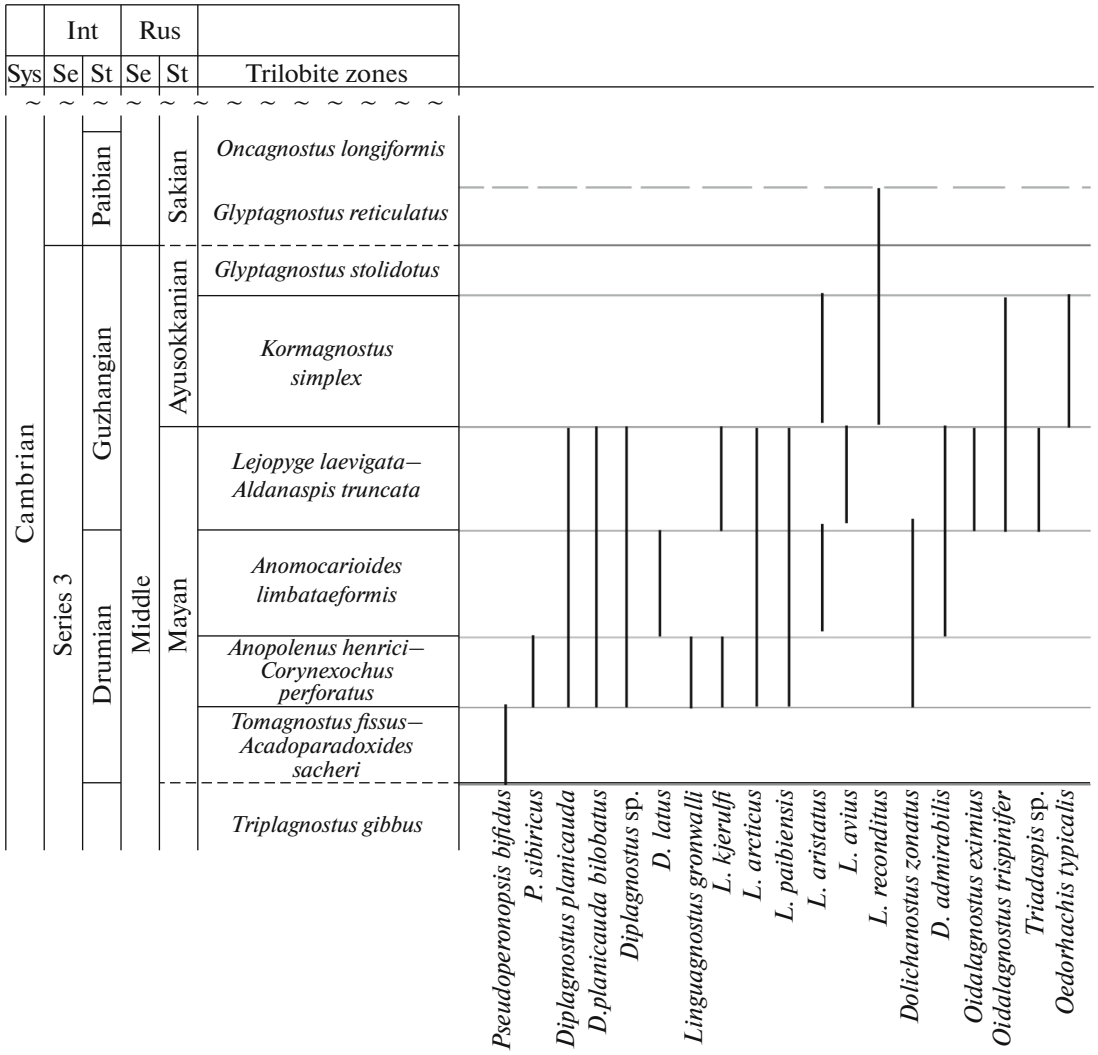


Fig. 6. Stratigraphic distribution of Diplagnostidae species known from Russia.

Type species. *Agnostus sallesi* Munier–Chalmas *et* Bergeron, 1889.

Diagnosis. Cephalon rounded in shape; median preglabellar furrow absent or partly developed at glabellar front; border narrow, border furrow from moderate to wide; posteroglabella with F3 straight or bent slightly backward; F2 weakly expressed at flanks. Pygidium subquadrate, border flattened, may have incipient zonation, bispinose; border furrow wide, axis unconstricted at M2, M3 unexpanded, F1 and F2 undeveloped, expressed as relief on axis, axis not reaching border furrow, lacking postaxial furrow.

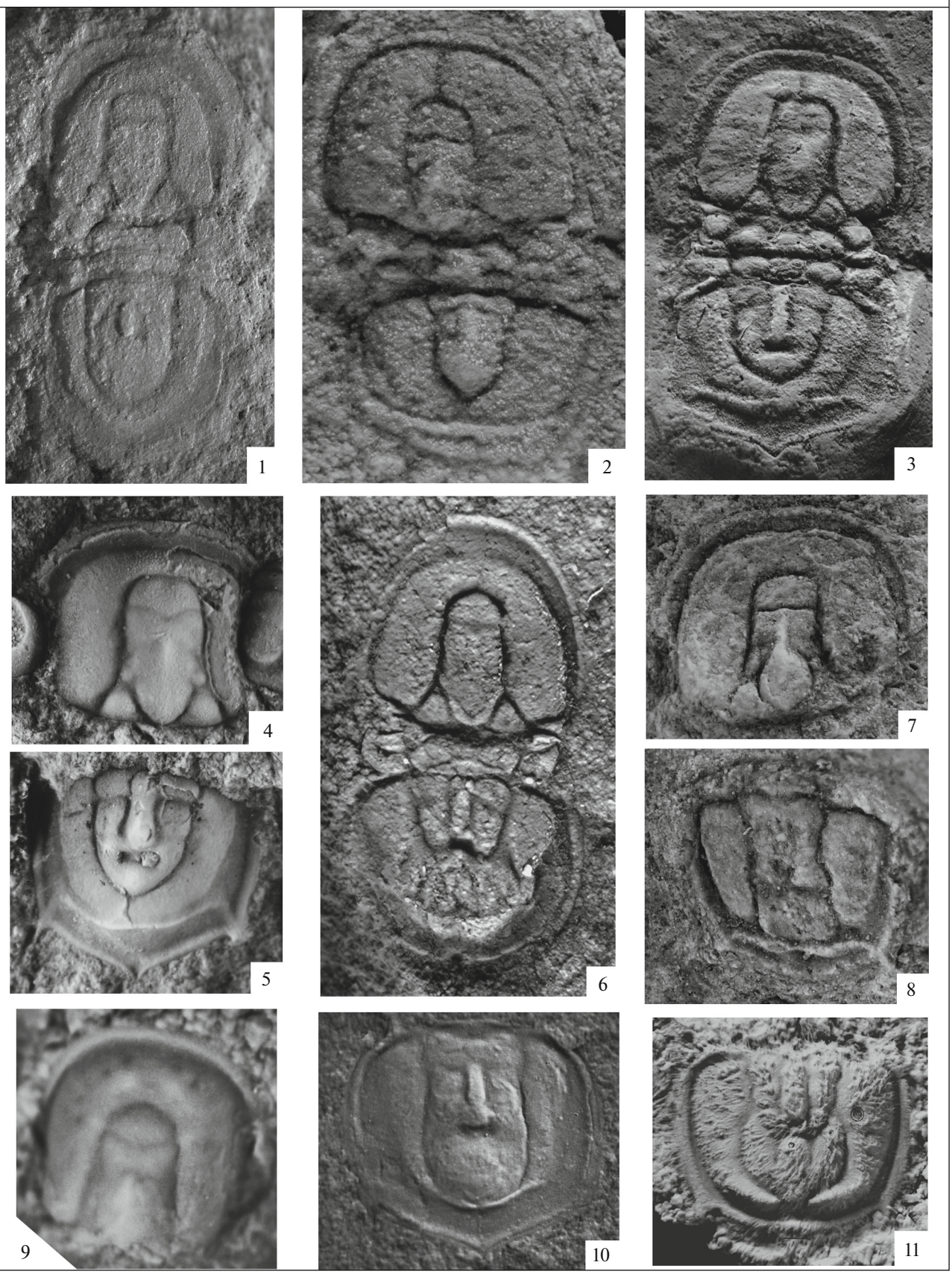
Remarks. Difficulties with the recognition of this genus usually arise with the including *Agnostus rakuroensis* Kobayashi, 1935 in this genus (see Sun, 1989). This species does not have the main diagnostic characters of the genus, that is, wide border furrows in both cephalon and pygidium, and variably expressed zonation on the pygidial border, leaving the only ambiguous shape of the pygidial axis. We transferred *A. rakuroensis* to *Baltagnostus*, thus, the generic diagnosis became more or less rigid. Also *P. minuscula* Buchholz, 2004a possessing a preglabellar feature agrees better with *Euagnostus* diagnosis and habitus.

P. bifidus (Hajrullina, 1975) has a recognizable zonation on the pygidial border with no postaxial furrow; therefore, the species was transferred from *Peronopsis* to *Pseudoperonopsis*.

P. sibiricus was originally described within the genus *Linguagnostus*. But it does not have specific pygidial characters, that is, very short third axial lobe with the clear depression. Therefore, the species is believed to belong to *Pseudoperonopsis* instead.

Species found in Russia. *P. bifidus* (Hajrullina, 1975 in Repina et al., 1975)—Siberian Platform: Lena River (middle reaches), lowermost Mayan Stage, *Tomagnostus fissus* Zone (Egorova et al., 1976, pl. 36; figs. 1, 2, 4, pl. 37, figs. 5, 6, pl. 38. figs. 5,

Plate 5



22 as *P. quadrata*); ?Maya River, Middle Cambrian (Pokrovskaya, 1960, pl. 1, fig. 9 as *P. fallax*; Egorova et al., 1982, pl. 9, figs. 3, 4 as *P. fallax*).

P. sibiricus (Pokrovskaya et Pegel, 1982) – Siberian Platform: Lena (middle reaches) and Botoma rivers, Mayan Stage, *Liostracus allachjunensis* Zone (*Anopolenus henrici* Subzone) (Egorova et al., 1982 as *Linguagnostus sibiricus* Pokrovskaya et Pegel, 1982).

Genus *Diplagnostus* Jaekel, 1909

Plate 5, fig. 2

Diplagnostus: Peng and Robison, 2000, p. 48 (see synonymy list except *Tasagnostus*); Ergaliev and Ergaliev, 2008, p. 46; Peng et al., 2009, p. 18.

Type species. *Agnostus planicauda* Angelin, 1851.

Diagnosis. Cephalon commonly scrobiculate; deliquiate to subdeliquiate border furrows with narrow border in cephalon and zonate in pygidium; unconstricted acrolobes; median preglabellar furrow variably developed; glabella with trapeziform to subrectangular anterior lobe, commonly with median sulcus; F3 straight, glabellar node at or slightly in front of F2. Pygidium bispinose, axis long, ogival, extending to border furrow or postaxial furrow; F1 impressed, except space of median node; F2 clearly impressed; posterior lobe ogival to subtriangular, commonly with poorly defined transverse depression, pygidial collar always well defined, extending across entire posterior margin between spines, but not extending onto acrolobe.

Remarks. *Diplagnostus latus* E. Romanenko, 1967 described from Gornyi Altai has the same cephalic characteristics as *Diplagnostus atavorum* Öpik, 1979. The latter was established based on a single cephalon. If the cephalic aspects are sufficient to compare these two species, *D. atavorum* appears to be a junior synonym of *D. latus*. Another representative of this species emerges from revised Siberian agnostoid diversity, that is, the form found in the Maya River section and published in open nomenclature (Egorova et al., 1982 as gen. et sp. indet. 2). Both cephalon and pygidia fit the original description, including the cephalic and pygidial sculpture of *D. latus.* Australian representative of *D. latus* confined to the *Ptychagnostus atavus* Zone, while the Siberian form is younger; the chronological distribution of the specimens from Gornyi Altai requires clarification.

Species found in Russia. *D. planicauda* Angelin, 1851—Siberian Platform: Maya River, *Anopolenus henrici* and *Anomocariodes limbataeformis* zones; Chabda River, *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982).

D. planicauda bilobatus Kobayashi, 1939—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone; Chabda River, upper Mayan Stage, *L. laevigata–A. truncata* zones (Pokrovskaya, 1960; Egorova et al., 1982).

D. latus E. Romanenko, 1967—Siberian Platform: Maya River, Mayan Stage, *Anomocarioides limbataeformis* Zone (Egorova et al., 1982); Altai-Sayany Folded Belt, Altai Mountains, Verkhnyaya Yinyrga River, upper Middle Cambrian (Mayan Stage) (Romanenko and Romanenko, 1967 as gen. et sp. indet. 2).

Diplagnostus sp.—Siberian Platform: Maya River, *Anopolenus henrici* and *Anomocariodes limbataeformis* zones; Chabda River, *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982, pl. 21, fig. 1, pl. 46, fig. 2b as *D. planicauda*).

Explanation of Plate 5

Diplagnostidae, Oidalagnostinae

Fig. 1. *Pseudoperonopsis sibiricus* (Pokrovskaya et Pegel, 1982); holotype TsNIGR, no. 2/10112, dorsal shield, 8.4 mm long (Egorova et al., 1982, pl. 61, fig. 10); Siberian Platform, Botoma River, loc. 6.

Fig. 2. *Diplagnostus latus* E. Romanenko, 1967; holotype TsSGM, no. 74/724, dorsal shield, 2.5 mm long (Romanenko and Romanenko, 1967, pl. 1, fig. 11); Altai-Sayany Folded Belt, Altai Mountains, Yynyrga River, loc. 146.

Fig. 3. *Linguagnostus aristatus* Fedjanina, 1977; holotype LFGI, no. 2112/4810, dorsal shield, 7.2 mm long (Fedjanina, 1977, pl. XIX, fig. 1); Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain, loc. 4810.

Figs. 4 and 5. *Linguagnostus avius* E. Romanenko, 1985: (4) holotype LFGI, no. 1595/196, cephalon, 3.5 mm long (Romanenko, 1985, pl. V, fig. 11); (5) syntype LFGI, no. 1595/195, pygidium, 3.1 mm long (Romanenko, 1985, pl. V, fig. 9); Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River, loc. 170.

Fig. 6. *Linguagnostus reconditus* Poletaeva et Romanenko, 1970; counterimpression of holotype LFGI, no. 1328/15, incomplete dorsal shield, 4.5 mm long (Poletaeva and Romanenko, 1970, pl. 10, fig. 11b); Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River.

Figs. 7 and 8. *Oidalagnostus eximius* E. Romanenko, 1967: (7) TsSGM, no. 77/724, cephalon, 2.3 mm long, (8) holotype TsSGM, no. 78/724, pygidium, 3.9 mm long (Romanenko and Romanenko, 1967, pl. 1, figs. 14 and 15, respectively); Altai-Sayany Folded Belt, Altai Mountains, Tandoshka River.

Figs. 9 and 10. *Dolichagnostus admirabilis* Pokrovskaya, 1958; represented by specimens from the eastern Siberian Platform, Maya River: (9) TsNIGR, no. 98/10112, cephalon, 1.8 mm long, loc. C–5 (Egorova et al., 1982, pl. 25, fig. 4); (10) TsNIGR, no. 101/10112, pygidium, 4.5 mm long, loc. C–2 (Egorova et al., 1982, pl. 27, fig. 15).

Fig. 11. *Triadaspis* sp., SNIIGGiMS no. 366/250, pygidium, 3.6 mm long (Pegel, 2010, pl. II, fig. 24); Siberian Platform, Kotui River (middle reaches), loc. 68c.

Genus *Linguagnostus* Kobayashi, 1939

Plate 5, figs. 3–6

Linguagnostus: Kobayashi, 1939, pp. 142–143; Westergård, 1946, p. 63; Moore, 1959, p. O175; Pokrovskaya, 1960, p. 57; Egorova et al., 1960, p. 158; 1963; pp. 61–62; Öpik, 1979, p. 52; Rushton, 1979, p. 58; Shergold et al., 1990, pp. 47–48; Robison, 1994, p. 33; Shergold and Laurie, 1997, p. 364; Peng and Robison, 2000, p. 52; Jell and Adrian, 2002, p. 361; Ergaliev and Ergaliev, 2008, p. 160.

Enetagnostus: Whitehouse, 1936, p. 91; Lermontova, 1940, p. 128.

Diplagnostus (Linguagnostus): Ivshin, 1953, pp. 33–34.

Cristagnostus: Rushton, 1978, pp. 262, 264; Shergold et al., 1990, p. 48; Ahlberg and Ahlgren, 1996, p. 138; Shergold and Laurie, 1997, pp. 365–366.

Type species. *Agnostus kjerulfi* Brögger, 1878.

Diagnosis. Nonscrobiculate, border furrows both in cephalon and pygidium deliquiate; cephalon with subrectangular anteroglabella, commonly with median sulcus; F3 straight; F2 weakly expressed at flanks or absent, glabellar node at about level with F2; posteroglabella tapering to angular or narrowly rounded rear; median preglabellar furrow absent. Pygidium bispinose or trispinose, acrolobe commonly constricted, zonate border; axis short, unconstricted at M2, posteroaxis short, subtriangular, with transverse depression at about midlength of posteroaxis; pygidial collar extending onto acrolobe.

Remarks. Peng and Robison (2000) assigned *L. aristatus* Fedjanina, 1977 to the type species *L. kjerulfi*. However, as Fedjanina has emphasized (1977), these species differ in some characters: the larger basal lobes in *L. aristatus*, zonate border is more complicated in *L. aristatus* in having the sinusoid ridge with the furrow between this ridge and the rear of the acrolobe, and the weak F2. These differences seem to be sufficient to consider this species valid. Ergaliev identified *L. kjerulfi* from the Kyrshabakty section (Malyi Karatau, southern Kazakhstan) (Ergaliev and Ergaliev, 2008, p. 160, pl. 13, fig. 17). But the imaged specimen fits the description of *L. aristatus;* therefore, it would be better to reassign it to this species.

Linguagnostus tricuspis from Gornyi Altai Region was briefly mentioned by Lermontova (1940), although neither formal description nor the holotype was provided. Lermontova marked this species with the sign MS in the place of an authorship and probably was going to publish the description in the close future, but this never had been done. Therefore, the name and the species itself cannot be considered valid. Dong (1991) established *Linguagnostus pibiensis,* which resembles *L. tricuspis* in both images and short text description. These two species are most probably the same. As *L. tricuspis* has not formally been described; *L. paibiensis* is validated, although *L. tricuspis* was published earlier. Other specimens from Gornyi Altai identified as *Linguagnostus* sp. (Romanenko, 1977, p. 167, pl. 23, figs. 21, 22) represent the same species and have earlier been assigned to *L. paibiensis* (Peng and Robison, 2000).

L. arcticus originally described by Holm and Westergård (1930) from Bennett Island may represent the same species as *L. reconditus*. A new collection from Bennett Island (Danukalova et al., 2014) contained *L. reconditus,* which only differs from the images of *L. arcticus* in the size of basal lobes on cephalon. To distinguish between these two species, the Holm and Westergård's collection needs to be reexamined.

Species found in Russia. *L. kjerulfi* (Brögger, 1878)—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* and *L. laevigata–A. truncata* zones (Lermontova, 1940 as *Enetagnostus kjerulfi* (Brögger); Egorova et al., 1982; Pegel, 2000).

L. grönwalli Kobayashi, 1939—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone (Pokrovskaya, 1960; Egorova et al., 1982); Kulyumbe River, *Pedinocephalina–Toxotis* Zone (lower part) (Lazarenko and Nikiforov, 1968 as *Oidalagnostus* sp.).

L. arcticus (Holm et Westergård, 1930)—Bennett Island, Mayan Stage, *Paradoxides forchhammeri* Zone (Lermontova, 1940 as *Enetagnostus arcticus* (Holm et Westergård, 1930)).

L. paibiensis Dong, 1991—Altai-Sayany Folded Belt: Salair Ridge, Orlinaya Mountain, Mayan Stage, *Paradoxides forchhammeri* Zone (Lermontova, 1940 as *Enetagnostus tricuspis* Lermontova (MS)); Altai Mountains, Bol'shaya Isha River, uppermost Middle Cambrian (Egorova et al., 1960 as *Linguagnostus tricuspis*; Romanenko, 1977 as *Linguagnostus sp*.).

L. avius E. Romanenko, 1985—Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River, Mayan Stage, *Anopolenus henrici* Zone (Romanenko, 1985).

L. aristatus Fedjanina, 1977—Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain, Mayan Stage, *Goniagnostus nathorsti* Zone (Fedjanina, 1977).

L. reconditus Poletaeva et Romanenko, 1970—Altai-Sayany Folded Belt, northeastern Altai Mountains, Bol'shaya Isha River, uppermost Middle Cambrian (Poletaeva and Romanenko, 1970 as *Linguagnostus? reconditus*; Romanenko, 1977 as *Linguagnostus? reconditus*); Bennett Island, *Glyptagnostus reticulatus* Zone (Danukalova et al., 2014 as *Linguagnostus kjerulfi*).

Genus *Dolichagnostus* Pokrovskaya, 1958

Plate 5, figs. 9 and 10

Dolichagnostus: Pokrovskaya, 1958, p. 36; Öpik, 1967, p. 132; Shergold et al., 1990, p. 47; Shergold and Laurie, 1997, p. 364.

Type species. *Dolichagnostus admirabilis* Pokrovskaya, 1958.

Diagnosis. Diplagnostidae with flat cephalic acrolobe, border narrow, border furrow wide; F3 weak or unexpressed, if present anterior glabellar lobe small, basal lobes large. Pygidium bispinose, with wide border furrow and narrow border; F1 and F2

very weak or unexpressed; posteroaxis wide with transverse depression.

Remarks. Öpik (1967) described pygidia from the Mungerebar limestone (central Queensland), which he questionably assigned to *Connagnostus,* and named this form as a new species, *?C. zonatus*. These pygidia did not display the diagnostic characters of *Connagnostus*, that is, they do not possess transaxial furrows in the axis, have transverse depression in the posteroaxis and large elongate node. Later, Pegel (1978) published a new species, *Dolichagnostus levis,* from the Siberian Platform; this form seems to be identical to *?C. zonatus*. There were both cephala and pygidia in the Siberian material, which allow this species to be correctly assigned to *Dolichagnostus*. Therefore, this taxon is referred to as the binomen *Dolichagnostus zonatus* (Öpik, 1967).

The holotype of *Dolichagnostus admirabilis* was lost.

Species found in Russia. *Dolichagnostus admirabilis* Pokrovskaya, 1958—Siberian Platform: Maya and Yudoma rivers, Mayan Stage, *Prohedinia–Forchhammeria–Anomocarioides limbataeformis* Zone (Pokrovskaya, 1958); Maya River, Mayan Stage, *Prohedinia–Forchhammeria–Anomocarioides limbataeformis* Zone (Pegel, 2000); Mayan Stage, *Anomocarioides limbataeformis* and *Anopolenus henrici* zones (Egorova et al., 1982).

D. zonatus (Öpik, 1967)—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Liostracus allachjunensis* Zone (*Anopolenus henrici* Subzone), *Anomocarioides? curtus* Zone (Pegel, 1978; Egorova et al., 1982 both as *D. levis*).

Genus *Oedorhachis* Resser, 1938

Oedorhachis: Resser, 1938, p. 50; Shimer and Shrock, 1944, p. 601; Moore, 1959, p. O185; Poulsen, 1960, p. 12; Öpik, 1967, p. 127; Robison, 1988, p. 35; Shergold et al., 1990, p. 48; Pratt, 1992, p. 42; Shergold and Laurie, 1997, p. 364; Ergaliev and Ergaliev, 2008, p. 162.

Acmarhachis Resser (part): Palmer, 1962, p. 19.

Type species. *Oedorhachis typicalis* Resser, 1938.

Diagnosis. Diplagnostinae with deliquiate border furrows both in cephalon and pygidium; cephalon with faint sculpture; glabella narrowing to angular rear; basal lobes comparatively large; pygidial axis with F1, F2 weakly developed, transverse depression absent.

Species found in Russia. *Oedorhachis typicalis* Resser, 1938—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Ayusokkanian Stage, *Clavagnostus spinosus* Zone (Chernysheva, 1961; Lazarenko et al., 2008a); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010, 2014 as *Pseudagnostus* sp.).

Subfamily Oidalagnostinae Öpik, 1967

Diagnosis. En grande tenue, scrobiculate, with deliquiate border furrows; zonate pygidial border; preglabellar median furrow usually weak. Glabella with trapeziform to subrectangular anterior lobe; F3 well developed; posterior lobe with variably developed F2; glabellar node about level with F2 furrows. Pygidium trispinose; axis long, extending to pygidial collar or posteriorly effaced; Fl variably impressed; Ml trilobate; F2 variably impressed, deflected by axial node; posterior lobe variably quadrate with deep transverse depression in anterior half, posterior portion subrectangular, tumid or effaced.

Genus *Oidalagnostus* Westergård, 1946

Plate 5, figs. 7 and 8

Oidalagnostus: Westergård, 1946, p. 65; Hupé, 1953, p. 121; Moore, 1959, p. O175; Pokrovskaya, 1960, p. 57; Lu et al., 1965, p. 24; Öpik, 1967, p. 134; Lu et al., 1974, p. 80; Jago, 1976, p. 160; Zhang, 1981, p. 135; Robison, 1988, p. 37 (except *Tasagnostus*); Lu and Lin, 1989, p. 79; Shergold et al., 1990, p. 48; Shergold and Laurie, 1997, p. 365; Peng and Robison, 2000, p. 56.

Ovalagnostus: Lu et al., 1974, p. 81; Qui et al., 1983, p. 32; Lu and Lin, 1989, p. 205.

Type species. *Oidalagnostus trispinifer* Westergård, 1946.

Diagnosis. Agnostids with unique shape of pygidium. Axis long extending marginal collar, posteroaxis with tumid subrectangular posterior portion; it separated from pleural fields by paired bosses and weak accessory furrows; pygidial collar acute, with median depression, sometimes with perforation at base of central spine or its analogue.

Remarks. Jago (1976) described a new genus, *Tasagnostus,* with the type species *T. debori* and another species *T. compani*. Robison (1988) suppressed this genus and transferred its type species to *Oidalagnostus* as a separate species, while *T. compani* was decided to be treated as a synonym of *O. trispinifer;* Robison argued that *T. compani* was erroneously described as a separate species due to its poor preservation. Later, *Tasagnostus* was considered valid (Shergold and Laurie, 1997, p. 364) and included in *Diplagnostinae*. The diagnosis suggested by these authors emphasizes the following characters: absence of scrobiculation and acute glabellar culmination, axis constricted across M2. Only the type species bears this set of characters, while *T. compani* does not. Here we refer *T. compani* to *Oidalagnostus,* although it has a bispinose pygidium and weak glabellar F3 like *Tasagnostus debori*. Actually, *T. compani* is well illustrated and supplied with a detailed description. Both allow us to reconsider it as a junior synonym of *O. eximius* E. Romanenko, 1967. Romanenko also emphasized in the description and diagnosis a weak glabellar F3 and two instead of three spines on the pygidium. Other characters in either case coincide. Therefore, *O. eximius* gains wider distribution than formerly recognized.

Species found in Russia. *O. trispinifer* Westergård, 1946—Siberian Platform: Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2000, 2010, 2014); Sette-Daban Ridge, Kerbi River mouth, beds with *Oidalagnostus trispinifer*, upper Mayan Stage (Gogin and Pegel, 1997); Kharaulakh Mountains, Khos-Nelege River, Mayan Stage, *Anopolenus henrici* and *Proagnostus bulbus* zones (Lazarenko et al., 2008a, 2008b); Kulyumbe River, upper Middle Cambrian, Mayan Stage, Saamsky Horizon (Rosova, 1964).

O. eximius E. Romanenko, 1967—Altai-Sayany Folded Belt, Altai Mountains, Tandoshka and Tagaza rivers; upper Mayan Stage (Romanenko and Romanenko, 1967).

Genus *Triadaspis* Öpik, 1967

Plate 5, fig. 11

Triadaspis: Öpik, 1967, p. 125; Shergold et al., 1990, p. 52; Shergold and Laurie, 1997, p. 373; Ergaliev and Ergaliev, 2008, p. 215.

Type species. *Triadaspis bigeneris* Öpik, 1967.

Diagnosis. Pygidium trispinose; border narrow; border furrow moderate to deliquate, M1, M2 parallel–sided; posteroaxis also with parallel sides or slightly expanded at two–thirds of posteroaxis length; rear of posteroaxis acuminate, running into border furrow, median tubercule extended to posteroaxis and subdivided by transverse depression; transverse depression laterally bent forwards, forming lateral lobes on posteroaxis; acrolobe with faint radial scrobicules on pleurae.

Remarks. This species was established by Öpik (1967, p. 125) based on a very poorly preserved pygidium. Until recently, no other material of the species has been published. In 2008, Ergaliev and Ergaliev (2008, p. 215, pl. 22, fig. 12) described a pygidium from the Kyrshy–Bacty section (Kazakhstan), which they assigned to this genus. But the Kazakhstan form lacks a transverse depression or any other transverse structures on the posteroaxis; in addition, the posteroaxis is widened posteriorly. Therefore, there is no doubt that this pygidium does not belong to *Triadaspis*. Later, Pegel (2010) illustrated the genus with a new material from Siberia, which again comprised the only pygidium, but of good preservation. This pygidium displays all diagnostic characters and even allows us the correction of the taxonomic position of the genus. The set of characters (see the diagnosis) readily transfers the genus to the subfamily Oidalagnostinae from Clavagnostidae (subfamily Aspidagnostinae). This genus is distinguished from *Oidalagnostus* by acutely tipped posteroaxis, while other species of *Oidalagnostus* bear expanded posteroaxis or with parallel sides, with its wide rear reaching the border furrow.

Species found in Russia. *Triadaspis* sp.—Siberian Platform, Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010, 2014).

Family Spinagnostidae Howell, 1935

Diagnosis. Anterior glabellar lobe mostly effaced with F3 variably expressed; preglabellar furrow absent; with narrow border structures; cephalon nonspinose; basal lobes simple. Pygidium nonspinose; border furrow narrow, border usually flat and narrow or moderately wide; axis usually long, but in some species, relatively short with effaced axial furrow; axis ogival, constricted across M2 with acuminated posteroaxis; pygidial axis with F1 and F2 from developed to effaced; axial node small to moderate; postaxial furrow present at least in juveniles.

Remarks. This family most probably aggregates phylogenetically unrelated genera with the tendency of anteroglabellar effacement. From this family, we excluded *Eoagnostus* (transferred to Peronopsidae) and *Euagnostus* (transferred to Doryagnostidae), as matching with other familial characters.

The summary of stratigraphic distribution for Spinagnostidae from Russia is shown in Fig. 7.

Genus *Hypagnostus* Jaekel, 1909

Plate 6, figs. 1–3

Hypagnostus: Jaekel, 1909, p. 399; Whitehouse, 1936, p. 103; Kobayshi, 1939, p. 122; Lermontova, 1940, p. 129; Westergård, 1936, p. 43; Rasetti, 1948, p. 320; Ivshin, 1953, p. 17; Moore, 1959, p. O184; Shergold et al., 1990, p. 43; Westrop et al., 1996, p. 822; Shergold and Laurie, 1997, p. 356; Peng and Robison, 2000, p. 60; Ergaliev and Ergaliev, 2008, p. 128; Peng et al., 2009, p. 20.

Spinagnostus: Howell, 1935b, p. 219; Moore, 1959, p. O184.

Cyclopagnostus: Howell, 1937, p. 1166, Moore, 1959, p. O175.

Hypagnostus (*Breviagnostus*): Liu, 1982.

Hypagnostus (*Metahypagnostus*) Qiu: Qiu et al., 1983.

Type species. *Agnostus parvifrons* Linnarsson, 1869.

Diagnosis. Spinagnostidae with nonscrobiculate or weakly scrobiculate cephalon and pygidium, with cephalic F3 present; pygidium with border flattened and slightly widened at rear, F1 and F2 absent; axial node very small.

Remarks. *Hypagnostus latirhachis* Lermontova, 1940 agrees with the diagnosis of *Cotalagnostus* in having effaced glabellar F3. However, the transglabellar F3 is clearly visible in small cephala (Pl. 6, Fig. 3), becoming effaced in the larger ones (Pl. 6, Fig. 2). This allows us to leave this species within the genus *Hypagnostus* instead of transferring it to *Cotalagnostus*. In addition, the shape of the pygidial border conforms more to *Hypagnostus*.

H. facetus Pokrovskaya et Egorova, 1982 represents a meraspis degree 1 of *H. brevifrons*: the incipient thoracic segment is clearly visible on the holotype pygidium (here Pl. 6, fig. 1).

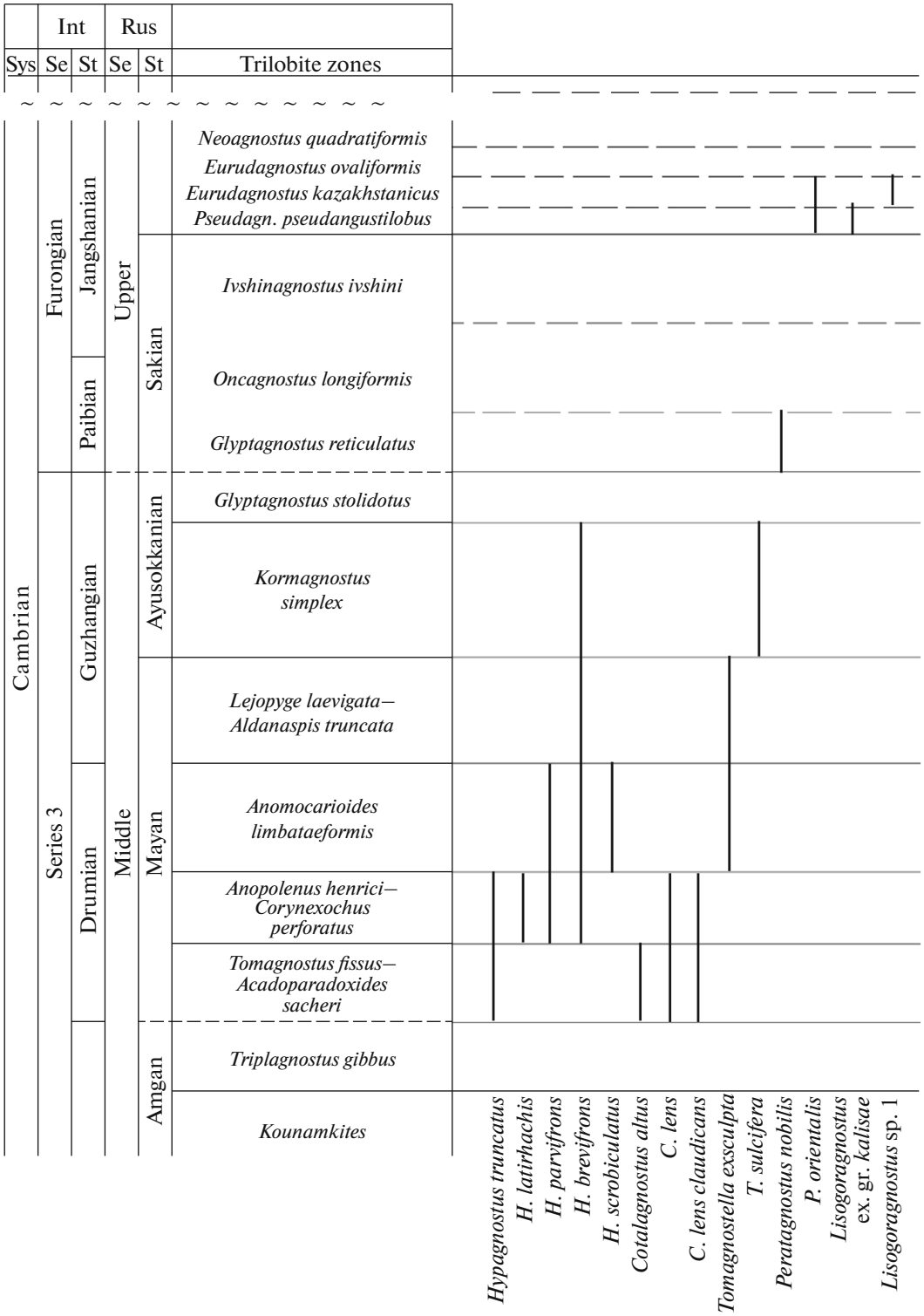
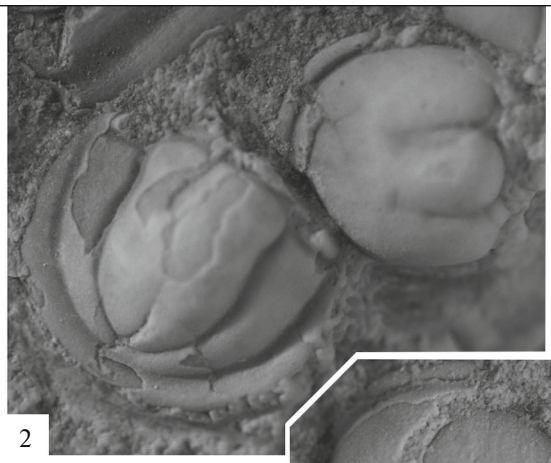


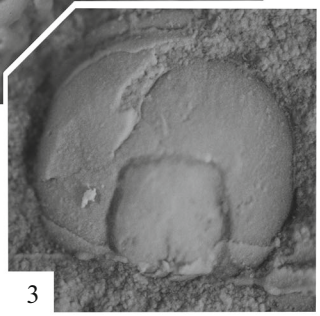
Fig. 7. Stratigraphic distribution of Spinagnostidae species known from Russia.

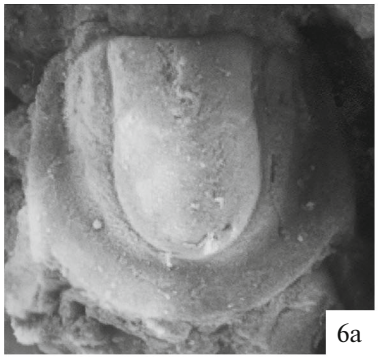
Species found in Russia. *H. truncatus* (Brögger, 1878)—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone (Pokrovskaya, 1960; Egorova et al., 1982; Pegel, 2000), lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone (Pokrovskaya, 1958); Lena River (middle reaches), Mayan Stage, *Liostracus allachjunensis* Zone; Yudoma River, *Tomagnostus fissus–Paradoxides hicksi* Zone (Pokrovskaya, 1958; Egorova et al., 1982); Botoma River, Mayan Stage, *Tomagnostus fissus–Par-*

Plate 6

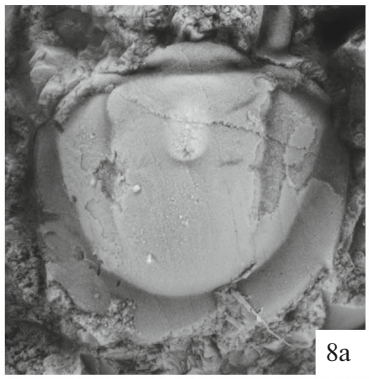

1

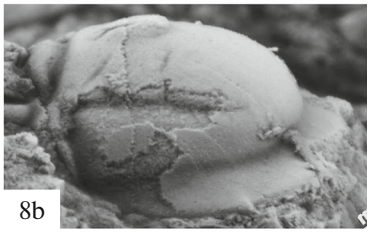

2

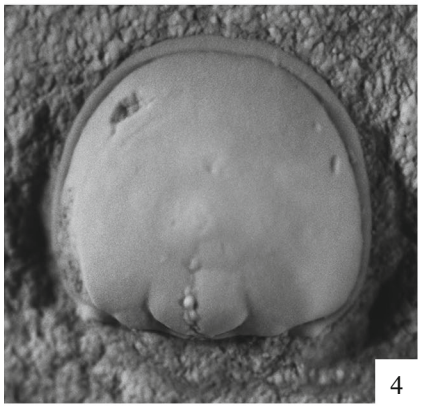

3


6a

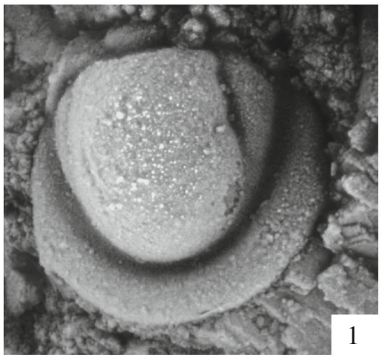

6b

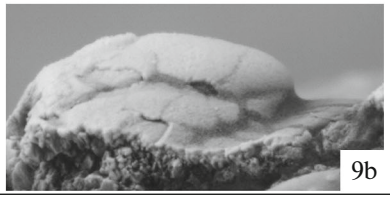

8a

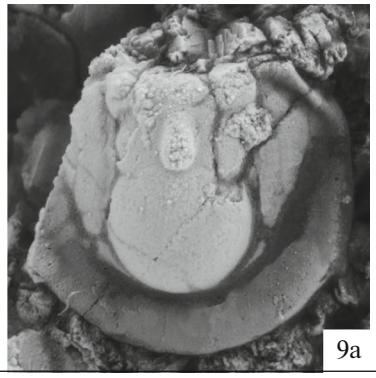

8b


4


5


1


9b


9a

adoxides hicksi and *Anopolenus henrici* zones (Pokrovskaya, 1958).

H. parvifrons (Linnarsson, 1869)—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone; Chabda River, Mayan Stage, *Anomocarioides limbataeformis* Zone (Egorova et al., 1982).

H. brevifrons (Angelin, 1851)—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone; Chabda River, Mayan Stage, *Anopolenus henrici*, *Anomocarioides limbataeformis* and *Aldanaspis truncata* zones (Egorova et al., 1982 as *H. facetus*); Kharaulakh Mountains, Khos-Nelege River, Mayan Stage, *Anopolenus henrici* and *Proagnostus bulbus* zones (Lazarenko et al., 2008a, 2008b). Altai-Sayany Folded Belt: Salair Ridge, Orlinaya Mountain, upper Middle Cambrian (Fedjanina, 1977, but not pl. 19, fig. 13); Altai Mountains, Bol'shaya Isha River, uppermost Middle Cambrian (Romanenko, 1977).

H. latirhachis (Lermontova, 1940)—Siberian Platform: Lena River (middle reaches), Middle Cambrian, *Paradoxides davidis* Zone (Lermontova, 1940).

H. scrobiculatus (Wallerius, 1895)—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Anomocarioides (?) curtus* Zone (Egorova et al., 1982).

Genus *Cotalagnostus* Whitehouse, 1936

Cotalagnostus: Whitehouse, 1936, p. 92; Kobayashi, 1939, p. 129; Lermontova, 1940, p. 129; Westergård, 1946, p. 53; Moore, 1959, p. O184; Robison, 1964, p. 528; Shergold et al., 1990, p. 43; Shergold and Laurie, 1997, p. 356; Ergaliev and Ergaliev, 2008, p. 132.

Type species. *Agnostus lens* Grönwall, 1902.

Diagnosis. Like *Hypagnostus,* but with glabellar F3 effaced and commonly with axial furrows surrounding posterior lobe of pygidial axis effaced (from Shergold and Laurie, 1997, p. 356).

Remarks. *Cotalagnostus globiceps* was mentioned by Lermontova as a provisional new species under consideration referred as "MS" (Lermontova, 1940). But she neither chose the type specimen among the three indicated ones (Lermontova, 1940, pl. 36, figs. 5, 5a, 5b), nor gave their good illustrations or accurate description. We did not find these three specimens in the collection, so there is no any possibility to recognize this species. Thus, this species should be considered as a *nomen nudum*.

Some specimens, which were defined previously as *Ciceragnostus cicer* (Egorova et al., 1982, pl. 18, fig. 1, pl. 19, fig. 4, pl. 23, fig. 3), we questionably referred to *Cotalagnostus* (see remarks to *Phaldagnostus*).

Species found in Russia. *Cotalagnostus lens* (Grönwall, 1902)—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Liostracus allachjunensis* Zone, *Triplagnostus lundgreni* Subzone; Yudoma River, lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone; Maya River, Mayan Stage, *Anopolenus henrici* Zone (Egorova et al., 1982).

C. lens claudicans Westergård, 1946—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Liostracus allachjunensis* Zone (Mayan Stage, *Anopolenus henrici* Subzone); Yudoma River, lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone, Maya River, Mayan Stage, *Anopolenus henrici* Zone (Egorova et al., 1982).

C. altus Grönwall, 1902—Siberian Platform: Maya River, Middle Cambrian (Pokrovskaya, 1960).

Cotalagnostus sp. 1—Siberian Platform: Maya River, *Anopolenus henrici* and *Anomocarioides limbataeformis* zones (Egorova et al., 1982, pl. 18, fig. 1, pl. 19, fig. 4, pl. 23, fig. 3 as *Ciceragnostus cicer*).

Genus *Tomagnostella* Kobayashi, 1939

Tomagnostella: Kobayashi, 1939, p. 150; Moore, 1959, p. O186; Öpik, 1963, p. 34; 1967, p. 81; 1979, p. 71; Robison, 1988, p. 51; Shergold et al., 1990, p. 44; Pratt, 1992, p. 40; Shergold and Laurie, 1997, p. 358; Peng and Robison, 2000, p. 84; Ergaliev and Ergaliev, 2008, p. 128; Peng et al., 2009, p. 23.

Explanation of Plate 6

Spinagnostidae, Peronopsidae, and Ammagnostidae

Fig. 1. *Hypagnostus brevifrons* (Linnarsson, 1969), TsNIGR, no. 4/10112, dorsal shield, 2.5 mm long (Egorova et al., 1982, pl. 42, fig. 4 as the holotype shield (late meraspis) of *Hypagnostus facetus*); Siberian Platform, Chabda River, loc. C-24.

Figs. 2 and 3. *Hypagnostus latirhachis* Lermontova, 1940: (2) lectotype TsNIGR, no. 64/9182, cephalon and pygidium, 2.6 and 3.1 mm long, respectively (Lermontova, 1940, pl. XXXVI, fig. 4); Sinsky Region; (3)TsNIGR, no. 66/9182, juvenile cephalon, 1.7 mm long, Botoma Region (Lermontova, 1940, pl. XXXVI, fig. 4a); Siberian Platform, Lena River (middle reaches).

Figs. 4 and 5. *Peratagnostus orientalis* (Lazarenko, 1966): (4) holotype TsNIGR, no. 1/8907, cephalon, 2.9 mm long, loc. 7 (Lazarenko, 1966, pl. I, fig. 1); (5) TsNIGR, no. 2/8907, pygidium, 2.0 mm long, loc. 137 (Lazarenko, 1966, pl. I, fig. 2 as paratype of *Cyclopagnostus orientalis*); northeastern Siberian Platform, Kjutjungde trough, Khoyguollakh Spring.

Fig. 6. *Ammagnostus simplexiformis* (Rosova, 1964), (6a) holotype TsSGM, no. 556/113, pygidium (plan view), 2.7 mm long (Rosova, 1964, pl. 13, fig. 9); (6b) lateral view; northwestern Siberian Platform, Kulyumbe River, loc. P-10.

Fig. 7. *Kormagnostus seclusus* (Walcott, 1884), TsSGM, no. 814/113, pygidium, 1.6 mm long (Rosova, 1964, pl. 16, fig. 9); northwestern Siberian Platform, Kulyumbe River, loc. P-12.

Fig. 8. *Connagnostus fritzi* Pratt, 1992, TsSGM, no. 1008/814, pygidium, 3.4 mm long (Rosova, 1964, pl. 16, fig. 6): (8a) plan and (8b) lateral views; northwestern Siberian Platform, Kulyumbe River, loc. P-12.

Fig. 9. *Kormagnostus beltensis* (Lochman in Lochman and Duncan, 1944), TsSGM, no. 814/1000, pygidium, 4.7 mm long (Rosova, 1964, pl. 16, fig. 6): (9a) plan and (9b) lateral views; northwestern Siberian Platform, Kulyumbe River, loc. P-12.

Type species. *Agnostus exsculptus* Angelin, 1851.

Diagnosis. Weakly scrobiculate, median preglabellar furrow weakly developed or as weak indentation at front outline of acrolobe; border and border furrow narrow, F3 present, F2, F1 as notches at glabellar flanks, glabellar node at about F2. Pygidium constricted across M2, F1, F2 developed, deflected by node, axial node comparatively large.

Species found in Russia. *T. exsculpta* (Angelin, 1851)—Siberian Platform: Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2000, 2014); Maya and Chabda rivers, Mayan Stage, *Anomocarioides limbataeformis* and *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982 as *Hypagnostus exsculptus* (Angelin, 1851)).

T. sulcifera (Wallerius, 1895)—Altai-Sayany Folded Belt: northeastern Altai Mountains, Bol'shaya Isha River, uppermost Middle Cambrian (Romanenko, 1977 as *H. exsculptus*); northwestern Kuznetsky Alatau, Kazennaya Vasil'evka River, Sakian Stage, *Glyptagnostus reticulatus* Zone, Ust'-Kul'bich Horizon (Petrunina and Gabova, 2008 as *Tomagnostella* cf. *sulcifera*).

Genus *Peratagnostus* Öpik, 1967

Plate 6, figs. 4 and 5

Peratagnostus: Öpik, 1967, p. 87; Palmer, 1968, p. B26; Shergold, 1980, p. 23; 1982, p. 21; Shergold et al., 1990, p. 43; Pratt, 1992, p. 40; Robison, 1994, p. 65; Shergold and Laurie, 1997, p. 357; Peng and Robison, 2000, p. 92; Choi et al., 2004, p. 185; Ergaliev and Ergaliev, 2008, p. 132.

Type species. *Peratagnostus nobilis* Öpik, 1967.

Diagnosis. Almost completely effaced, cephalic border absent or narrow, pygidial border moderately wide, nonspinose; both border furrows narrow if present. Glabella discernible by vestigial relief and faint axial furrow at rear of posteroglabella, pygidial axis outlined with very faint furrows (or they effaced) and with median node; axis not reaching border furrow.

Remarks. *Peratagnostus orientalis* (Lazarenko, 1966) shows the resemblance to *P. nobilis*. It differs, however, in the presence of a cephalic border, which usually absent in the species of *Peratagnostus*. Following the formal generic diagnoses would address this species to *Cotalagnostus,* but the overall cephalic constitution of the species does not fit the peronopsid habitus of *Cotalagnostus*. Therefore, we emended the *Peratagnostus* diagnosis to include *P. orientalis*. *P. orientalis* corresponds well to *P. hillardensis* Palmer, 1968. Pratt (1992) synonymized *P. hillardensis* with *P. nobilis,* but did not explain the difference in the cephalic border condition, although this feature has been ranked as the generic definition (Öpik, 1967). Therefore, we consider this synonymy inconsistent, and *P. orientalis* is a valid species and its junior synonym is *P. hillardensis*. *P. orientalis* is therefore found in Siberia and Alaska (*Elvinia* Zone, lower Franconian fauna).

Peratagnostus sp. from northern Siberian, Chopko River known by three destroyed pygidia (Varlamov et al., 2005, pl. 1, figs. 11–13) may represent other effaced genera, that is, *Toragnostus, Pseudophalacroma,* and *Skryjagnostus*.

Species found in Russia. *Peratagnostus nobilis* Öpik, 1967—Siberian Platform: Chopko River, Sakian Stage, *Erixanium sentum* Zone (Varlamov and Rosova, 2009 as *Peratagnostus* aff. *nobilis*).

P. orientalis (Lazarenko, 1966)—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Sakian Stage, *Eugonocare (Pseudeugonocare) borealis* and *Maladioidella abdita* zones (Pegel, 2000; Lazarenko et al., 2008a, 2008b), downstream of the Lena River near the village of Chekurovka, Sakian Stage, *Irvingella–Cedarellus felix (=Maladioidella abdita)* zones (Lazarenko, 1966 as *Cyclopagnostus orientalis*).

Peratagnostus sp.—Siberian Platform: Chopko River, Sakian Stage, *Glyptagnostus reticulatus* Zone (upper part), beds with *Erixanium sentum* (Varlamov et al., 2005), Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010, 2014).

Genus *Lisogoragnostus* Rosova in Lisogor et al., 1988

Lisogoragnostus: Lisogor et al., 1988, p. 64; Shergold et al., 1990, p. 58; Shergold and Laurie, 1997, p. 381; Peng and Robison, 2000, p. 64 (see synonymy); Jago and Brown, 2001, p. 8; Hong et al., 2003, p. 897; Choi et al., 2004, p. 185; Ergaliev and Ergaliev, 2008, p. 220.

Type species. *Lisogoragnostus kalisae* Rosova, 1988.

Diagnosis. Cephalon partly effaced, with vestigial basal lobes and glabellar culmination, well defined border furrow. Pygidium in holaspids apparently lacking border furrow or it extremely narrow, with wide, short (approximately half pygidium length), more or less tumid axis bearing low axial node placed anteriorly; F1 and F2 completely absent.

Remarks. Peng and Robison (2000, pp. 64–65) discussed the genus in detail, but one missed representative of the genus should be taken into consideration. This is Agnostinarum gen. et sp. indet. described by Shergold and Sdzuy (1984, p. 73, pl. 3, fig. 31). This form was found in central Turkey, Sultan Dag, from the Upper Cambrian beds (with *Homagnostus* and *Pseudagnostus cyclopyge*). This specimen has a very small convex cephalon with a convex border and narrow border furrow and effaced anteroglabella. This cephalon resembles *L. hybus* Peng *et* Robison, 2000 by the proportions of the glabellar parts; the specimen from Turkey extends the geographical range of the species and genus.

Phalagnostus shergoldi Pratt, 1992 corresponds to the diagnosis and the overall habitus of *Lisogoragnos-*

tus (Peng and Robison, 2000). Adding to extended discussion of Peng and Robison, we note that this species is based on juvenile specimens, with the holotype representing meraspid degree 1 (Pratt, 1992, pl. 7, fig. 29). This follows from both the original figures and description of this species (Pratt, 1992, p. 44): "faint oblique furrows crossing the anterior portions of the pygidial acrolobes, but they are not readily visible on most specimens..." The feature mentioned in this line inevitably refers us to meraspid degrees in agnostids (Naimark, 2006, 2007, 2008). If this inference is correct, than *L. shergoldi* would become a junior synonym of *L. minor* (Kobayashi, 1962); the description of this latter species has been complemented by Choi et al. (2004) with the species' cephalic characters. These authors distinguished *L. minor* from *L. shergoldi* only by these anterolateral oblique furrows.

When the genus *Lisogoragnostus* was first established by Rosova, she mentioned two species for this genus; one is the type species *L. kalisae* and the second is *L. egorovae*. Rosova indicated two specimens for this second species, as Egorova et al. (1982, pl. 4, fig. 13, pl. 5, fig. 3), both from the Yudoma River, *Tomagnostus fissus* Zone. But she gave neither a description nor differential diagnosis for this new species. Thus, the species appeared to be invalid according to the *International Code* (1999, Art. 13.1.1). This form is close to *L. minor* in having cephalon without border, highly effaced cephalic axial furrow, and cephalic acrolobe with equal length and width; it differs from *L. mictus* Peng et Robison, 2000 in the narrower cephalic acrolobe. More material is needed to compare it with *L. minor*. In Korea, this species was found in younger strata, in the *Agnostotes orientalis* Zone (Lee and Choi, 1995; Choi et al., 2004).

Species found in Russia. *Lisogoragnostus* ex gr. *kalisae* Rosova, 1988—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Sakian Stage, *Maladioidella abdita* Zone (Lazarenko et al., 2008a as *Lisogoragnostus* cf. *kalisae*); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2000; 2010 as *Lisogoragnostus sp.*).

Lisogoragnostus sp. 1—Siberian Platform, Khos-Nelege River, Aksayan Stage, *Plicatolina perlata* Zone (Lazarenko et al., 2008a as *Lisogoragnostus sp.*).

L. ?minor—Yudoma River, *Tomagnostus fissus* Zone (Egorova et al., 1982, pl. 4, fig. 13, pl. 5 as *Phalacroma calva*).

Family Doryagnostidae Shergold and Laurie et Sun, 1990

Diagnosis. En grand tenue, nonscrobiculate, borders narrow to moderate; border furrows narrow to moderate. Cephalon with median preglabellar furrow variably expressed, but commonly present, basal lobes small. Pygidium bispinose; axis triangular or unexpanded posteroaxis; F1, F2 undeveloped but with transverse variably expressed depression; postaxial furrow commonly present.

Genus *Doryagnostus* Kobayashi, 1939

Doryagnostus: Peng and Robison, 2000, p. 58 (see synonymy except *Rhodotypiscus* Öpik, 1979); Ergaliev and Ergaliev, 2008, p. 140.

Type species. *Agnostus incertus* Brögger, 1878.

Diagnosis. Cephalon and pygidium semiovate or semicircular; median preglabellar furrow well developed, expanding into deltoid area anteriorly, anteroglabella ogival, posterior lobe slightly expanded at rear; F2 weakly developed.

Species found in Russia. *D. incertus* (Brögger, 1878)—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* and *Anomocarioides limbataeformis* zones (Egorova et al., 1982).

Genus *Euagnostus* Whitehouse, 1936

Euagnostus: Whitehouse, 1936, p. 87; Moore, 1959, p. O184; Öpik, 1979, p. 74; Shergold et al., 1990, p. 43; Shergold and Laurie, 1997, p. 356; Laurie, 2004, p. 245; Naimark, 2012, p. 1009.

Type species. *Euagnostus opimus* Whitehouse, 1936.

Diagnosis. Cephalon semiovate to subquadrate, with narrow border structures; glabella bipartite, with rounded anteroglabella partly or almost fully effaced; basal lobes small to moderate. Pygidium subquadrate, with narrow or moderate border structures, minutely bispinose; axis conical or with parallel sides, posteroaxis not expanded; F1, F2 as very short lateral grooves, posteroaxis not reaching border furrow; postaxial furrow usually present, but may be effaced in large holaspids.

Species found in Russia. *E. opimus* Whitehouse, 1936—Siberian Platform: Lena River (middle reaches), lowermost Mayan Stage, *Tomagnostus fissus* Zone (Egorova et al., 1982 as *Hypagnostus tessella*).

Euagnostus aff. *opimus*—Siberian Platform: Yudoma River, lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone, Maspakiyskiy key horizon (Egorova et al., 1982, pl. 4, fig. 2 as *Peronopsis* ex gr. *fallax*); Daldyn–Alakit Region, Amgan Stage, *Kounamkites* Zone (Ogienko and Garina, 2001, pl. 2, fig. 14 as *Peronopsis scutalis*).

Family Ammagnostidae Öpik, 1967

Diagnosis. Agnostoids with deliquiate cephalic and pygidial border furrows; cephalon with incomplete median preglabellar furrow or sometimes it completely effaced; pygidial posteroaxis long and variably expanded; transverse F1 and F2 variably developed;

median node relatively large, rounded in shape; pygidial border bispinose.

The summary of stratigraphic distribution for Ammagnostidae from Russia is shown in Fig. 8.

Genus *Ammagnostus* Öpik, 1967

Plate 6, fig. 6; Plate 7, figs. 1–5

Ammagnostus: Öpik, 1967, p. 138; Peng and Robison, 2000 (see for additional synonymy); Ergaliev and Ergaliev, 2008, p. 67; Peng et al., 2009, p. 14; Naimark, 2012, p. 1010.

Type species. *Ammagnostus psammius* Öpik, 1967.

Diagnosis. Cephalon with incomplete or absent preglabellar furrow, transglabellar F3 bent slightly backward, F2 well developed, median node in mid–length of posterior lobe, posterior lobe rounded at rear. Pygidium subcircular to ovoid; posteroaxis subcylindrical to weakly pisiform; F1, F2 variably developed, secondary node usually present.

Remarks. We refer *Connagnostus tandoshkensis* E. Romanenko, 1970 to *Ammagnostus,* because all generic diagnostic characters are present in this species. Those are glabellar F3 bowed backward, wide border and border furrow on the cephalon, expanded pygidial posteroaxis, and weak F1 and F2 on the pygidial axis. These characters contradict the diagnosis of *Connagnostus*. The only *connagnostus'* character is the long median node on the cephalon, but the position of the node in *Ammagnostus* may actually be variable.

After the revision of the type material, *Peronopsis crassa* Lermontova, 1940 was reassigned to *Ammagnostus* as it possesses all generic diagnostic characters. The type collection contains a complete shield (holotype), external mold of a shield, and a separate cephalon; all specimens are very poorly preserved. Of these specimens, the cephalon may represent another species, but other two resemble *A. histus* Peng et Robison, 2000, although due to obscure morphology of given specimens, we cannot compare these species with sufficient confidence.

The specimens originally assigned to *"Agnostus" simplexiformis* were revised and refigured (here Pl. 6, figs. 6–9). There are four different species in the collection combined under this specific name; thus, only the holotype is referred to this species. Its generic identification meets better the *Ammagnostus*' criteria, although there are no cephala for this species in the type collection. Rosova erroneously mentioned the cranidium to be the holotype, but both the image and specimen under the reference number in the collection is the same pygidium. Its specific characters are the same as for *Ammagnostus wangcunensis* Peng et Robison, 2000. The authors of this species suggested provisional synonymy with *A. simplexiformis* with the priority of the latter, but left this question open until *A. simplexiformis* could be restudied. Here we agree with this synonymy.

We identified the second species of the ensemble of *"Agnostus" simplexiformis* as *Kormagnostus seclusus* (Walcott, 1884), the third as *Kormagnostus beltensis* (Lochman in Lochman and Duncan, 1944), and the fourth as *Connagnostus fritzi* Pratt, 1992, and illustrated them here in Pl. 6, figs. 7–9.

Species found in Russia. *Ammagnostus psammius* Öpik, 1967—Siberian Platform, Kulyumbe River, Sakian Stage, *Faciura–Garbiella* Zone. Novaya Zemlya, Upper Cambrian (Lazarenko and Nikiforov, 1968 as *Agnostus ?holtedahli* Walcott et Resser, 1924).

A. laiwuensis—Siberian Platform: Lena River (middle reaches), Middle Cambrian, *Paradoxides davidis* Zone (Lermontova, 1940, pl. 36, fig. 1c, as *P. fallax*); Kulyumbe River, upper *Pedinocephalina–Toxotis* Zone (Lazarenko and Nikiforov, 1968 as *Baltagnostus* (?) sp.); Anabar Anticline, Yurung–Tas–Suluda River, Mayan Stage, *Hatangia* and *Proasaphiscus privus* zones (Egorova and Savitzkiy, 1969, pl. 6, figs. 2–7 as *Peronopsis* ex gr. *fallax*). Altai-Sayany Folded Belt, Altai Mountains, Verkhnyaya Elanda River, Mayan Stage (in the same slab with the holotype of *A. jegorovae*).

A. jegorovae (Romanenko, 1985)—Altai-Sayany Folded Belt, Altai Mountains, Verkhnyaya Elanda River, Mayan Stage, *Anopolenus henrici* Zone (Romanenko, 1985 as *Peronopsis jegorovae*).

A. tandoshkensis (E. Romanenko, 1970)—Altai-Sayany Folded Belt: northwestern Kuznetsky Alatau, lower Upper Cambrian (Ust'-Kul'bich Horizon) (Petrunina and Gabova, 2008 as *Connagnostus* cf. *tandoshkensis*); Altai Mountains, Tandoshka, and Tagaza rivers, upper Middle Cambrian (upper Mayan Stage), lower Upper Cambrian (Poletaeva and Romanenko, 1970 as *Connagnostus tandoshkensis*).

A. bassa Öpik, 1967—Siberian Platform: Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010).

A. crassa (Lermontova, 1940)—Altai-Sayany Folded Belt: Salair Ridge, Orlinaya Mountain, upper Middle Cambrian (Lermontova, 1940, pl. 36, figs. 2, 2a as *Peronopsis crassa;* here Pl. 7, figs. 1, 2).

A. adchinensis (Schrank, 1975)—Siberian Platform: Aldan River, near the Kerbi River mouth, Ayusokkanian Stage, *Toxotis venustus* and *Maspakites* zones, beds with *Plethopeltoides kulyumbensis* (Gogin and Pegel, 1997 as *Agnostus (?) simplexiformis* Rosova, 1964, as *Homagnostus fusus* E. Romanenko, 1988). Altai-Sayany Folded Belt: Altai Mountains, Isha River, lowermost Sakian Stage, *Glyptagnostus reticulatus* Zone (Romanenko, 1988 as *Homagnostus fusus*).

A. simplexiformis (Rosova, 1964)—Siberian Platform: Kulyumbe River, Ayusokkanian Stage, Sakhaisky Horizon (Rosova, 1964, pl. 13, fig. 9 as *Agnostus simplexiformis*); Kharaulakh Mountains, Khos-Nelege River, Ayusokkanian Stage, *Clavagnostus spinosus* Zone (Lazarenko et al., 2008a as *Ammag-*

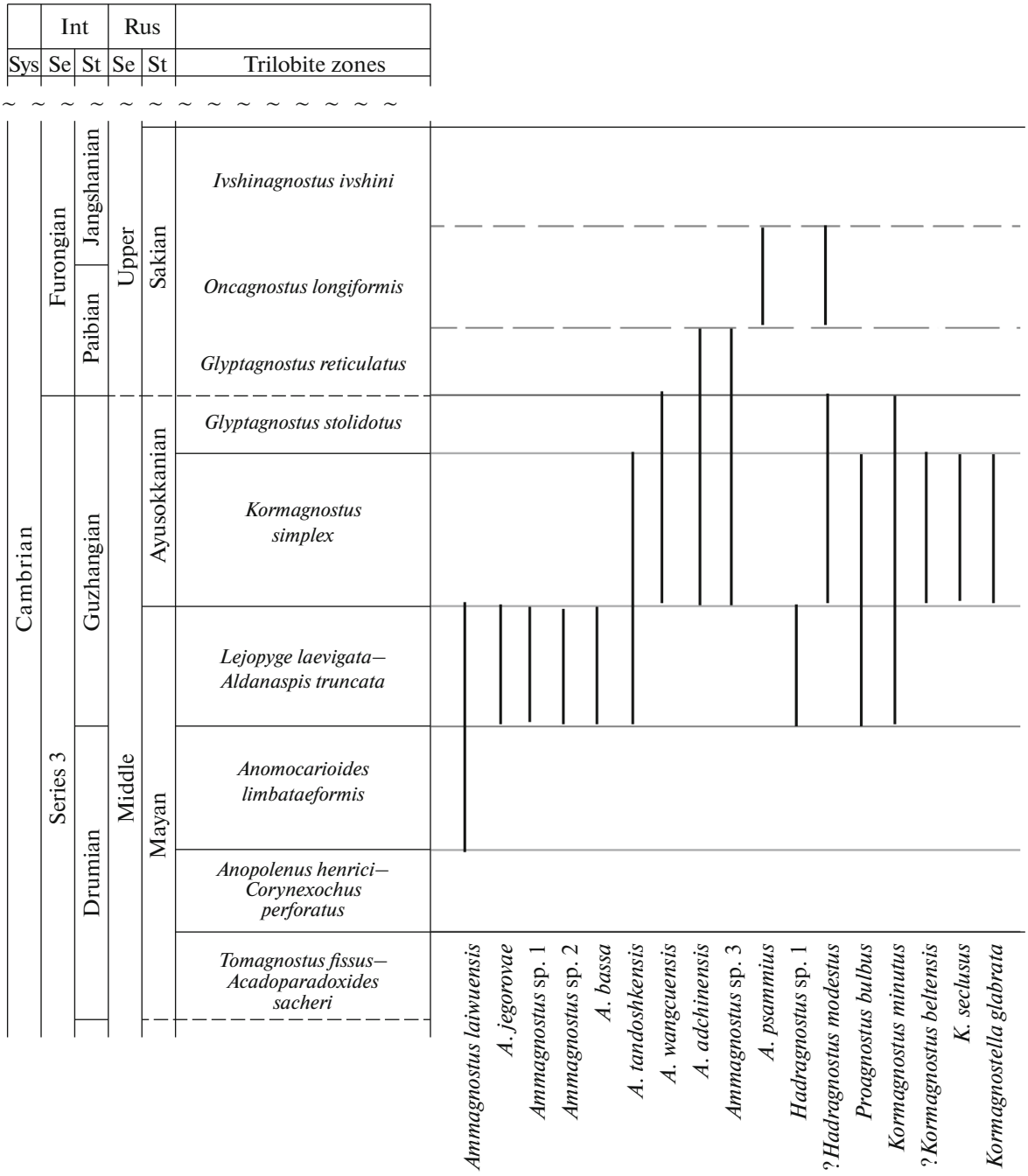


Fig. 8. Stratigraphic distribution of Ammagnostidae species known from Russia.

nostus (A.) cf. *wangcunensis*, as *Ammagnostus psammius,* pl. 14, fig. 24).

Ammagnostus sp. 1—Siberian Platform: Chabda River, Mayan Stage, *Leopyge laevigata–Aldanaspis truncata* Zone (Egorova et al., 1982, pl. 41 figs. 3–5, 11 as *Peronopsis fallax*).

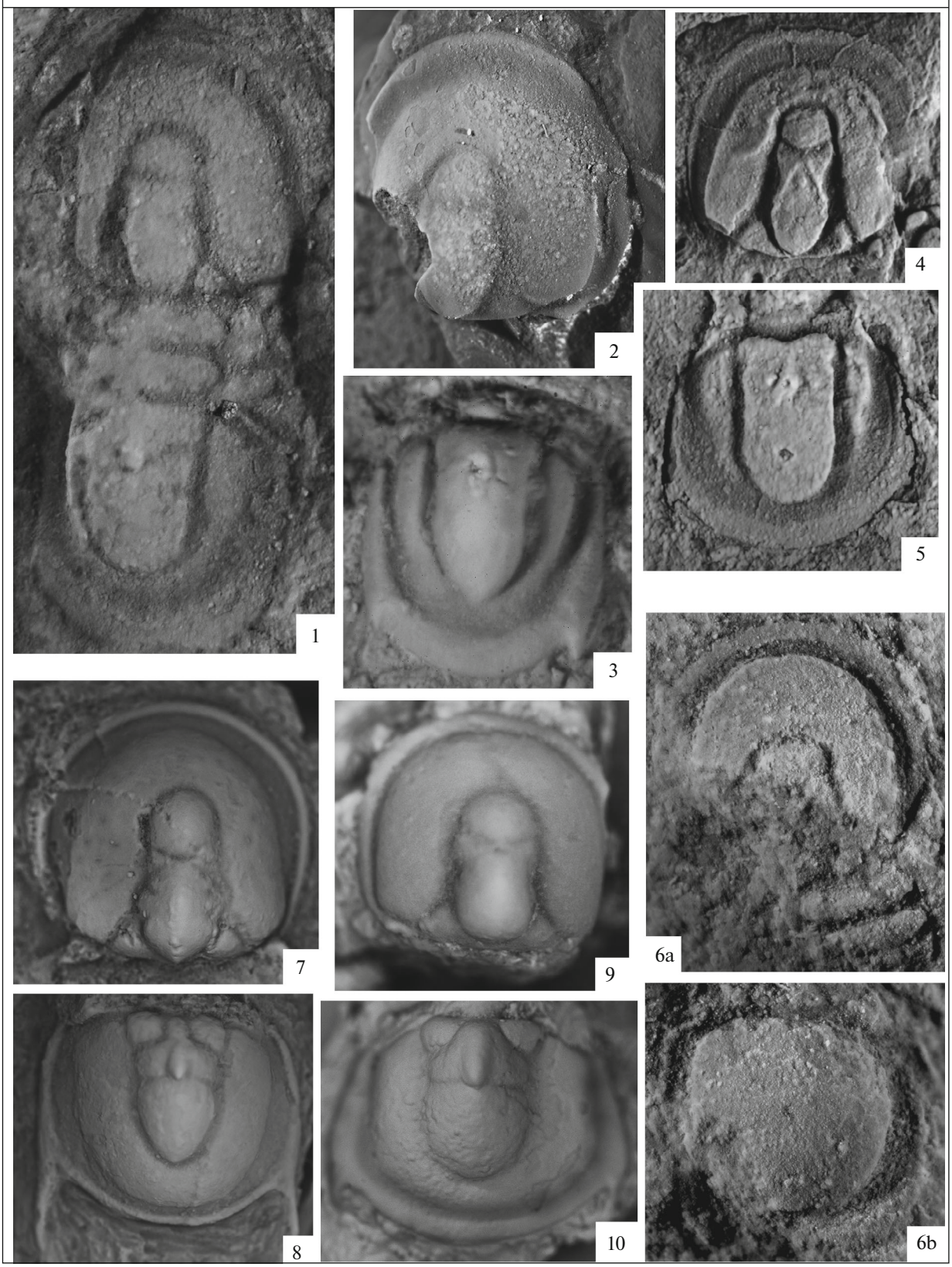
Ammagnostus sp. 2—Altai-Sayany Folded Belt: Altai Mountains, Verkhnyaya Elanda River, Middle Cambrian (Egorova et al., 1955, pl. 11, fig. 1b as *Peronopsis* ex gr. *fallax*).

Ammagnostus sp. 3—Siberian Platform: Kulyumbe River, Ayusokkanian and lowermost Sakian stages, *Pedinocephalina–Toxotis* and *Maspakites–Idahoia–Raashellina* zones (Lazarenko and Nikiforov, 1968 as *Agnostus (?)* aff. *simplexiformis* Rosova, 1964).

Genus *Hadragnostus* Öpik, 1967

Hadragnostus: Peng and Robison , 2000, p. 30 (see synonymy list, except *Formosagnostus* Ergaliev, 1980); Ergaliev and Ergaliev, 2008, p. 79.

Plate 7



Type species. *Hadragnostus las* Öpik, 1967.

Diagnosis. Cephalon and pygidium en grande tenue, with subdeliquiate border furrows and narrow border in cephalon and moderately wide in pygidium; median preglabellar furrow wide and short; glabella relatively long, with short subtriangular or ogival anterior lobe; F2 weakly developed, glabellar node absent. Pygidium bispinose; pygidial axis tapering forwards from middle of posterior lobe; constriction across M2 weak or absent; F1, F2 effaced, terminal node sometimes present.

Species found in Russia. *Hadragnostus* sp. 1—Altai-Sayany Folded Belt: Altai Mountains, Verkhnyaya Elanda River, Middle Cambrian, Orlinogorskii assemblage horizon (Egorova et al., 1955, pl. 11, figs. 1a, 1c as *Peronopsis* ex. gr. *fallax*).

H.? modestus (Lochman, 1944)—Siberian Platform: Sette–Daban Ridge, Aldan River near the Kerbi River mouth, lowermost Sakian Stage, beds with *Plethopeltoides kulyumbensis* (Gogin and Pegel, 1997 as *Homagnostus* sp.); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010, 2014 as *Pseudagnostus* sp.). Western Siberia, Tomsk Region, Vostok-1 well, Upper Cambrian, Sakian Stage, Entsiysky Horizon (Korovnikov et al., 2010 as *Pseudagnostus* sp.).

Genus *Proagnostus* Butts, 1926

Proagnostus: Peng and Robison, 2000, p. 35 (see synonymy list); Ergaliev and Ergaliev, 2008, p. 85; Peng et al., 2009, p. 14.

Type species. *Proagnostus bulbus* Butts, 1926.

Diagnosis. Ammagnostidae having cephalon with preglabellar furrow, acrolobe constricted, F3 straight or bent forwards, F2 developed, glabellar node in front of F2. Pygidium reaching border furrow, F1 and F2 effaced, axis constricted across M2.

Species found in Russia. *P. bulbus*—Siberian Platform: Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2010, 2014); Kharaulakh Mountains, Khos-Nelege River, uppermost Mayan Stage, *Proagnostus bulbus* Zone and lowermost Sakian Stage, *Clavagnostus spinosus* Zone (Pegel, 2000), (Lazarenko et al., 2008a), *Clavagnostus spinosus* Zone (Lazarenko et al., 2008a). Altai-Sayany Folded Belt: northeastern Altai Mountains, Bol'shaya Isha River, uppermost Mayan Stage (Romanenko, 1977 as *Homagnostus bulbus*).

Genus *Kormagnostus* Resser, 1938

Plate 6, figs. 7 and 9

Kormagnostus: Peng and Robison, 2000, p. 35 (see synonymy list, except *Kormagnostella* E. Romanenko); Ergaliev and Ergaliev, 2008, p. 85.

Type species. *Kormagnostus simplex* Resser, 1938.

Diagnosis. Ammagnostidae with anterior glabellar lobe more or less effaced; pygidial axis reaching border furrow, axial furrows fully outlining posteroaxis or effaced at rear, border commonly widened and flattened.

Species found in Russia. *?K. beltensis* (Lochman in Lochman and Duncan, 1944)—Siberian Platform: Sette–Daban Ridge, Aldan River (near the Kerbi River mouth), Ayusokkanian Stage, *Toxotis venustus* Zone (Gogin and Pegel, 1997 as *Ammagnostus psammius*); Kulyumbe River, Nganasansky Horizon (Rosova, 1964, pl. 16, fig. 6 as *"Agnostus" simplexiformis*; here Pl. 6, fig. 9)

K. minutus (Schrank, 1975)—Siberian Platform: Sette–Daban Ridge, Aldan River (near the Kerbi River mouth), Ayusokkanian Stage, *Maspakites* Zone (Gogin and Pegel, 1997 as gen. et sp. indet. 2); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2000, figs. 12: 6, 9; 2010; 2014 as gen. and sp. indet.);

Explanation of Plate 7

Ammagnostidae and Agnostidae.

Figs. 1 and 2. *Ammagnostus crassa* (Lermontova, 1940): (1) lectotype TsNIGR, no. 28/9182, dorsal shield, 8 mm long (Lermontova, 1940, pl. 36, fig. 2); (2) TsNIGR, no. 29/9182, cephalon (Lermontova, 1940, pl. 36, fig. 2a); Altai-Sayany Folded Belt, Salair Ridge, in the vicinity of Orlinaya Mountain.

Fig. 3. *Ammagnostus jegorovae* (Romanenko, 1985); holotype LFGI, no. 189/1595, pygidium, 1.8 mm long (Romanenko, 1985, pl. V, fig. 1 as *Peronopsis jegorovae*); Altai-Sayany Folded Belt, Altai Mountains, Verkhnyaya Elanda River.

Figs. 4 and 5. *Ammagnostus tandoshkensis* (E. Romanenko, 1970): (4) holotype LFGI, no. 21/1328, cephalon, 5 mm long (Poletaeva and Romanenko, 1970, pl. 10, fig. 13), Tagasa River, loc. 716; (5) LFGI, no. 20/1328, pygidium, 3.7 mm long (Poletaeva and Romanenko, 1970, pl. 10, figs. 14a, 14b); Altai-Sayany Folded Belt, Altai Mountains; Tandoshka River, loc. 625.

Fig. 6. *Kormagnostella glabrata* E. Romanenko, 1967; (6a and 6b) holotype TsSGM, no. 86/724, shield with slightly disjoined cephalon and pygidium, dorsal shield 4.7 mm long (Romanenko and Romanenko, 1967, pl. 1, fig. 23); Altai-Sayany Folded Belt, Altai Mountains, Kul'bich Spring. loc. 152.

Figs. 7 and 8. *Eurudagnostus grandis* Lermontova, 1951a. (7) holotype TsNIGR, no. 131/7350, cephalon, 5 mm long (Lermontova, 1951a, pl. 2, fig. 1); (8) TsNIGR, no. 102/7350, pygidium, 5.2 mm long (Lermontova, 1951a, pl. 2, fig. 2); Kazakhstan, Boshchekul' borehole.

Figs. 9 and 10. *Eurudagnostus chiushuensis* (Kobayashi, 1931): (9) TsNIGR, no. 10/7350, cephalon, 2.5 mm long (Lermontova, 1951a, pl. II, fig. 7); (10) TsNIGR, no. 11/7350, pygidium, 2.3 mm long (Lermontova, 1951a, pl. II, fig. 5); Kazakhstan, Boshchekul' borehole.

Kharaulakh Mountains, Khos-Nelege River, uppermost Mayan Stage, upper *Proagnostus bulbus* Zone and Ayusokkanian Stage, *Clavagnostus spinosus* Zone (Lazarenko et al., 2008b).

K. seclusus (Walcott, 1884)—northwestern Siberian Platform: Igarka Region, Kulyumbe River, Ayusokkanian Stage, Nganasansky Horizon (Rosova, 1964, pl. 1, fig. 10 as "*Agnostus*" *simplexiformis* Rosova, 1964; here Pl. 6, fig. 7); Norilsk Region, Chopko River, Ayusokkanian Stage, Nganasansky Horizon (Rosova, 1977).

Genus *Kormagnostella* E. Romanenko, 1967

Plate 7, fig. 7

Kormagnostella: Romanenko and Romanenko, 1967, p. 74; Shergold, 1982, p. 24; Shergold et al., 1990, p. 36; Shergold and Webers, 1992, p. 133; Cooper et al., 1996, p. 369; Shergold and Laurie, 1997, p. 345; Ergaliev and Ergaliev, 2008, p. 82; Westrop and Adrain, 2013, p. 808.

Type species. *Kormagnostella glabrata* E. Romanenko, 1967.

Diagnosis. Cephalon and pygidium subquadrate, convex acrolobes; anteroglabella completely effaced; glabellar F3 straight, posteroglabella with parallel sides. Pygidial axial furrows effaced; median node large and rounded; border furrow deliquiate, border wide, nonspinose.

Species found in Russia. *Kormagnostella glabrata* E. Romanenko, 1967—Altai-Sayany Folded Belt, Altai Mountains, Kul'bich Spring, lower Upper Cambrian (Romanenko and Romanenko, 1967).

Family Agnostidae M'Coy, 1849

Diagnosis. Agnostids with comparatively short pygidial posteroaxis, deliquiate or nondeliquiate pygidial border furrow, and usually narrow border; transaxial F1 and F2 well developed. Cephalon with preglabellar furrow variably developed. Pygidium with small spines.

Remarks. Generic identification within the family is based upon the following characters: presence or absence of the median preglabellar furrow, the length of the pygidial axis, presence or absence of the lanceolate field on the posteroaxis, the shape and subdivision of pygidial M1, and the shape of border furrows both in cephalon and pygidium. Of these characters, the former and the latter seem to be the most concervative. The former is the development of a preglabellar furrow; it may display intraspecies variation and varies between two marginal points, while the latter one stays more or less constant. Other characters change due to the mode of preservation or/and growth stage or/and geographical variations.

This set of diagnostic characters represents the essence from the diagnoses of all valid genera established to the date. It helped to construct more accurate generic diagnoses with reestablishing *Eurudagnostus* Lermontova, 1951 and placing *Barrandagnostus* to the correct position between other Agnostidae. The obtained set of genera does not have any phylogenetic sense, as the diagnoses include both meaningful and formal characteristics, but it helps to review and order the diversity of known species (for detailed discussion, see Naimark, 2014).

Here we summarize some diagnostic characteristics of genera in this complicated cluster of Agnostidae to get a clearer view (Table 2).

The summary of stratigraphic distribution for Agnostidae from Russia is shown in Fig. 9.

Genus *Agnostus* Brongniart, 1822

Agnostus: Jaekel, 1909, p. 399; Westergård, 1946, p. 68; Moore, 1959, p. O172; Pokrovskaya, 1960, p. 68; Egorova et al., 1960, p. 159; Öpik, 1961a, p. 74; Palmer, 1962, p. F12; Öpik, 1967, p. 95; Pratt, 1992, p. 26; Robison, 1994, p. 29; Nielsen, 1997, p. 466; Buchholz, 1999, p. 239; Ergaliev and Ergaliev, 2008, p. 32.

Agnostus (Agnostus): Shergold et al., 1990, p. 33; Shergold and Laurie, 1997, p. 339; Peng and Robison, 2000, p. 11.

Type species. *Enthomostracites pisiformis* Wahlenberg, 1818.

Diagnosis. En grande tenue, narrow borders and moderate border furrows in cephalon and pygidium. Cephalon with ogival or rounded anteroglabella; basal lobes simple, moderate to large in size, posterior lobe rounded at rear, preglabellar furrow full or effaced partly anteriorly; F2 expressed. Pygidium with axis not reaching border furrow, with nonexpanded posteroaxis, F1, F2 weak, median node of moderate size, terminal node sometimes present.

Species found in Russia. *A. pater* Westergård, 1930—Bennett Island, Mayan Stage, *Paradoxides forchhammeri* Zone (Lermontova, 1940 as *Homagnostus pater*).

Agnostus pisiformis—Bennett Isl., Sakian Stage, *Glyptagnostus reticulatus* Zone (Danukalova et al., 2014, pl. 3, figs. 12, 13).

?Agnostus subsulcatus Westergård, 1946—central Russia, Yaroslavl Region, lower Upper Cambrian (Korobov and Yankauskas, 1982).

Genus *Homagnostus* Howell, 1935

Plate 8, figs. 6 and 7

Homagnostus: Howell, 1935b, p. 15; Kobayashi, 1939, p. 162; Whitehouse, 1939, p. 261; Lochman and Duncan, 1944, p. 139; Shaw, 1951, p. 110; Moore, 1959, p. O173; Palmer, 1960, p. 62; Robison, 1964, p. 531; Rushton, 1978, p. 259; Shergold and Sdzuy, 1984, p. 64; Robison, 1988, p. 33; Pratt, 1992, p. 27; Buchholz, 1999, p. 245; 2004b, p. 539; Peng and Robison, 2000, p. 13; Choi et al., 2004, p. 165; Ergaliev and Ergaliev, 2008, p. 33; Westrop and Eoff, 2012, p. 215.

Agnostus (Homagnostus): Shergold et al., 1990, p. 33; Shergold and Laurie, 1997, p. 339.

Type species. *Agnostus pisiformis* var. *obesus* Belt, 1867.

Diagnosis. En grande tenue, narrow borders and moderate border furrows in cephalon and pygid-

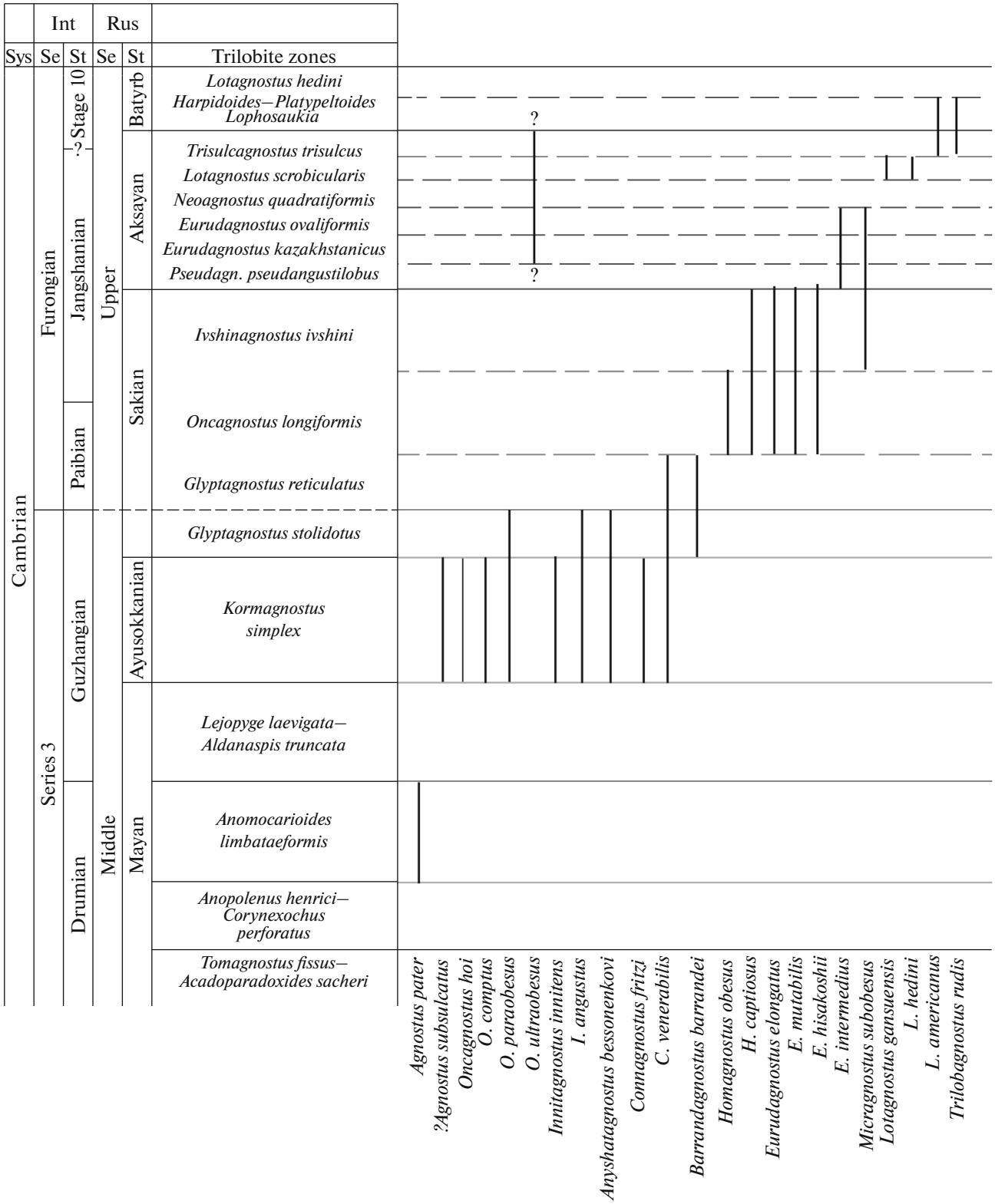


Fig. 9. Stratigraphic distribution of Spinagnostidae species known from Russia.

ium. Cephalon with ogival or rounded anteroglabella, basal lobes simple, moderate to large in size, preglabellar furrow full, F2 only weakly expressed, posterior lobe rounded at rear. Pygidium with long axis almost reaching border furrow, with relatively wide, usually expanded posteroaxis; F1 impressed on flanks and only occasionally impressed medially, F2 well developed; median node of moderate size.

Table 2. Diagnostic characteristics of some Agnostidae genera: preglabellar furrow (+) full, (±) incomplete, (–) absent; cephalic and pygidial border furrows deliquiate or nondeliquaite; length of pygidial axis short, moderate, long; M2: M1 > M2 < M3 (constricted), M1 > M2 > M3 (M1 > M2), M2 = M1 (unconstructed); lanceolate field on the posteroaxis (+) present or (–) absent; pygidial F1 full or appears as lateral parts, sometimes bent forward, otherwise straight

	Cephalon		Pygidium				
Feature / Genus	preglabellar furrow	border furrow	length of axis	shape of M2	lanceolate field	border furrow	shape of F1
Agnostus	±, +	deliq	short, moderate	unconstr	–	deliq	full, bent forwards
Lotagnostus	+	nondeliq	short, moderate	constr.	+	deliq	full or lateral parts
Eurudagnostus	–, ±	deliq	short	M1 > M2	–	deliq	lateral parts
Salagnostus	–, ±	deliq	short	M1 > M2	–	deliq	lateral parts
Micragnostus	–, ±	nondeliq	short	unconstr	–	moderate	lateral parts
Trilobagnostus	–	nondeliq	short	M1 > M2	–	deliq	full, bent forwards
Oncagnostus	–, ±	deliq	long	unconstr	–	deliq	lateral parts
Strictagnostus	–	deliq	short	M1 > M2	–	nondeliq	lateral parts
Acutatagnostus	±	nondeliq	long	constr	–	nondeliq	lateral parts
Homagnostus	±, +	nondeliq	long	unconstr	–	nondeliq	full or lateral parts
Innitagnostus	±, –	nondeliq	short, moderate	unconstr	–	nondeliq	full, bent forwards
Barrandagnostus	+	nondeliq	short, moderate	unconstr	–	nondeliq	full, bent forwards
Ivshinagnostus	–	deliq	short	M1 > M2	–	deliq	lateral parts
Anyshtagnostus	±	deliq	short	unconstr	–	deliq	lateral parts
?Aistagnostus	–	nondeliq	short	unconstr	–	nondeliq	full
?Connagnostus	–	nondeliq	long	unconstr	–	deliq	full

Species found in Russia. *H. obesus* (Belt, 1867)—Siberian Platform: Chopko River, Sakian Stage, beds with *Erixanium centum* (Varlamov and Rosova, 2009); Kharaulakh Mountains, lower part of Upper Cambrian (Lermontova, 1940); Sette–Daban Ridge, Aldan River (near the Kerbi River mouth), lower Sakian Stage, beds with *Plethopeltoides kulyumbensis* (Gogin and Pegel, 1997 as gen. et sp. indet. 1). Altai-Sayany Folded Belt: Altai Mountains, Kul'bich Spring, lower Upper Cambrian, Ust'-Kul'bichsky Horizon (Egorova et al., 1960).

Explanation of Plate 8

Agnostidae

Fig. 1. *Innitagnostus angustus* Pokrovskaya et Pegel, 1997; holotype TsNIGR, no. 1/12718, dorsal shield, 4 mm long (Gogin and Pegel, 1997, pl. 23, fig. 3); southeastern Siberian Platform, Aldan River (near the Kerbi River mouth), loc. P-7.

Figs. 2 and 3. *Barrandagnostus barrandei* Ivshin, 1960: (2) neotype LFGI, no. 19/2613, dorsal shield, 7.5 mm long (Petrunina and Gabova, 2008, pl. 2, fig. 4); Altai-Sayany Folded Belt, northeastern Altai Mountains, Kul'bich Spring, loc. 1219; (3) TsNIGR, no. 14/8378, dorsal shield, 5.5 mm long (Borovikov and Krys'kov, 1963, pl. I, fig. 13 as the holotype dorsal shield of *Tomagnostus tchatertensis*); southern Kazakhstan, Kendyktas Mountains, loc. 503.

Fig. 4. *Oncagnostus ultraobesus* (Lermontova, 1940); 4a) holotype TsNIGR, no. 36/9182, cephalon, 3.3 mm long (Lermontova, 1940, pl. 49, figs. 9, 9'): (4a) plan and (4b) lateral views; Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain.

Fig. 5. *Anyshtagnostus bessonenkovi* Petrunina, 2008; holotype LFGI, no. 26/2613, cephalon, 3.1 mm long (Petrunina and Gabova, 2008, pl. 2, fig. 11); Altai-Sayany Folded Belt, southern Salair Range, Anyshtaikha River, loc. 2100.

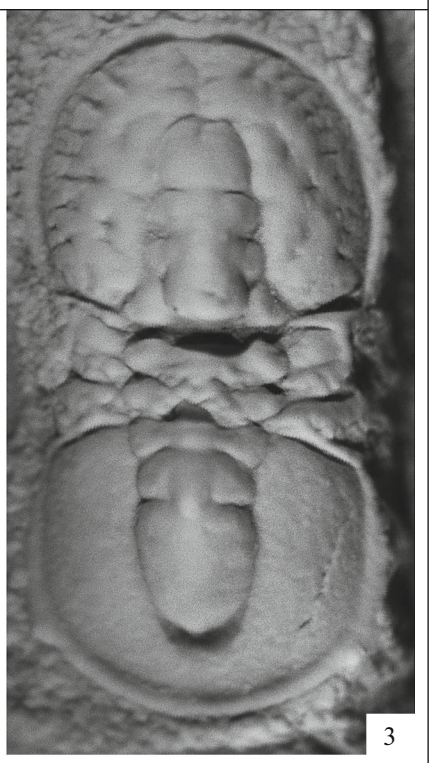
Figs. 6 and 7. *Homagnostus captiosus* (Lazarenko, 1966): (6) holotype TsNIGR, no. 13/8907, cephalon, 2.8 mm long (Lazarenko, 1966, pl. 1, fig. 13); (7) TsNIGR, no. 12/8907, pygidium, 2.6 mm long (Lazarenko, 1966, pl. 1, fig. 15); northeastern Siberian Platform, Kjutjungde trough, Khoyguollakh Spring.

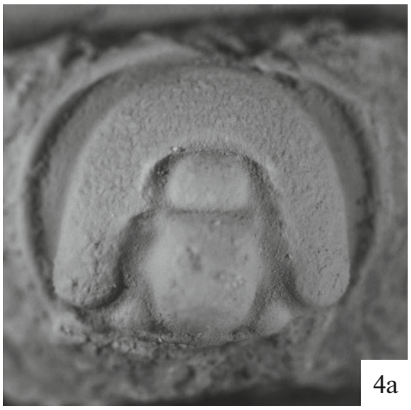
Fig. 8. *Ivshinagnostus intermedius* (Petrunina, 2008); holotype LFGI, no. 5/2613, dorsal shield, 7.0 mm long (Petrunina and Gabova, 2008, pl. I, fig. 5); Altai-Sayany Folded Belt, southern Salair Ridge, Anyshtaikha River, loc. 2100.

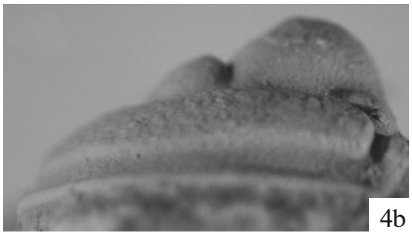
Plate 8


1


2

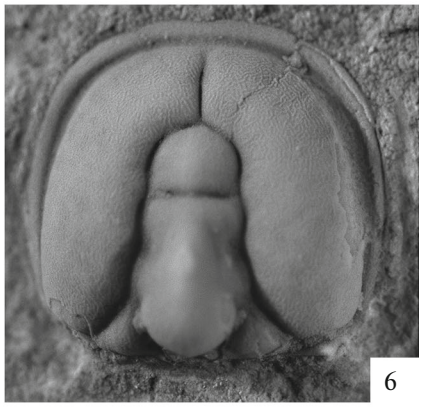

3

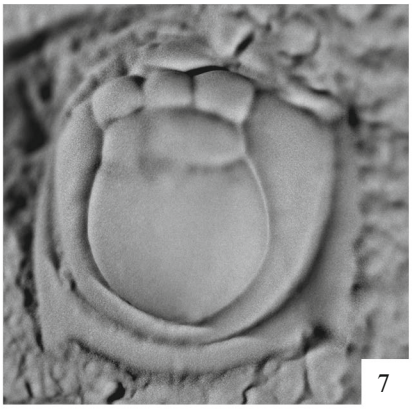

4a


4b


5


8


6


7

H. captiosus—Siberian Platform: Chopko River, Sakian Stage, from *A. clavatus–Irvingella angustilimbata* to *I. cipita* zones (Varlamov et al., 2005; Varlamov and Rosova, 2009 as *"Agnostus"* sp. aff. *A. captiosus*); Olenek River (lower reach, Khoyguollakh Spring) and Kharaulakh Mountains (near the village of Chekurovka), Sakian Stage, *Irvingella–Cedarellus felix* zones (Lazarenko, 1966 as *Agnostus captiosus*); Khos-Nelege River, Sakian Stage, *Agnostotes orientalis–Irvingella* Zone (Lazarenko et al., 2008b as *Agnostus (Homagnostus) captiosus*).

Genus Lotagnostus Whitehouse, 1936

Lotagnostus: Peng, Babcock, 2005, p. 110 (see list of synonyms); Ergaliev and Ergaliev, 2008, p. 46; Westrop et al., 2011, p. 571.

Type species. *Agnostus trisectus* Salter, 1864 [=*Lotagnostus americanus* (Billings, 1860)].

Diagnosis. Variably effaced, border structures narrow, unconstricted acrolobes. Cephalon with or without median preglabellar furrow, its absence coinciding with high degree of effacement; basal lobes large; glabella with straight F3, well developed F2, F1 variably developed due to mode of effacement; glabellar node located between F1 and F2. Pygidium bispinose, axis not reaching border furrow, slightly constricted across M2; F1 and F2 well developed, F1 may be full or expressed only at flanks or lateral parts may bent forwards to articulating furrow; M1 tripartite, posterior lobe elongate, semiovate to ogival, with terminal node.

Remarks. The genus is subdivided into three subgenera according to the degree of effacement. Here we follow this taxonomy.

L. americanus (Billings, 1860), being a provisional index species for the terminal Zone of the Cambrian, provoked a vivid discussion concerning its morphology variability and distribution (Peng and Babcock, 2005; Rushton, 2009; Westrop et al., 2011). While first authors tended to combine close species *L. americanus, L. asiaticus, L. trisectus*, and *L. punctatus*, the last ones insisted on the separating all of them. As we have only the Siberian material in hand to compare with the good images of the type species (Allen et al., 1981, pl. 17, figs. 1, 2; Rushton, 2009, p. 276; Westrop et al., 2011, figs. 5, 6), thus, we are not able to conclude about the validity of all these species, but inclined to follow Rushton's view, considering these forms as inevitable geographical intraspecies variations of *L. americanus*. We could infer the similarity of the Siberian specimens (for example, see Lazarenko et al., 2008a, pl. 23, figs. 1, 2, 5) to *L. americanus*. Westrop et al. (2011, p. 582) indicated the difference as "... the strongly defined trisection of the pygidial posteroaxis and by longer basal glabellar lobes that are notched into the posteroaxis behind M2." The degree of the axial pygidial trisecting may vary within the species and the notches, which mark the central part of glabellar posteroaxis are clearly visible on the images of *L. americanus* from Quebec (Westrop et al., 2011, figs. 5A, 5B) as well as from northern Siberia (Lazarenko et al., 2008b, pl. 23, fig. 2).

Species found in Russia. *L. americanus* (Billings, 1860)—Siberian Platform: Khos-Nelege River, upper Aksayan and lower Batyrbayan stages, *L. americanus* Zone (Pegel, 2000 as *L. trisectus*; Lazarenko et al., 2008b).

L. hedini (Troedsson, 1937)—Siberian Platform: Khos-Nelege River, Aksayan Stage, *Parabolinites rectus* Zone (Pegel, 2000, only pl. 15(12); Lazarenko et al., 2008b, not pl. 23, figs. 3, 4); Aldan River, Upper Cambrian (Pokrovskaya, 1960 as *Lotagnostus grandis* Lermontova, msc.).

Genus *Eurudagnostus* Lermontova, 1951

Plate 7, figs. 7–10

Eurudagnostus: Lermontova, 1951, p. 7; Ergaliev and Ergaliev, 2008, p. 57 (see synonymy list); Lazarenko et al., 2008a, p. 17; Naimark, 2014, p. 171.

Salagnostus: Gabova in Petrunina and Gabova, 2008, p. 19.

Type species. *Eurudagnostus grandis* Lermontova, 1951.

Diagnosis. Transglabellar furrow curving backward, median preglabellar furrow partly developed as short notch in front of glabella; cephalic spines present, deliquiate border furrows on both shields, borders narrow, pygidial axis short; transaxial F1 furrow impressed only laterally.

Remarks. The genus *Eurudagnostus* was established by Lermontova (1951, p. 7). Then, it was suppressed as a junior synonym of *Oncagnostus* (Shergold et al., 1990). A review of the further discussion on this genus was later made by Neilsen (1997, p. 467) and he advocated the validity of *Eurudagnostus*. The validity of the genus was accepted by some specialists (Ergaliev and Ergaliev, 2008, p. 57; Lazarenko et al., 2008a, p. 17) and recent revision of the type species clarified its morphology (Naimark, 2014). The originally defined holotype of *E. grandis* consisted of two parts (cephalon and pygidium), which belong to different animals and, moreover, to different species. We left the cephalon as the holotype for this species.

Also, according to Table 2, other numerous combinations of characters of Agnostidae open the possibilities for synonymy of *Eurudagnostus* with *Micragnostus, Oncagnostus, Homagnostus, Trilobagnostus, Agnostus, Innitagnostus,* etc.).

Table 2 shows that *Eurudagnostus* is distinguished from *Micragnostus* by having a deliquiate border furrow in cephalon and specific shape of the pygidial axis and from *Oncagnostus* by the short pygidial axis. This point of view became a background for the revision of the genus and an emended list of species with its stratigraphic and geographic distribution was provided (Naimark, 2014).

Salagnostus Gabova in Petrunina et Gabova, 2008 does not differ from *Eurudagnostus* by any characters placed in Table 2; other characters were not specified in the original diagnosis of *Salagnostus*. Gabova (Petrunina and Gabova, 2008, p. 19) compared *Salagnostus* with *Micragnostus,* pointing out its short preglabellar furrow and very wide border furrow both in cephalon and pygidium as differential characters. She did not provide a comparison with *Oncagnostus,* which was considered to embrace *Eurudagnostus*. Here we separate the genus *Eurudagnostus* as a valid unit, while *Salagnostus* becomes its junior synonym.

There were three species in *Salagnostus: S. gorskinus* Gabova in Petrunina et Gabova, 2008, *S. intermedius* Petrunina in Petrunina et Gabova, 2008, and *S. orbiculatus* Gabova in Petrunina et Gabova, 2008. These species can be distinguished one from another by the shape of the pygidial shield and axis and by the shape of cephalic F3. *S. gorskinus* has a rounded pygidial shield, straight cephalic F3, and very deep axial furrows; *S. orbiculatus* has a comparatively high pentagonal pygidial shield and rounded posteroaxis and F3 straight. *S. intermedius* differs from these two in many other characters*:* it has a pentagonal pygidial shield with acuminated posteroaxis and F3 bent backward, pygidial F1 and F2 are very weak, glabellar basal lobes are very small and sometimes indistinct, glabellar front lobe bent rearward. This third species covers the diagnoses of *Ivshinagnostus* and, thus, should be transferred to it.

Choi et al. (2004), having described the fauna from the Machari Formation (Korea), identified three species of *Micragnostus: M. elongatus* (Chien, 1961), *M. hisakoshii* (Kobayashi, 1962), and *Micragnostus* aff. *intermedius* (Palmer, 1968). Their diagnosis of *Micragnostus* allowed forms with the deliquiate cephalic border furrow and nonparallel axis on the pygidium to be included. However, according to the concept accepted here, their species should be assigned to *Eurudagnostus*. *Micragnostus hisakoshii* (Kobayashi, 1962) from Korea resembles *Salagnostus orbiculatus* Gabova, 2008 and there are the slightest differences between *Salagnostus gorskinus* and *Micragnostus* aff. *intermedius* from Korea. Also in Kazakhstan, section Kyrshabakty, there are four species of *Eurudagnostus,* which cover the same range of diversity; those are forms with round or triangular pygidia shield and straight or bending backward glabellar F3 and pygidial axis variable in width (Ergaliev and Ergaliev, 2008). The Kazakhstan species resembling species of *Salagnostus* are *Eurudagnostus minor* Ergaliev, 1980, *Eurudagnostus ovaliformis* Ergaliev, 1980, and *Eurudagnostus ovalis* Ergaliev, 2008. *S. gorskinus* seems to be equivalent to *E. minor* and *S. orbiculatus* has very subtle differences in comparison with *Eurudagnostus ovalis.* These triads from the Salair Ridge (Altai–Sayan Folded Belt), Korea, and Kazakhstan demonstrate, on the one hand, the closeness of the faunas, but, on the other hand, the overestimated species diversity from overlooked regional species lists. Following the example of *Salagnostus,* I infer the species of *Eurudagnostus* from Salair as *E. minor* (=*S. gorskinus*), *E. hisakoshii* (Kobayashii, 1962) (=*S. orbiculatus*).

Also *Geragnostus nesossii* Harrington et Leanza, 1957 from Argentina is a possible representative of this genus (Tortello and Esteban, 2014, p. 959, figs. 3.10, 3.11). It is characterized by all generic diagnostic characters, while lacking the *Geragnostus* characters especially in the cephalon. This form was found in the Upper Tremadocian of the Nazareno area.

Agnostus gladiator Clark, 1923 (Clark, 1923, p. 122, text-fig. 10) described from Levis Limestone in Quebec resembles the type species *E. grandis*. If these species are synonyms, then the type species should be referred to *E. gladiator,* but the original material was represented by a single damaged, schematically outlined pygidium. Whether or not they are synonyms, the known distribution of the genus was expanded to the *L. americanus* Zone in Laurentia.

Species found in Russia. *E. intermedius*—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, uppermost Sakian Stage, *Maladioidella abdita* Zone (Lazarenko et al., 2008a, 2008b both as *E.* cf. *minor*). Altai-Sayany Folded Belt, northeastern Salair Ridge, lower Upper Cambrian (Petrunina and Gabova, 2008).

E. hisakoshii—Altai-Sayany Folded Belt, northeastern Salair Ridge, lower Upper Cambrian (Petrunina and Gabova, 2008 as *Salagnostus orbiculatus* Gabova, 2008).

Eurudagnostus mutabilis—Altai-Sayany Folded Belt, northeastern Salair Ridge, lower Upper Cambrian (Petrunina and Gabova, 2008 as *Salagnostus gorskinus*).

Genus *Oncagnostus* Whitehouse, 1936

Plate 8, figs. 4 and 4a

Oncagnostus: Shergold et al., 1990, p. 34; Nielsen, 1997 p. 466; Shergold and Laurie, 1997, p. 339; Buchholz, 1999, p. 247; 2004b, p. 550; Ergaliev and Ergaliev, 2008, p. 55.

Type species. *Agnostus hoi* Sun, 1924.

Diagnosis. Nonscrobiculate, transglabellar furrow straight or bent slightly backward, median preglabellar furrow absent or as very short notch in front of glabella, cephalic spines absent, deliquiate border furrows; borders narrow, sometimes flattened. Pygidium minutely spinose, pygidial axis long with parallel sides, rounded at rear, transaxial F1 impressed as only lateral parts.

Remarks. We failed to find specimens of *Oncagnostus paraobesus* (Lermontova, 1940) in the type collection in TsNIGR. Therefore, there is no a refigured holotype or paratypes in this work. It is noteworthy that *Oncagnostus paraobesus* differs from *O. ultraobesus* only in the wider pygidial axis. *O. ultraobesus* was geographically distributed more widely than *O. parao-*

besus, as it is known from Andrarum, Sweden (Ahlberg and Terfelt, 2012), Siberia, and Altai. Some specimens of *O. obesus* reported from Canada, Rabbitkettle Formation were very similar to *O. paraobesus* (Pratt, 1992, pl. 1, figs. 33, 34).

Species found in Russia. *O. hoi* (Sun, 1924)—Siberian Platform, Kharaulakh Mountains, lower part of the Upper Cambrian (Lermontova, 1940 as *Homagnostus obesus* (Belt, 1867)).

O. paraobesus (Lermontova, 1940)—Siberian Platform: Kharaulakh Mountains, lower part of the Upper Cambrian (Lermontova, 1940 as *Homagnostus paraobesus*), Kulyumbe River, Ayusokkanian Stage, *Pedinocephalina–Toxotis* Zone, Olenek River (middle reaches), Upper Cambrian (Lazarenko and Nikiforov, 1968 as *Homagnostus paraobesus*).

O. ultraobesus (Lermontova, 1940)—Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain, uppermost Upper Cambrian (Lermontova, 1940 as *Homagnostus ultraobesus*; Pokrovskaya, 1960 as *Homagnostus ultraobesus*).

O. comptus (Palmer, 1962)—Siberian Platform: Kulyumbe River, Ayusokkanian Stage, Nganasansky Horizon (Rosova, 1964 as *"Agnostus" comptus*).

Genus *Micragnostus* Howell, 1935

Micragnostus: Howell, 1935b, p. 233; Moore, 1959, p. O179; Fortey, 1980, p. 21; Shergold and Sdzuy, 1984, p. 65; Shergold et al., 1990, p. 34; Nielsen, 1997, p. 467; Shergold and Laurie, 1997, p. 342; Sohn and Choi, 2002, p. 63; Choi et al., 2004, p. 167; Ergaliev and Ergaliev, 2008, p. 33.

Geragnostus (Micragnostus): Kobayashi, 1939, p. 168; Shergold, 1971, p. 22; Ludvigsen, 1982, p. 44.

Type species. *Agnostus calvus* Lake, 1906.

Diagnosis. Nonscrobiculate, transglabellar furrow straight or bent slightly backward, median preglabellar furrow absent or as very short notch in front of glabella, cephalic spines absent, nondeliquiate border furrows, borders narrow, minutely spinose in pygidium, pygidial axis short with parallel sides, first transaxial furrow transversely impressed or having only lateral parts.

Species found in Russia. *Micragnostus subobesus* (Kobayashi, 1936)—Siberian Platform: Aksayan Stage, Khos-Nelege River, upper *Plicatolina perlata* Zone, lower *Parabolinites rectus* Zone (Lazarenko et al., 2008a; 2008b both as *Eurudagnostus* cf. *brevispinus*), Aksayan Stage (Pegel, 2000 as *?Geragnostus sp.*).

Genus *Trilobagnostus* Harrington, 1938

Trilobagnostus: Harrington, 1938, p. 148; Moore, 1959, p. O179; Ludvigsen et al., 1989, p. 106; Shergold et al., 1990, p. 35; Shergold and Laurie, 1997, p. 343; Nielsen, 1997, p. 470; Buchholz, 1999, p. 249; Żylińska, 2001, p. 350; Jell and Adrain, 2003, p. 355; Buchholz, 2004b, p. 550; Ergaliev and Ergaliev, 2008, p. 61.

Lotagnostus (Trilobagnostus): Shergold, 1975, p. 48.

Rudagnostus: Lermontova, 1951a, p. 7; Shergold, 1972, p. 21.

Type species. *Agnostus innocens* Clark, 1923.

Diagnosis. Nonscrobiculate, transglabellar furrow straight or bent slightly backward, median preglabellar furrow absent, cephalic spines absent, border furrows flat and of medium width, pygidial border minutely spinose, pygidial axis short, widest at M1, first transaxial furrow transversely impressed or having only lateral parts.

Species found in Russia. *T. rudis* (Salter, 1964)—northeastern Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, uppermost Aksayan Syage, *Lotagnostus americanus* Zone (Lazarenko et al., 2008a, 2008b).

Trilobagnostus sp. 1—Altai-Sayany Folded Belt, southern Salair Ridge, Anyshtaikha River, Ust'-Kul'bich Horizon (lower Upper Cambrian) (Petrunina and Gabova, 2008 as Agnostidae gen. et sp. ind. 1).

Trilobagnostus sp. 2—Altai-Sayany Folded Belt, southern Salair Ridge, Anyshtaikha River, Ust'-Kul'bich Horizon (lower Upper Cambrian) (Petrunina and Gabova, 2008 as Agnostidae gen. et sp. ind. 2)

Genus *Innitagnostus* Öpik, 1967

Plate 8, fig. 1

Innitagnostus: Öpik, 1967, p. 98; Shergold, 1980, p. 22; Shergold, 1982, p. 20; Shergold et al., 1990, p. 33; Pratt, 1992, p. 26; Shergold and Laurie, 1997, p. 341; Buchholz, 1999, p. 248; Buchholz, 2004b, p. 548; Ergaliev and Ergaliev, 2008, p. 42; Petrunina and Gabova, 2008, p. 23; Westrop and Eoff, 2012, p. 231.

Type species. *Innitagnostus innitens* Öpik, 1967.

Diagnosis. Cephalon semiovate, border narrow, border furrow of moderate width; median preglabellar furrow incomplete; anterior glabellar lobe trapeziform, with truncated (exsagittal) front outline, F2 and F1 developed. Pygidium with narrow border and narrow to moderate border furrow; F1, F2 well developed, F1 impressed transversely; axis of moderate length, constricted across M2, M1 trilobate.

Species found in Russia. *I. innitens* Öpik, 1967—Siberian Platform: Chopko River, lowermost Sakian Stage, *Glyptagnostus reticulatus* Zone (upper part) (Rosova, 1977 as *Innitagnostus* aff. *innitens;* Varlamov and Rosova, 2009); Khos-Nelege River, *Clavagnostus spinosus* Zone (Lazarenko et al., 2008a); Olenek River, Upper Cambrian (Pokrovskaya, 1960 as *Agnostus pisiformis*).

I. angustus Pokrovskaya et Pegel, 1997—Siberian Platform: western part of Sette–Daban Ridge, Aldan River (near the Kerbi River mouth), Ayusokkanian Stage, *Toxotis venustus* Zone (Gogin and Pegel, 1997); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2000, 2010, 2014); Kharaulakh Mountains, Khos-Nelege River, Ayusokkanian Stage, *Clavagnostus spinosus* Zone (Lazarenko et al., 2008a). Altai-Sayany Folded Belt: northeastern Altai Moun-

tains, Bol'shaya Isha River, upper Middle Cambrian (Romanenko, 1977 as *Agnostus* sp. pl. 23, fig. 3 as *"Agnostus"* sp., pl. 23, figs. 4–8), northwestern Kuznetsky Alatau, Kazennaya Vasil'evka River, Ust'-Kul'bich Horizon (lower Upper Cambrian) (Petrunina and Gabova, 2008 as *Innitagnostus?* aff. *angustus*).

Genus *Barrandagnostus* Ivshin, 1960

Plate 8, figs. 2 and 3

Barrandagnostus Ivshin: Egorova et al., 1960, p. 166, Petrunina and Gabova, 2008, p. 23.

Hozediasagnostus Ergaliev: Ergaliev and Ergaliev, 2008, p. 23.

Type species. *Barrandagnostus barrandei* Ivshin, 1960.

Diagnosis. Preglabellar median furrow complete or effaced at junction with border furrow, indented as short sulcus in front of anteroglabella, anteroglabella with truncate (exsagittal) front outline; cephalic cheeks with faint or well discernible rugae and, sometimes, with arcuate scrobicules around anteroglabella. Both cephalic and pygidium border structures narrow to moderate; glabellar F2 and F3 well developed. Pygidium bispinose, F1 and F2 straight and well developed, axis constricted across M2; posteroaxis moderately wide.

Remarks. This genus with the only type species was established by Ivshin from the Altai Region, who did not supply the description with adequate images. He gave only drawings and this prevented the usage of the genus (Shergold, 1982). Shergold (1982) mentioned this genus as a possible synonym of *Glyptagnostus* or *Innitagnostus*. Gabova and Petrunina (2008) investigated the section, from which the type material of *B. barrandei* originated. They found specimens (complete shields, cephala, and pygidia) that fitted both the description and drawings provided by Ivshin (1960). They supposed their specimens belonged to the same species and designated the neotype for the type species. The morphology of the specimens assigned to *B. barrandei* resembles the diagnosis of *Innitagnostus;* therefore, Petrunina and Gabova suggested *Innitagnostus* was a junior synonym of *Barrandagnostus*, invoking principle of nomenclatural priority. Here we distinguish these genera by the shape of the preglabellar furrow whether complete in *Barrandagnostus* or incomplete or absent in *Innitagnostus*. According to this difference, *I. inexpectans* (Kobayashi, 1938) should be assigned to *Barrandagnostus*.

G. Ergaliev (Ergaliev and Ergaliev, 2008) described two specimens (both cephala), which were very close to the specimens imaged by Petrunina and Gabova (2008). But he hesitated to relate his specimens with the Petrunina and Gabova's neotype. Due to this, he established the new genus *Hosediazagnostus* Ergaliev, 2008 with the type species *Tomagnostus tchatertensis* Krys'kov, 1963. Petrunina and Gabova had previously considered this species as a junior synonym of *B. barrandei* Ivshin, 1960. Therefore, the validity of *Hosediazagnostus* depends on distinguishing between *Tomagnostus tchatertensis* and the neotype of *B. barrandei*. Here we followed the concept of Petrunina and Gabova and, therefore, included *Hosediazagnostus* in the list of synonyms. *Barrandagnostus* resembles *Innitagnostus* in many aspects, but they differ in the longer preglabellar furrow as well as the development of scrobiculs on the cephalon in the former genus. The generic rank of these characters seems to be a matter of opinion.

The agnostoid with the sulcate anteroglabella was described from the Machari Formation in Korea as *Homagnostus? sulcatus* Choi, Lee et Sheen, 2004 (Choi et al., 2004). It is also characterized by a truncate front of anteroglabella and narrow border and border furrow of the cephalon. But the pygidium is much wider and with wide border structures, nonspinose. We accounted this for an example of parallel evolution, when similar cephalic characters evolved independently in "*Homagnostus*" and "*Agnostus*" lineages.

Species found in Russia. *B. barrandei* Ivshin, 1960—Altai-Sayany Folded Belt: Kuznetsky Alatau, Kazennaya Vasil'evka River, lowermost Sakian Stage, near (below and above) the lower boundary of the *Glyptagnostus reticulatus* Zone; Altai Mountains, Kul'bich Spring, lowermost Sakian Stage, *Glyptagnostus reticulatus* Zone (Petrunina and Gabova, 2008); Bol'shaya Isha River, upper Middle Cambrian (Romanenko, 1977 as *Barrandagnostus* sp.).

Genus *Ivshinagnostus* Ergaliev, 1980

Plate 8, fig. 8

Ivshinagnostus: Ergaliev, 1980, p. 65; Shergold and Laurie, 1997, p. 341; Choi et al., 2004, p. 169.

Type species. *Ivshinagnostus ivshini* Ergaliev, 1980.

Diagnosis. Cephalon and pygidium subquadrate; median preglabellar furrow absent or rudimentary, border furrow on both cephalon and pygidium wide, pygidium bispinose, axis comparatively short, axial F1 and F2 weak or absent.

Remarks. We assigned to this genus *Salagnostus intermedius* Petrunina, 2008. Other two species originally described within *Salagnostus* were transferred to *Eurudagnostus*. *Salagnostus intermedius* has all diagnostic characters of *Ivshinagnostus* and is separated from *Eurudagnostus* by smoothed F1 and F2 and triangular pygidial axis.

Species found in Russia. *I. intermedius* (Petrunina, 2008 in Petrunina and Gabova, 2008)—Altai-Sayany Folded Belt: Anyshtaikha River, lower Arinichevskaya Formation, Ust'-Kul'bich Horizon (lower Upper Cambrian) (Petrunina and Gabova, 2008).

Genus *Anyshtagnostus* Petrunina in Petrunina et Gabova, 2008

Plate 8, fig. 5

Anyshtagnostus: Petrunina in Petrunina and Gabova, 2008, p. 24.

Type species. *Anyshtagnostus bessonenkovi* Petrunina, 2008.

Diagnosis. Cephalic shield widened on anterolateral sides with rounded anterior outline; border narrow, border furrow widened on sides; preglabellar furrow partly developed, glabella short and narrow, anteroglabella short and triangular, F3 straight, F2 discernible at sides, basal lobes small.

Remarks. The genus *Anyshtagnostus* Petrunina, 2008 has pygidium similar to that of *Eurudagnostus* and *Trilobagnostus*, but strikingly different cephalic characteristics. Its cephalon has a triangular anteroglabella, pronounced partly developed preglabellar furrow, border furrow widened at sides, making the whole cephalic shape semicircular. A triangular anteroglabella with partly developed preglabellar furrow is known in species *Nahannagnostus pratti* Choi, Lee et Sheen, 2004, but though without any doubts this latter species does not belong to either *Nahannagnostus* or Pseudagnostidae and differs from *Anyshtagnostus* in many other characters.

Species found in Russia. *A. bessonenkovi*—Altai-Sayany Folded Belt: southern Salair Ridge, Anyshtaikha River, Ust'-Kul'bich Horizon (lower Upper Cambrian) (Petrunina and Gabova, 2008).

Subfamily Uncertain

Genus *Connagnostus* Öpik, 1967

Plate 6, fig. 8

Connagnostus: Öpik, 1967, p. 128; Shergold, 1971, p. 24; Shergold, 1975, p. 56; Shergold, 1980, p. 24; Shergold et al., 1990, p. 38; Pratt, 1992, p. 28; Westrop et al., 1996, p. 815; Shergold and Laurie, 1997, p. 349; Ergaliev and Ergaliev, 2008, p. 94; Naimark, 2012, p. 1009.

Type species. *Connagnostus venerabilis* Öpik, 1967.

Diagnosis. Cephalon with narrow border and moderate border furrow; preglabellar median furrow absent, anteroglabella rounded in outline; posterior lobe rounded and expanded at rear; median node elongate and shifted to transglabellar F3, F3 straight to bending forwards. Pygidium with narrow border and deliquiate border furrow; F1, F2 well developed, F1 deflected forwards by median node; median node elongate, axis long, reaching border furrow.

Species found in Russia. *Connagnostus venerabilis*—Altai-Sayany Folded Belt: northwestern Kuznetsky Alatau, Kazennaya Vasil'evka River, Ust'-Kul'bich Horizon (lower Upper Cambrian) (Petrunina and Gabova, 2008). Siberian Platform: Sette–Daban Ridge, Aldan River (near the Kerbi River mouth), uppermost Ayusokkanian Stage, *Maspakites* Zone (Gogin and Pegel, 1997 as *Connagnostus* aff. *venerabilis*).

Connagnostus aff. *venerabilis*—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone (Egorova et al., 1982, pl. 10, fig. 3 as *Peronopsis fallax*).

C. fritzi—Siberian Platform: Kulyumbe River, Ayusokkanian Stage, lower *Pedinocephalina–Toxotis* Zone, Nganasansky Horizon (Rosova, 1964 as *Peronopsis* aff. *insignis* in pl. 16, fig. 7, 8; as *"Agnostus" simplexiformis* pl. 16, fig. 5; here Pl. 6, fig. 8).

Connagnostus sp. 1—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Anomocarioides? curtus* Zone (Egorova et al., 1982, pl. 62, fig. 7 as *Peronopsis* aff. *integra*).

Connagnostus sp. 2—Siberian Platform: Kulyumbe River, uppermost Mayan Stage and Ayusokkanian Stage, *Pedinocaphalina–Toxotis* Zone (Lazarenko and Nikiforov, 1968 as *Agnostus (?) simplexiformis* Rosova, 1964).

Family Pseudagnostidae Whitehouse, 1936

Diagnosis. Agnostidae with pygidium variably deuterolobate, axis reaching border furrow, usually with accessory furrows, F1 absent, F2 well developed; cephalon with or without median preglabellar furrow, border bispinose or trispinose.

Remarks. There are a set of genera which always impose difficulties in identification. The reason seems to be not only in unclear taxonomic diagnoses, but also in unclear phylogeny of these genera. The confusing node of genera includes *Pseudagnostus*, *Rhaptagnostus*, *Neoagnostus*, *Sulcatagnostus*, *Xestagnostus*, and *Pseudagnostina*. Peng and Robison (2000) suggested to combine them under the name *Pseudagnostus* (except *Neoagnostus,* which was believed to be a senior synonym of *Pseudorhaptagnostus*). *Xestagnostus* Öpik, 1967 and *Yongwolagnostus* Choi, Lee et Sheen, 2004 lack a preglabellar furrow. In the former genus, the absence of a preglabellar furrow may reflect an advanced effacement. Other characters of the genus are consistent with *Pseudagnostus* (especially border structures), so *Xestagnostus* is regarded here as the weakly furrowed and effaced *Pseudagnostus* representative and synonymized with *Pseudagnostus* (Peng and Robison, 2000). *Yongwolagnostus* possesses short preglabellar furrow on some specimens (Choi et al., 2004, pl. 11, figs. 2–4). Therefore, *Pseudagnostina* is a unique genus with completely absent preglabellar furrow. There is no evidence of the effacement of this furrow during the ontogeny in *Pseudagnostina*. This feature introduces the generic rank in other families (Agnostidae, Peronopsidae). Given other differential characters (full effacement of posteroaxis and F2, no hints for lanceolate field on the posteroaxis, glabella without traces of F1, F2), we consider *Pseudagnostina* as a valid genus.

Rhaptagnostus, as the original diagnosis indicates, differs from other genera of Pseudagnostidae in the ovoid shape of the pygidium, nondeliquiate border furrows both on cephalon and pygidium, and narrow nonspinous (or with extremely tiny pygidial spines) borders both on cephalon and pygidium. *Pseudagnostus* usually possesses moderate or wide border structures usually bispinous on the pygidium. Of these, border structures seem to be the most reliable characters (the same as for agnostid and peronopsid genera). Given this peculiarity, we keep to separate *Rhaptagnostus* from *Pseudagnostus* as a genus or at least to delineate it as a subgenus.

Sulcatagnostus differs in possessing the third spine on the pygidial margin, which is emphasized in its diagnosis. The third marginal spine is accentuated at the subfamilial diagnostic level (Oidalagnostinae), generic level (*Aspidagnostus*, *Utagnostus*), or species level (*Clavagnostus*, *Linguagnostus*, *Oedorhachis*). So, this feature does not earn a constant taxonomic rank in diplagnostids. However, as representatives of *Sulcatagnostus* are the only ones among Pseudagnostidae bearing a third spine, we thought it was taxonomically justifiable to refer *Sulcatagnostus* to a separate genus.

The last genus in this taxonomic node is *Neoagnostus*. Two problems are referred to this genus. The first is addressed to recognizing the genus itself and the second concerns a zoological nomenclature problem (Naimark, 2015, 2016). Possessing deliquiate border furrows and variably effaced preglabellar median furrow, lanceolate field and posteroaxis differently delineated, it is usually confused with *Pseudagnostus*. The small anteroglabella, the spectacles shape of the posteroglabella or the V–shape glabellar F3 cannot distinguish this genus from *Pseudagnostus*. The revision of the type material for *Pseudorhaptagnostus*, which was frequently considered as a junior synonym of *Neoagnostus*, allowed us to subdivide a number of "neoagnostid" species into five genera. These genera (*Pseudorhaptagnostus, Neoagnostus, Norilagnostus, Idolagnostus, Machairagnostus*) represent a mosaic combination of pygidial and cephalic characters. Their resemblance indicates a parallel development rather than a monophyletic origin.

From this set, *Neoagnostus* and *Idolagnostus* have not been found in Russia. They differ from *Pseudorhaptagnostus* in the glabellar characters, that is, the presence of full or almost full lateral glabellar furrows (Naimark, 2016).

The summary of stratigraphic distribution for Pseudagnostidae from Russia is shown in Fig. 10.

Subfamily Pseudagnostinae Whitehouse, 1936

Genus *Pseudagnostus* Jaekel, 1909

Plate 9, figs. 1–10, Plate 10, figs. 11 and 12

Pseudagnostus: Jaekel, 1909, p. 400; Ivshin, 1956, p. 11; Moore, 1959, p. O182; Öpik, 1967, p. 149; Shergold, 1971, p. 27; 1975, p. 58; 1977, pp. 69–100 (see for additional synonymy); Shergold, 1980, p. 27; Shergold and Sdzuy, 1984, p. 69; Westrop, 1986, p. 26; Pratt, 1992, p. 33; Peng and Robison, 2000, p. 15; Choi et al., 2004, p. 177; Westrop and Eoff, 2012, p. 205.

Pseudagnostus (Pseudagnostus): Shergold and Sdzuy, 1984, p. 69; Shergold et al., 1990, p. 49; Shergold and Laurie, 1997, p. 366; Ergaliev and Ergaliev, 2008, p. 165 (but note the discrepancies with the validity of *Pseudagnostina* on p. 180).

Xestagnostus: Öpik, 1967, p. 161; Shergold et al., 1990, p. 51; Shergold and Laurie, 1997, p. 371; Ergaliev and Ergaliev, 2008, p. 208.

Type species. *Agnostus cyclopyge* Tullberg, 1880.

Diagnosis. Need revision. Here we group species of deuterolobate pygidium with narrow border structures and often bispinose.

Remarks. Peng and Robison (2000) provided a detailed revision of *P. josepha* (Hall, 1863) and 18 other species and subspecies of *Pseudagnostus* were included in it. *P. intermedius* Pack, 2005, which was described based on the holotype cephalon (Varlamov et al., 2005, pl. 10, fig. 2) and paratype pygidia shares the specific characteristics, except the position of pygidial spines (they are positioned slightly anterolaterally). Therefore, we combine this species with other 18 synonyms of *P. josepha*.

Another Siberian species, *P. impressus* Lermontova, 1940, shares almost all characters with *P. josepha,* but it has an advanced position of the glabellar node and narrower pygidium and narrow, not delicate pygidial border furrow. Such difference seems to be sufficient to consider this species valid. Separated cephala and pygidia of *P. impressus* were found among the type material of *Pseudorhaptagnostus simplex* and *Rhaptagnostus obsoletus* (Naimark, 2015, 2016) (these specimens are shown here in Pl. 9, figs. 5, 6).

P. rotundatus Lermontova, 1940 represented by two cephala and two pygidia is most probably an erroneous combination. These two cephala differ from each other; one of them (Lermontova, 1940, pl. 49, fig. 12; here Pl. 9, fig. 1) represents *P. rotundatus,* while the second (Lermontova, 1940, pl. 49, fig. 12a) would belong to a certain other species within a hundred species of *Pseudagnostus*. The closest appears to be *P. orbiculatus*. The pygidia of *P. rotundatus* have a very common habitus and resemble *P. cyclopyge* or species (Lermontova, 1940, pl. 49, fig. 12b; here Pl. 9, fig. 2). As Lermontova did not indicate the holotype of *P. rotundatus,* we suggested the lectotype from the original species type series to be the first of the mentioned cephala.

P. salairicus Petrunina, 2008 from Altai may represent *P. sericatus* Öpik, 1967 described from Queensland, Australia. The latter is known by the only cephalon and no pygidia have been ascribed to this cephalon. Given the lack of pygidia in the latter species and poorly preserved material of the former species, there are justified doubts on the synonymy of these two species. But if the close resemblance of the cephala is taken into account, *P. salairicus* would be found to be a junior synonym of the Australian species.

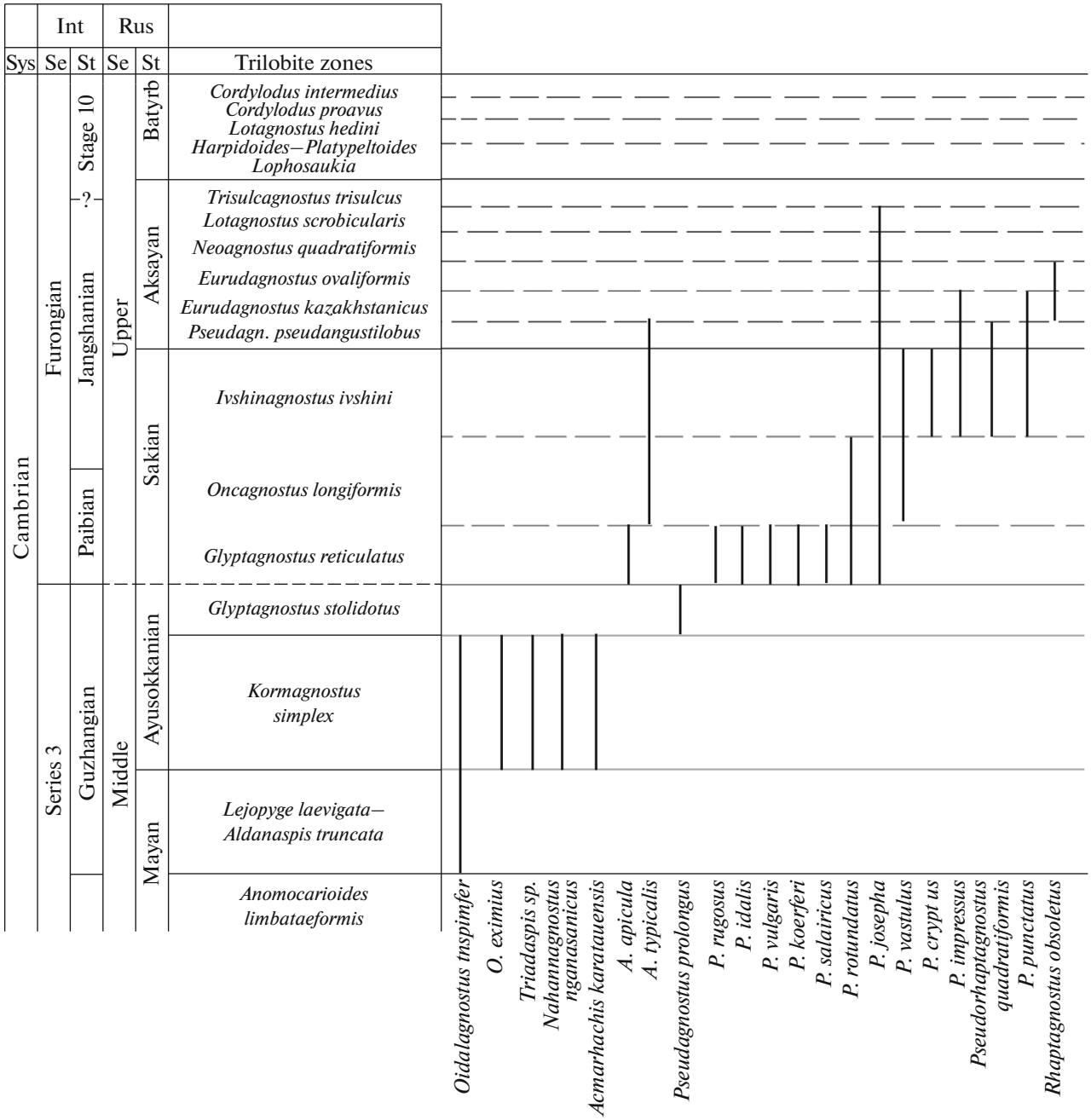


Fig. 10. Stratigraphic distribution of Pseudagnostidae species known from Russia.

Two species, *P. levatus* E. Romanenko, 1967 and *P. cryptus* Pack, 2005, demonstrate gradual degree of effacement of anteroglabella. *P. levatus* possesses completely effaced furrow around anteroglabella, while *P. cryptus* has less effaced axial glabellar furrows. Both species have traces of a preglabellar furrow; that is why they would better be associated with *Pseudagnostus* rather than *Pseudagnostina,* although their pygidial characters conform to those of *Pseudagnostina koerferi* (Monke, 1903).

P. vulgaris Rosova, 1960 is similar to *Neoagnostus sabulosus* Peng, 1992 (in both species, the holotypes are represented by pygidia). Cephala of these species differ in the less expressed glabellar furrows in *P. vulgaris*, but this feature may vary in pseudagnostid species.*P. vulgaris* and *Neoagnostus sabulosus* do not possess the third annulation on the pygidium; thus, they better fit the diagnosis of *Pseudagnostus* than *Neoagnostus*, with *N. sabulosus* being the synonym of the former species.

P. vulgaris resembles *Pseudagnostus tumidus* (Sun, 1989). Their pygidia do not differ, but the cephala can be separated with relatively wider preglabellar field and expanded posteroglabellar rear in *P. tumidus* (Sun, 1989). The Korean representatives of *P. tumidus* look much like the Siberian *P. vulgaris* in having a slender posteroglabella and, in some specimens, narrower preglabellar field (Choi et al., 2004, text-fig. 15: 1, 4). Thus, the Korean form should be reassigned to *P. vulgaris*.

P. cavernosus (Rosova, 1960) (Rosova, 1960; Egorova et al., 1960; here Pl. 10, fig. 11) known by the pygidia resembles *Neoagnostus* cf. *sabulosus* Peng, 1992 from the Khos-Nelege River (Lazarenko et al., 2008a, 2008b, 2011) by the overall outline and the sculptural pattern. This latter differs from *P. cavernosus* in the nonexpressed posterolateral annulation in the axis, less widened border furrow at posterolateral spines. This difference seems sufficient to distinguish the species.

Xestagnostus sp. described by Petrunina and Gabova (2008) looks very close to Australian species *X. rasilis* Öpik, 1967. But we hesitate to synonymize them as more material is needed to consider the variability in these species.

Species found in Russia. *P. josepha* (Hall, 1863)—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Upper Cambrian, Sakian Stage, *Glyptagnostus reticulatus* and *Eugonocare borealis* zones and Aksayan Stage, *Parabolinites rectus* Zone (Pegel, 2000 as *Pseudagnostus communis*; Lazarenko et al., 2008a as *Pseudagnostus idalis*, as *Pseudagnostus* ex. gr. *rotundatus* Lermontova, but not pl. 16, fig. 11, as *Pseudagnostus* sp. pl. 21, figs. 7, 8; 2008b as *Pseudagnostus idalis*); Chopko River, Upper Cambrian, from upper Sakian Stage, *Pseudoglyptagnostus clavatus–Irvingella angustilimbatus* Zone to lower Aksayan Stage, *Irvingella norilica* Zone (Varlamov et al., 2005 as *Pseudagnostus intermedius* Pack, 2005; Varlamov and Rosova, 2009 as *P. intermedius*).

P. (Sulcatagnostus) rugosus Ergaliev, 1980—Siberian Platform: Chopko River, Sakian Stage, lowermost *Glyptagnostus reticulatus* Zone (Varlamov and Rosova, 2009 as *Sulcatagnostus antecedens* Rosova et Makarova, 2009).

P. vastulus Whitehouse, 1936—Siberian Platform: Chopko River, upper Sakian Stage, *Pseudoglyptagnostus clavatus–Irvingella angustilimbata* Zone to the base of the *Mokutella mokutica* Zone (Varlamov et al., 2005; Varlamov and Rosova, 2009).

P. idalis Öpik, 1967—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Sakian Stage, *Eugonocare (Pseudeugonocare) borealis* and *Maladioidella abdita* zones (Lazarenko et al., 2008a as *Pseudagnostus* ex gr. *rotundatus* in pl. 16, fig. 11, pl. 18, figs. 6, 7).

P. rajovopsis Pratt, 1992—Siberian Platform, Chopko River, Sakian Stage, base of the *Pseudoglyptagnostus clavatus–Irvingella angustilimbata* Zone (Varlamov and Rosova, 2009 as *Pseudagnostus* sp. aff. *P. rajovopsis*).

P. prolongus (Hall et Whitefield, 1877)—Siberian Platform, Kharaulakh Mountains, Khos-Nelege River, uppermost Ayusokkanian Stage, *Glyptagnostus stolidotus* Zone (Lazarenko et al., 2008a).

P. cryptus Pack, 2005 —Siberian Platform, Chopko River, Aksayan Stage, *Irvingella norilica* Zone (Varlamov et al., 2005).

P. levatus E. Romanenko, 1967—Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River, lower Upper Cambrian (Romanenko, 1967).

P. vulgaris Rosova, 1960—Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain, near the villages of Gorskino and Arinichevo (Egorova et al., 1960; Petrunina and Gabova, 2008 as *Pseudagnostus* cf. *cyclopyge*).

P. salairicus Petrunina, 2008—Altai-Sayany Folded Belt, southern Salair Ridge, Anyshtaikha River, lower Upper Cambrian, Ust'-Kul'bich Horizon (Petrunina and Gabova, 2008 ?= *P. sericatus* Öpik, 1967).

P. impressus Lermontova, 1940—Siberian Platform, Kharaulakh Mountains (Lermontova, 1940), Khos-Nelege River, Sakian Stage, *Agnostotes orientalis–Irvingella* and *Maladioidella abdita* zones, and Aksayan Stage, *Plicatolina perlata* and *Parabolinites rectus* zones (Lazarenko et al., 2008a, pl. 21, figs. 7, 8 as *Pseudagnostus* sp., pl. 20, figs. 1, 5 as *Pseudagnostus communis*; 2008b as *Rhaptagnostus impressus*).

Pseudagnostus sp.—Altai-Sayany Folded Belt, southern Salair Ridge, Anyshtaikha River, lower Upper Cambrian, Ust'-Kul'bich Horizon (Petrunina and Gabova, 2008 as *Xestagnostus* sp.).

Genus *Pseudagnostina* Palmer, 1962

Psedagnostina: Palmer, 1962, p. 21; Pratt, 1992, p. 37; Ergaliev and Ergaliev, 2008, p. 180.

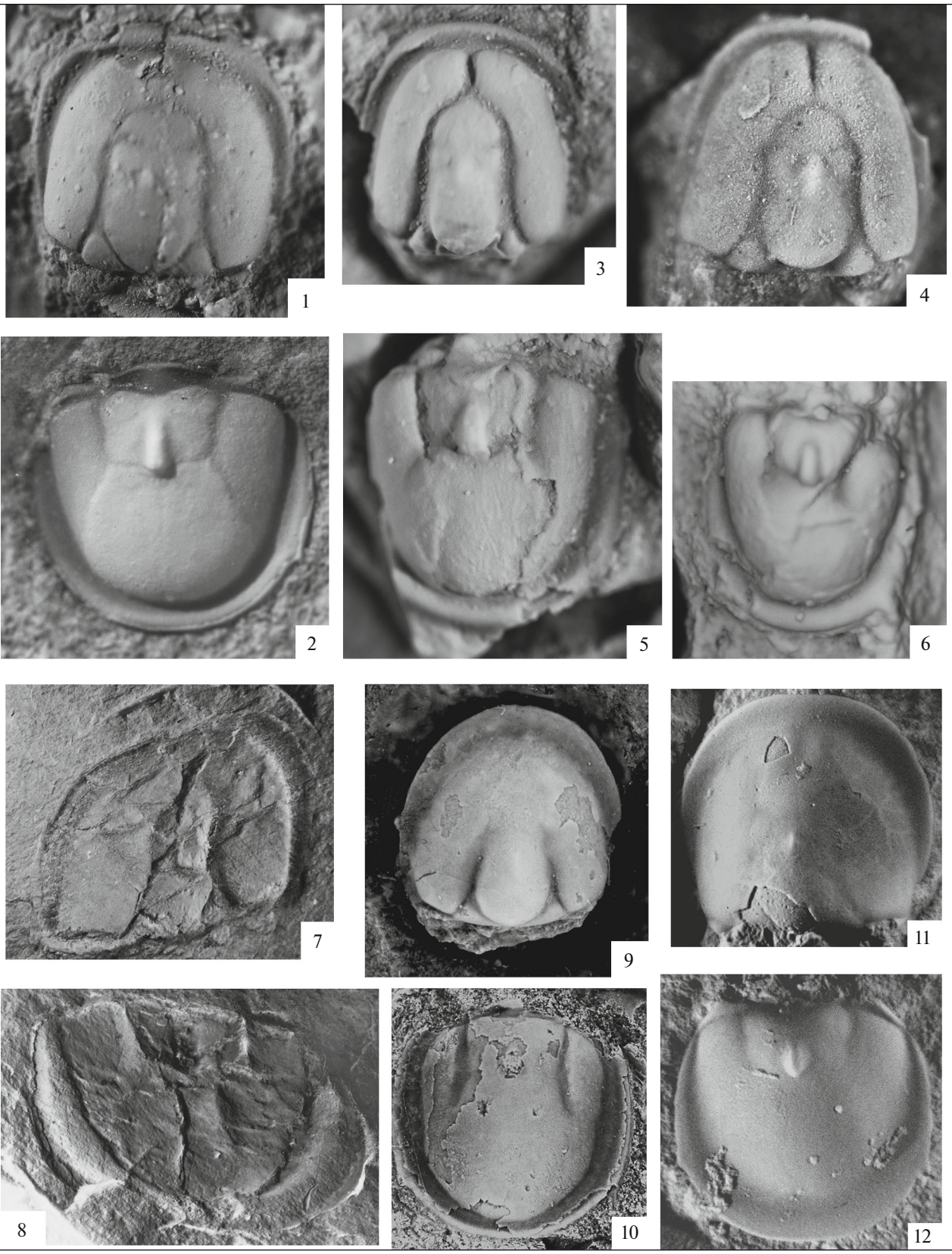
Pseudagnostus (Pseudagnostina): Shergold, 1977, p. 92; Ergaliev, 1980, p. 111; Sun, 1989, p. 81; Shergold et al., 1990, p. 49; Shergold and Laurie, 1997, 366.

Type species. *Psedagnostina contracta* Palmer, 1962.

Diagnosis. Pseudagnostids with anteroglabella outlined by axial furrow and preglabellar furrow completely absent. Pygidium usually with posteroaxis and F2 undeveloped.

Species found in Russia. *P. koerferi* (Monke, 1903)—Altai-Sayany Folded Belt, northeastern Altai Mountains, Bol'shaya Isha River, lowermost Upper Cambrian (Romanenko, 1977 as *Pseudagnostus* aff. *levatus*).

Plate 9



Genus *Rhaptagnostus* Whitehouse, 1936

Plate 10, figs. 1–3

Rhaptagnostus: Whitehouse, 1936, p. 97; Moore, 1959, p. O183; Shergold, 1977, pp. 69–100 (see for additional synonymy); 1980, p. 34; Shergold and Sdzuy, 1984, p. 71; Shergold et al., 1990, p. 51; Nielsen, 1997, p. 474; Shergold and Laurie, 1997, p. 370; Ergaliev and Ergaliev, 2008, p. 198.

Type species. *Agnostus cyclopygeformis* Sun, 1924.

Diagnosis. As *Pseudagnostus*, but with oval elongate shape pygidium; pygidial spines absent or minutely small, cephalic border furrow moderate, pygidial border furrow and border narrow.

Remarks. Lermontova defined two "holotypes" for *Rhaptagnostus obsoletus*—one was for a cephalon and the second, for a pygidium (Lermontova, 1951). As noted in the discussion above, the "holotype pygidium" actually belongs to *Pseudagnostus impressus.* Therefore, this species was composed of the "holotype cephalon" associated with two different types of pygidia: impressus–like and some different one. That second type shows a more or less narrow range of variation: oval shape, narrow border structures, pygidial deuterolobe smoothed. Such combination of cephala and pygidia—the "holotype cephalon" and the second type of pygidia—makes *Rhaptagnostus obsoletus* a senior synonym of *R. convergens* (Palmer, 1955).

Species found in Russia. *R. obsoletus* Lermontova, 1951—Altai-Sayany Folded Belt: Salair, Orlinaya Mountain, uppermost Cambrian (Lermontova, 1940 as *Pseudagnostus* cf. *obsoletus*).

Genus *Pseudorhaptagnostus* Lermontova, 1951

Plate 10, figs. 4–6

Pseudorhaptagnostus: Lermontova, 1940, p. 126; 1951, p. 12; Nielsen, 1997, p. 472; Choi et al., 2004, p. 181; Jago and Cooper, 2005, p. 668; Tortello, 2014, p. 301; Naimark, 2016, p. 58.

Neoagnostus (Pseudorhaptagnostus): Shergold, 1975, p. 58; 1977, p. 79; 1980, p. 39.

Type species. *Pseudorhaptagnostus punctatus* Lermontova, 1940 (=*P. simplex* Lermontova, 1951).

Diagnosis. Pseudagnostids with subquadrate cephalon and pygidium, border structures wide on both cephalon and pygidium. Cephalon with preglabellar furrow; glabella with shallow V-shaped transglabellar furrow, anteroglabella small. Glabellar node located in middle of posteroglabella, lateral furrows undeveloped. Pygidium spinous, axis wide, two first segments wide, F1 absent, F2 weak, posterior annulation expressed in low relief and not outlined by furrows, lanceolate field frequently present as two rows of dots or fossae, terminal node small.

Remarks. The revision of the type series has shown that the definition of *P. simplex* was based on erroneous combination of cephala and pygidia. *Pseudorhaptagnostus simplex* seems to be a junior synonym of *P. punctatus.* The redescription of the type species allowed us to clarify species groupings for the close genera *Neoagnostus, Machairagnostus, Norilagnostus,* and *Idolagnostus* (Naimark, 2016).

Pseudagnostus bituberculatus Ivshin, 1960 (Egorova et al., 1960) is probably a synonym of the type species as well. But the collection with the material of this species was lost, and no new material has appeared since the species was first established. Ivshin indicated the presence of posterior annulation on the posteroaxis as a main diagnostic feature for the species, but this feature may not be displayed very clearly and depends on preservation.

We referred the form *P.* cf. *sabulosus* from the Khos-Nelege River to *Pseudorhaptagnostus,* as it possessed all diagnostic generic characters in both cephalon and pygidium (see also the remarks to *Pseudognostus cavernosus*). Investigation of the type material of *Neoagnostus sabulosus* Peng, 1992 is needed to consider if this species belonged to *Pseudorhaptagnostus*.

The monotypic genus *Euplethagnostus* Lermontova, 1940, with the type species *E. subangulatus*

Explanation of Plate 9

Pseudagnostus Jaekel, 1909

Figs. 1 and 2. *Pseudagnostus rotundatus* Lermontova, 1940: (1) lectotype TsNIGR, no. 40/9182, cephalon (Lermontova, 1940, pl. 49, fig. 12), 3.2 mm long, (2) TsNIGR, no. 42/9182, pygidium (Lermontova, 1940, pl. 49, fig. 12b), 4 mm long; both from northeastern Siberian Platform, Kharaulakh Mountains.

Figs. 3–6. *Pseudagnostus impressus* Lermontova, 1940: (3) lectotype TsNIGR, no. 44/9182, cephalon, 3.1 mm long (Lermontova, 1940, pl. 49, fig. 13); (5) TsNIGR, no. 45/9182, pygidium, 2.5 mm long (Lermontova, 1940, pl. 49, fig. 13a); northeastern Siberian Platform, Kharaulakh Mountains; (4) TsNIGR, no. 12/7350, cephalon, 3 mm long (Lermontova, 1951a, pl. 2, fig. 16 originally indicated as the second holotype (cephalon) of *Pseudorhaptagnostus simplex*); (6) TsNIGR, no. 108/7350, pygidium, 2.5 mm long, (labeled as *Pseudagnostus obsoletus*).

Figs. 7 and 8. *Pseudagnostus salairicus* Petrunina, 2008: (7) LFGI, no. 44/2613, cephalon, 5.0 mm long (Petrunina and Gabova, 2008, pl. 3, fig. 12); (8) holotype LFGI, no. 42/2613, pygidium (inversed image of a cast), 4.9 mm long (Petrunina and Gabova, 2008, pl. III, fig. 10); Altai-Sayany Folded Belt, southern Salair Ridge, Anyshtaikha River, loc. 2100.

Figs. 9 and 10. *Pseudagnostus levatus* Romanenko, 1967: (9) TSSGM, no. 724/81, cephalon, 3.6 mm long (Romanenko and Romanenko, 1967, pl. I, fig. 18); (10) holotype TsSGM, no. 724/81b, pygidium, 3.4 mm long (Romanenko and Romanenko, 1967, pl. I, fig. 18); Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River.

Figs. 11 and 12. *Pseudagnostus cryptus* Pack, 2005: (11) holotype TsSGM, no. 8/749, cephalon, 4.5 mm long, loc. Ch-22a-II-1 (Varlamov et al., 2005, pl. 10, fig. 8); (12) TsSGM, no. 13/749, pygidium, 4 mm long, loc. Ch-24a-3 (Varlamov et al., 2005, pl. 11, fig. 1); northwestern Siberian Platform, Chopko River.

Lermontova, 1940 is usually referred to *Pseudorhaptagnostus* as its junior synonym. In the original description, Lermontova denoted the transaxial furrows of the pygidium as being completely effaced. As this feature is not diagnostic for *Pseudorhaptagnostus* and appears in some other genera, this synonymy seems to be unsound. The material for the species is lost, so the revision became impossible.

Species found in Russia. *Pseudorhaptagnostus punctatus*—Altai-Sayany Folded Belt: Salair Ridge, Orlinaya Mountain, uppermost Upper Cambrian (Lermontova, 1940).

P. cf. *sabulosus* (Peng, 1992)—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Aksayan Stage and lowermost of Batyrbayan Stage, *Parabolinites rectus* and *Lotagnostus americanus* zones (Lazarenko et al., 2008a, 2008b, 2011 as *Neoagnostus* cf. *sabulosus* Peng, 1992).

?P. bituberculatus (Ivshin, 1960)—Altai-Sayany Folded Belt: Altai Mountains, Kul'bich Spring, southern Salair Ridge, Ust'-Kul'bich Chumysh River, lower Upper Cambrian (Egorova et al., 1960 as *Pseudagnostus bituberculatus*).

Genus *Machairagnostus* Harrington et Leanza, 1957

Machairagnostus: Harrington and Leanza, 1957, p. 63; Moore, 1959, p. O182; Lisogor, 1977, p. 209; Alonso et al., 1982, p. 21; Naimark, 2016, p. 63.

Neoagnostus (Machairagnostus): Shergold et al., 1990, p. 50; Shergold and Laurie, 1997, p. 370; Lazarenko et al., 2008b, p. 22.

Pseudorhaptagnostus (Machairagnostus): Tortello and Acenolaza, 1993, p. 161; Nielsen, 1997, p. 473; Sohn and Choi, 2002, p. 65; Tortello and Esteban, 2005, p. 162; 2007, p. 159.

Tarayagnostus Suarez–Soruco: Suárez Soruco, 1975, p. 133.

Type species. *Machairagnostus tmetus* Harrington et Leanza, 1957.

Diagnosis. Pseudagnostids with rounded or oval cephalon and rounded or subquadrate pygidium, cephalic and pygidial acrolobes low in height, border furrows narrow, brims from moderate to narrow; preglabellar furrow expressed, transglabellar furrow smoothed, glabellar node shaped as long tubercule. Pygidium with well expressed lanceolate field, which outlined by two rows of deep fossae or furrows, lanceolate field terminating into terminal node.

Remarks. Siberian specimens of *Machairagnostus* sp. (Lazarenko et al., 2008b, pl. 20, figs. 12, 14, pl. 21, fig. 12) look similar to *Xestagnostus tianshanicus* Zhang, 1981 from northern Tian–Shan, *Agnostotes tianshanicus* Zone (Xiang and Zhang, 1985, p. 89, pl. 8, figs. 8, 10). These specimens from China neither fit the descriptions and images of the types of *Xestagnostus tianshanicus,* nor do they agree with the morphology of the whole specimens from Tian–Shan (Xiang and Zhang, 1985, p. 89, pl. 8, fig. 3). Therefore, the Siberian and Chinese material represent the same species, which is referred to *Machairagnostus*.

Species found in Russia. *Machairagnostus* sp.—Siberian Platform, Kharaulakh Mountains, Khos-Nelege River, Aksayan Stage, *Plicatolina perlata* and *Parabolinites rectus* zones (Lazarenko et al., 2008a as *Neoagnostus (Machairagnostus)* sp.).

Genus *Norilagnostus* Pack, 2005

Plate 10, figs. 7 and 8

Norilagnostus Pack: Varlamov et al., 2005, p. 43; Naimark, 2016, p. 64.

Type species. *Pseudagnostus quadratus* Lazarenko, 1966.

Diagnosis. Pseudagnostids with subquadrate or suboval cephalon and pygidium, wide border furrows. Cephalic preglabellar furrow smoothed or weakly expressed in front of glabella, transglabellar furrow mostly effaced, when expressed it thin and V-shaped; lateral furrows not expressed, glabellar node small, located in center of posteroglabella. Pygidium with narrow axis, only slightly expanded posteroaxis; pos-

Explanation of Plate 10

Pseudagnostidae

Figs. 1–3, 10. *Rhaptagnostus obsoletus* (Lermontova, 1951): (1) holotype TsNIGR, no. 115/7350, cephalon, 2.4 mm long (Lermontova, 1951a, pl. 2, fig. 9); (2) TsNIGR, no. 117/ 7350, cephalon, 2.4 mm long (Lermontova, 1951a, pl. 2, fig. 10); (3)TsNIGR, no. 129/7350, pygidium, 2.9 mm long; (10)TsNIGR, no. 114/7350, pygidium, 3.2 mm long; northeastern Kazakhstan, Boshche Kul'.

Figs. 4–6. *Pseudorhaptagnostus punctatus* Lermontova, 1940: (4) lectotype TsNIGR, no. 47/9182, pygidium, 3.5 mm long (Lermontova, 1940, pl. 49, fig. 14a); (5) TsNIGR, no. 48/9182, cephalon, 3.5 mm long (Lermontova, 1940, pl. 49, fig. 14); Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain; (6) TsNIGR, no. 127/7350, juvenile pygidium, 1.6 mm long (previously unpublished specimen from the type collection); Kazakhstan, Boshche–Kul'.

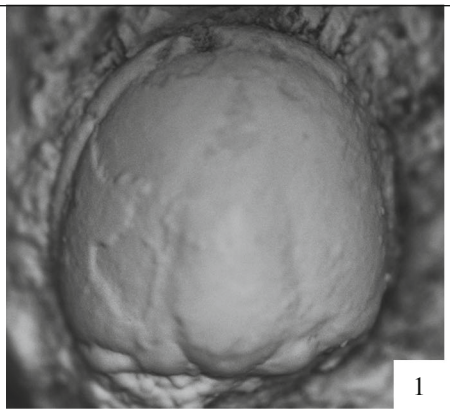
Figs. 7 and 8. *Norilagnostus quadratus* (Lazarenko, 1966): (7) holotype TsNIGR, no. 36/89007, cephalon, 5.1 mm long (Lazarenko, 1966, pl. 1, fig. 24); northeastern Siberian Platform, Kjutjungde trough, Khoyguollakh Spring, loc. 8-c.; (8) TsSGM, no. 749/20, pygidium, 2.8 mm long (Varlamov et al., 2005, pl. 11, fig. 9); northwestern Siberian Platform, Chopko River, loc. Ch-24a-3.

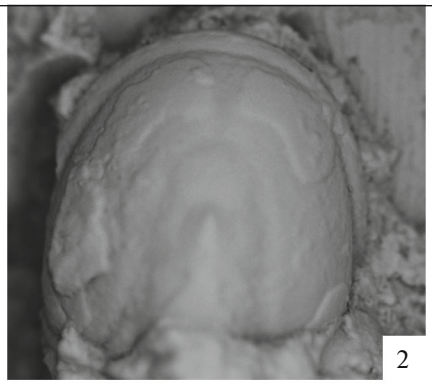
Fig. 9. *Nahannagnostus nganasanicus* (Rosova, 1964); holotype TSSGM, no. 113/875, pygidium, 2.4 mm long (Rosova, 1964, pl. XVI, fig. 3); northwestern Siberian Platform, Kulyumbe River, loc. R-12.

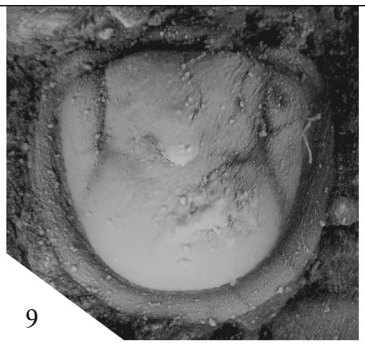
Fig. 11. *Pseudagnostus cavernosus* Rosova, 1960; holotype TsSGM, no. 1/731, pygidium, 3.7 mm long (Rosova, 1960, pl. 1, fig. 7); Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain, Tolstochikhinsky Horizon.

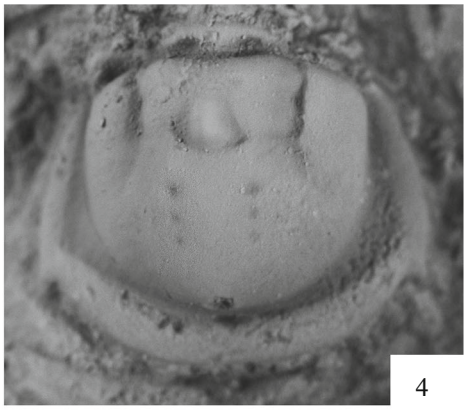
Fig. 12. *Pseudagnostus vulgaris* Rosova, 1960; holotype TsSGM, no. 11/731, pygidium, 3.5 mm long (Rosova, 1960, pl. 1, fig. 1); Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain, Tolstochikhinsky Horizon.

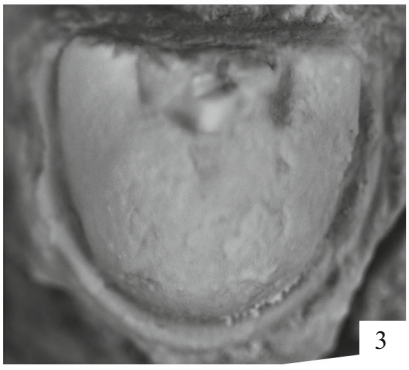
Plate 10

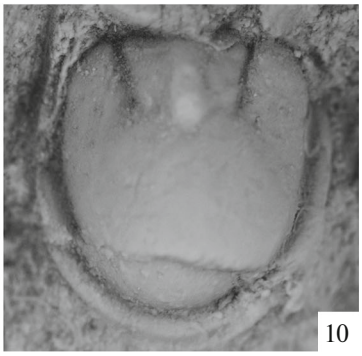

1

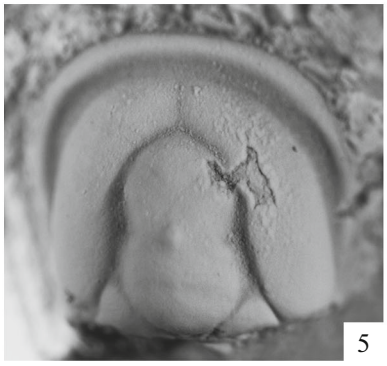

2

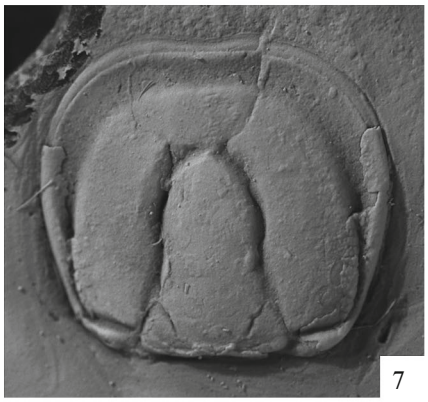

9

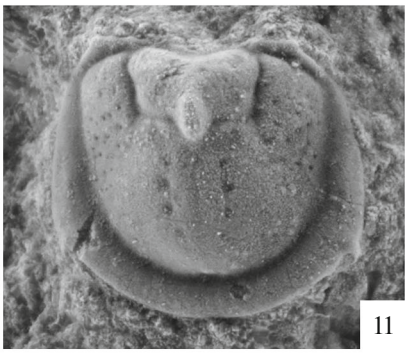

4

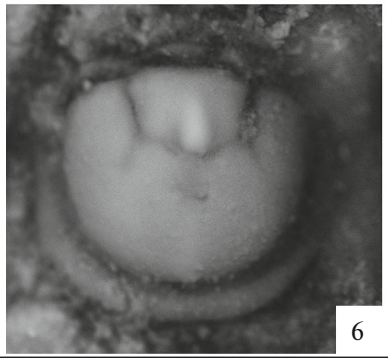

3

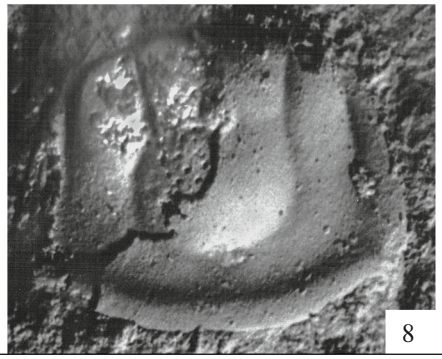

10

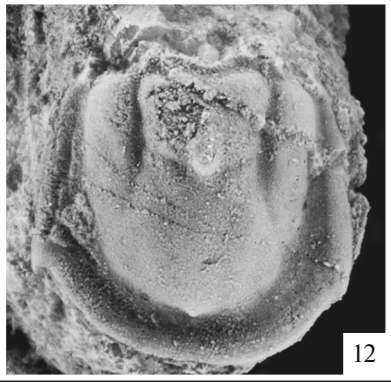

5


7


11


6


8


12

teroaxis delineated by full axial furrow or may be partly efface around its rear; posterior annulation on posteroaxis absent; terminal node usually large, sometimes overhanging border furrow; prosopon smooth or very weakly sculptured.

Species found in Russia. *N. quadratus* (Lazarenko, 1966)—Siberian Platform: Olenek River (lower reach) and Kharaulakh Mountains, Sakian Stage, *Irvingella* and *Maladioidella abdita* (=*Cedarellus felix*) zones and Aksayan Stage, *Plicatolina perlata* Zone (Lazarenko, 1966); Kharaulakh Mountains, Khos-Nelege River, Sakian Stage, *Agnostotes orientalis–Irvingella* Zone (Lazarenko et al., 2008a as *Pseudagnostus quadratus*); Chopko River, *Norilagnostus quadratus–Irvingella cipita* and *Irvingella norilica* zones, Aksayan Stage (Varlamov et al., 2005).

N. quadratiformis—Siberian Platform, Khos-Nelege River, Sakian Stage, *Agnostotes orientalis–Irvingella* Zone (Lazarenko et al., 2008a as *Neoagnostus (N.) quadratiformis*).

Genus *Sulcatagnostus* Kobayashi, 1937

Pseudagnostus (Sulcatagnostus): Taylor, Rushton, 1972, p. 20; Shergold, 1977, p. 89; Shergold et al., 1990, p. 49; Pratt, 1992, p. 35; Shergold and Laurie, 1997, p. 366.

Sulcatagnostus: Kobayashi, 1937, p. 451; 1939, p. 159; Moore, 1959, p. O186; Ergaliev and Ergaliev, 2008, p. 180.

Type species. *Agnostus securiger* Lake, 1906.

Diagnosis. *Pseudagnostus* with third central spine on pygidial border.

Species found in Russia. *Sulcatagnostus* sp. aff. *S. securiger* (Lake, 1906)—Siberian Platform: Chopko River, Sakian Stage, base of the *Pseudoglyptagnostus clavatus–Irvingella angustilimbata* Zone (Varlamov et al., 2005 as *Pseudagnostus (Sulcatagnostus)* sp. aff. *P. securiger*; Varlamov and Rosova, 2009).

Sulcatagnostus sp.—Siberian Platform: Khos-Nelege River, lowermost Aksayan Stage, *Maladioidella abdita* and *Plicatolina perlata* zones (Lazarenko et al., 2008b as *Pseudagnostus (Sulcatagnostus)* sp.).

Genus *Nahannagnostus* Pratt, 1992

Plate 10, fig. 9

Nahannagnostus: Pratt, 1992, p. 36; Peng and Robison, 2000, p. 23; Choi et al., 2004, p. 176; Ergaliev and Ergaliev, 2008, p. 187.

Type species. *Pseudagnostus nganasanicus* Rosova, 1964.

Diagnosis. Pseudagnostidae with convex cephalon and pygidium; preglabellar furrow well defined, with small anteroglabella, sometimes with effaced front part, F3 may be partly effaced; pygidial axis with shortened inflated posterior lobe, F2 straight, small posterolateral spines on border.

Species found in Russia. *N. nganasanicus* (Rosova, 1964)—Siberian Platform: Kulyumbe River, Ayusokkanian Stage, lower Nganasansky Horizon (Rosova, 1964 as *Pseudagnostus nganasanicus* and *"Agnostus" valentinus*), Kharaulakh Mountains, Khos-Nelege River, Ayusokkanian Stage, *Clavagnostus spinosus* and *Glyptagnostus stolidotus* zones (Lazarenko et al., 2008a).

Genus *Agnostotes* Öpik, 1963

Agnostotes: Öpik, 1963, p. 43; Zhu et al., 1979, p. 83; Xiang and Zhang, 1985, p. 88; Lu and Lin, 1989, p. 89; Shergold et al., 1990, p. 49; Pratt, 1992, p. 39; Peng, 1992, p. 25; Shergold and Laurie, 1997, p. 366; Zhang, 2000, p. 96; Choi et al., 2004, p. 173, Peng and Babcock, 2005, p. 107; Ergaliev and Ergaliev, 2008, p. 182; Westrop and Eoff, 2012, p. 219.

Type species. *Agnostotes inconstans* Öpik, 1963.

Diagnosis. Large; variably en grande tenue, variably scrobiculate, with nondeliquiate border furrows, and unconstricted acrolobes; median preglabellar furrow well developed. Glabella with broad anterior lobe; F3 bent forwards; posterior lobe with well-developed, forwardly directed F2 and broadly rounded glabellar culmination, glabellar node slightly in front of F2 furrows. Pygidium bispinose, deuterolobate subcircular to subpyriform, with terminal node; notular lines usually developed (from Shergold and Laurie, 1997, p. 367).

Subgenus *Agnostotes* sensu stricto

Diagnosis. Weakly scrobiculate; cephalic axial furrows relatively weakly impressed. Pygidial axis with weakly impressed F1, F2, and accessory lines, notular lines erratically developed.

Species found in Russia. *Agnostotes* sp.—Siberian Platform: Chopko River, Sakian Stage, *Agnostotes (Pseudoglyptagnostus) clavatus–Irvingella perfecta* Zone (Varlamov et al., 2005, only pl. 2, fig. 6 as *Agnostotes (Agnostotes)?* sp.).

Subgenus *Agnostotes (Pseudoglyptagnostus)* Lu, 1964

Pseudoglyptagnostus: Lu, 1964, p. 42; Lu et al., 1965, p. 33; 1974, p. 83.

Glyptagnostotes: Lazarenko, 1966, p. 42; Ergaliev, 1980, p. 101.

Type species. *Pseudoglyptagnostus clavatus* Lu, 1964.

Diagnosis. Strongly scrobiculate; cephalic axial furrows relatively strongly impressed, and glabellar F1 furrow also strong; lateral portions of glabellar M2 commonly separated from glabella by longitudinal (exsagittal) furrows. Pygidial axis with well-developed F1, F2, and accessory lines, notular lines as deep notches, which sometimes coalescing in dashed furrow.

Species found in Russia. *A. (Pseudoglyptagnostus) orientalis* (Kobayashi, 1935)—Siberian Platform: Olenek River (lower reach) and Kharaulakh Mountains near the village of Chekurovka, Sakian Stage, *Irvingella* and *Cedarellus felix* zones (Laza-

renko, 1966 as *Glyptagnostotes elegans*); Kharaulakh Mountains, Khos-Nelege River, Sakian Stage, *Agnostotes orientalis–Irvingella* Zone (Pegel, 2000, 2001 as *Agnostotes clavatus*; Lazarenko et al., 2008a, 2008b); Chopko River, from upper Sakian Stage to lower Aksayan Stage, *Pseudoglyptagnostus clavatus–Irvingella angustilimbata* and *Irvingella cipita* zones (Varlamov et al., 2005 *Agnostotes (Pseudoglyptagnostus) clavatus*; Varlamov and Rosova, 2009 as *Pseudoglyptagnostus clavatus*).

Genus *Acmarhachis* Resser, 1938

Acmarhachis: Peng and Robison, 2000, p. 20 (see synonymy list); Ergaliev and Ergaliev, 2008, p. 89; Westrop and Eoff, 2012, p. 219.

Type species. *Acmarhachis typicalis* Resser, 1938.

Diagnosis. Pseudagnostidae with border furrows from narrow to moderately wide, pygidial axial furrow outlining posterior lobe. Median preglabellar furrow variably developed. Anterior lobe relatively large, transglabellar F3 straight or bent forward, glabellar culmination acuminate. Pygidial axis constricted at M2; F1 directed forwards, sometimes half effaced, F2 deflected backward; posteroaxis ogival or narrowly rounded at rear, with terminal node. Acrolobes unconstricted or weakly constricted.

Species found in Russia. *A. typicalis* Resser, 1938—northeastern Siberian Platform: Kharaulakh Mountains, lower Upper Cambrian (with *Homagnostus obesus*) (Lermontova, 1940 as *Cyclagnostus elegans* Lermontova (MS)); Olenek River, upper Mayan Stage, *Anopolenus henrici* Zone (Pokrovskaya, 1960); Khos-Nelege River, Ayusokkanian Stage, *Clavagnostus spinosus* Zone, uppermost Sakian Stage, *Maladioidella abdita* Zone (Pegel, 2000 as *Acmarhachis acutus* (Kobayashi); Lazarenko et al., 2008b).

Acmarhachis apicula (Öpik, 1967)—northwestern Siberian Platform: Chopko River, Sakian Stage, *Glyptagnostus reticulatus* Zone (lowermost part) (Varlamov and Rosova, 2009 as *Formosagnostus primus* Rosova et Makarova, 2009).

A. karatauensis Ergaliev, 1980—Siberian Platform, Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2000, 2010, 2014).

Acmarhachis sp.—Altai-Sayany Folded Belt, northeastern Salair Ridge, village of Arinichevo, Ust'-Kul'bich Horizon (lower Upper Cambrian) (Petrunina and Gabova, 2008).

Family Clavagnostidae Howell, 1937

Diagnosis. En grande tenue; with variably zonate pygidial border and narrow or moderate border structures. Transglabellar furrow absent or weakly developed, glabellar node elongate, located near middle or in anterior half of glabella; basal lobes simple, small. Pygidium bispinose or trispinose, narrow, ogival or subtriangular, constricted across M2, F2 if present, strongly deflected by large tubercule, posteroaxis extending to border furrow, with transverse depression as pair of pits, which sometimes joining by deep furrow.

Remarks. *Triadaspis* previously considered as a member of this family has been assigned to Diplagnostidae (see above).

Subfamily Aspidagnostinae Pokrovskaya, 1960

Genus *Aspidagnostus* Whitehouse, 1936

Plate 11, figs. 1 and 2

Aspidagnostus: Peng and Robison, 2000, p. 43 (see synonymy list); Ergaliev and Ergaliev, 2008, p. 213.

Type species. *Aspidagnostus parmatus* Whitehouse, 1936.

Diagnosis. Clavagnostidae with preglabellar furrow present, basal lobes divided, pygidium trispinose, with F1, F2 developed, secondary node well developed, zonate border with collar crossed by median gap.

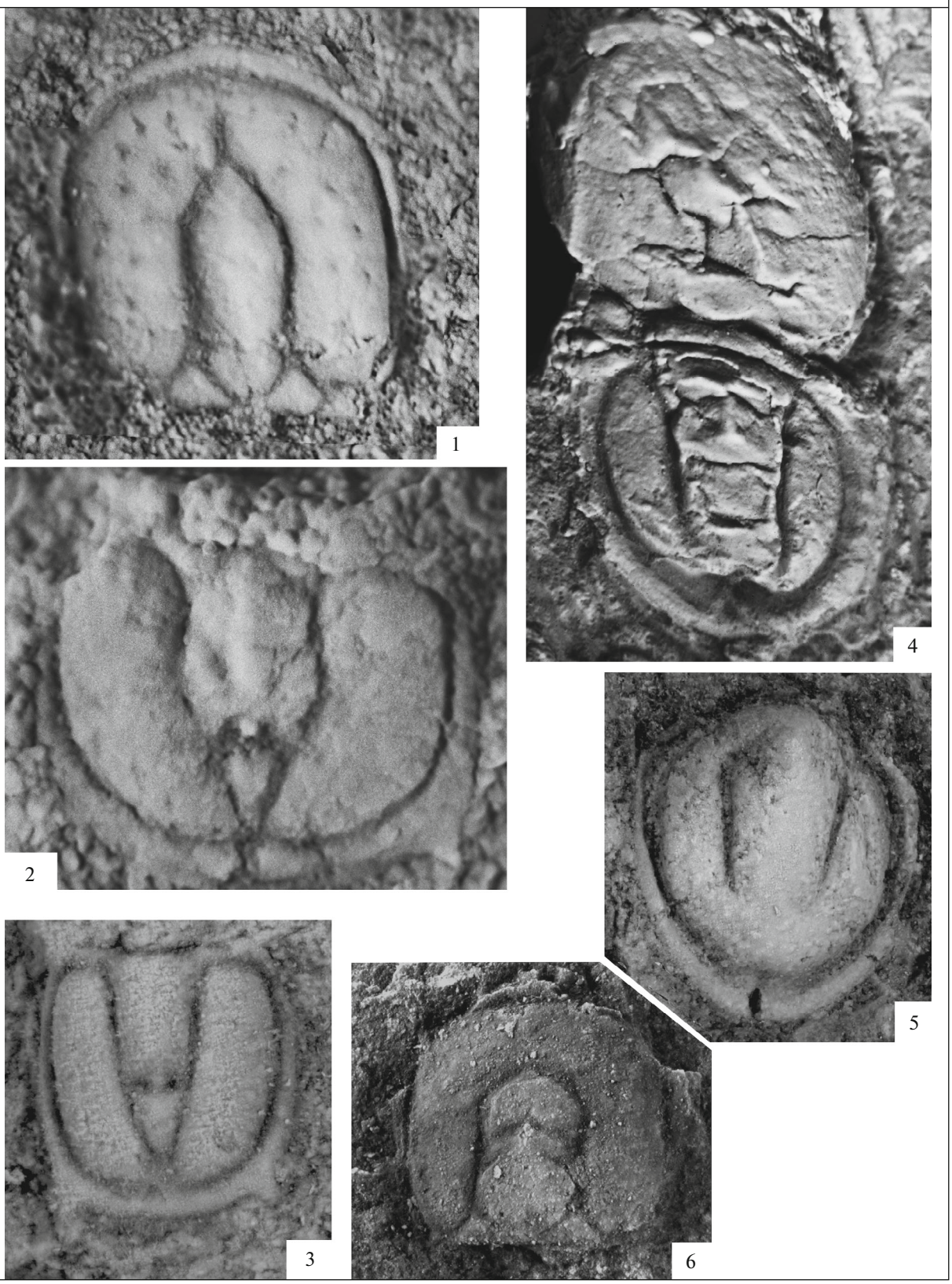
Remarks. *A. laevis* and *A. actuosus* are very close to each other; their difference seems to be quite subtle. The former has less prominent frontal dent in the cephalon and slightly more constricted M2 on the pygidium. These two species should better be combined into one as two subspecies or geographic varieties (Pratt, 1992, Peng and Robison, 2000).

?Biragnostus altaicus Ivshin, 1960 is known by the short description and schematic drawing; the type collection was lost and no additional material has appeared since that first reference of this species. According to the given information, we suggested the synonymy with *Aspidagnostus lunulosus* (Krys'kov, 1963), but due to obscure imaging and description of the older species, the more recently described species was considered to be valid.

Species found in Russia. *Aspidagnostus rugosus* Palmer, 1962—Siberian Platform: Khos-Nelege River, Sakian Stage, *Glyptagnostus reticulatus* Zone (Lazarenko et al., 2008a); Chopko River, *Glyptagnostus reticulatus* Zone (uppermost part) (Varlamov et al., 2005; Varlamov and Rosova, 2009). Altai-Sayany Folded Belt: Altai Mountains, Kul'bich and Bol'shaya Isha rivers, lower Upper Cambrian (Romanenko, 1977).

A. lunulosus (Krys'kov, 1963)—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Sakian Stage, base of *Glyptagnostus reticulatus* Zone (Pegel, 2000; Lazarenko et al., 2008a). Altai-Sayany Folded Belt: Altai Mountains, Kul'bich River, lower Upper Cambrian (Egorova et al., 1960 as *Biragnostus altaicus* Ivshin, 1960); northwestern Kuznetsky Alatau, Kazennaya Vasil'evka River, lower Upper Cambrian,

Plate 11



Ust'-Kul'bichsky Horizon (Petrunina and Gabova, 2008 as *Aspidagnostus* sp.).

A. laevis Palmer, 1962—Siberian Platform: Kharaulakh Mountains, Khos-Nelege River, Ayusakkanian Stage, *Glyptagnostus stolidotus* Zone and Sakian Stage, base of *Glyptagnostus reticulatus* Zone (Lazarenko et al., 2008a); Altai-Sayany Folded Belt, northeastern Altai Mountains, Bol'shaya Isha River, beds transitional from the Middle to Upper Cambrian (Romanenko, 1977 as *A. actuosus* E. Romanenko, 1977).

Subfamily Clavagnostinae Howell, 1937

Genus *Clavagnostus* Howell, 1937

Plate 11, fig. 3

Clavagnostus: Peng and Robison, 2000, p. 38 (see synonymy list); Ergaliev and Ergaliev, 2008, p. 209; Peng et al., 2009, p. 15.

Type species. *Agnostus repandus* Westergård, 1930.

Diagnosis. Clavagnostidae with nonscrobiculate cephalon and pygidium, preglabellar furrow variably developed, basal lobes undivided. Pygidium bispinose or trispinose, posterior lobe of axis reaching border furrow or connected with it by postaxial furrow, transverse depression on posteroaxis present, border simple (azonate) without median gap.

Remarks. *Clavagnostus spinosus* (as *Tomorhachis spinosa*) was briefly described by Resser (1938) on the basis of the only poorly preserved pygidium. Westergård (1946, p. 56) established a new species, *C. sulcatus,* with the cephalon being the holotype; he compared these two species and noted that they both bear a postaxial furrow on the pygidium. Meanwhile, the lack of a cephalon in the former species did not allow an adequate comparison. Siberian species ascribed to *C. spinosus* and *C. sulcatus* do not differ one from another in both cephala and pygidia; therefore, they represent the same species. Here we tentatively refer Siberian forms to the former species for the priority reason.

Clavagnostus cuneatus from Gornyi Altai was established by E. Romanenko (Romanenko and Romanenko, 1967), but she compared it only with the type species and omitted *C. spinosus* (=*?C sulcatus*). Meanwhile, both cephalon and pygidium of *C. cuneatus* completely fit its morphology. Lazarenko et al. (2008a) illustrated *C. spinosus* from Kos-Nelege section (Siberian Platform) and this material appeared to be identical to both American and Altaian species. Here we refer the forms from Gornyi Altai to *C. spinosus*.

Specimens of *Clavagnostus repandus* displayed by Pokrovskaya (1960) were excluded from the species list by Pratt (1992, p. 43). He denoted the rounded outline and more centered posterolateral spines to be a reason to discount these specimens. Pratt based on the illustrations made with artistic retouch, which slightly deformed the original outline. These specimens belong to this species and resemble its other Siberian representatives.

Species found in Russia. *C. spinosus* (Resser, 1938)—Siberian Platform: Kulyumbe River, Ayusokkanian Stage, *Pedinocephalina–Toxotis* Zone (Lazarenko and Nikiforov, 1968); Kotui River (middle reaches), uppermost Middle Cambrian, beds with *Proagnostus bulbus–Toxotis venustus* (Pegel, 2000, 2010, 2014); Khos-Nelege River, Ayusokkanian Stage, *Clavagnostus spinosus* and *Glyptagnostus stolidotus* zones (Lazarenko et al., 2008b). Altai-Sayany Folded Belt: Altai Mountains, Bol'shaya Isha, Tandoshka, and Tagaza rivers, upper Middle Cambrian and lower Upper Cambrian (Romanenko and Romanenko, 1967; Romanenko, 1977 as *Clavagnostus cuneatus*).

C. repandus (Holm et Westergård, 1930)—Bennett Island, Mayan Stage, *Paradoxides forchhammeri* Zone (Lermontova, 1940). Siberian Platform: Yudoma River, Middle Cambrian (Pokrovskaya, 1960); Maya River, upper Mayan Stage, *Anopolenus henrici–Aldanaspis truncata* zones (Egorova et al., 1982); Khos-Nelege River, Mayan Stage, *Anomocarioides limbataeformis*, *Anopolenus henrici*, and *Proagnostus bulbus* zones (Lazarenko et al., 2008a). Altai-Sayany Folded Belt: Altai Region (no time references mentioned) (Lermontova, 1940), Salair Ridge, Orlinaya Mountain, Mayan Stage, Altyrgainsky Horizon, beds with *Goniagnostus nathorsti* (Fedjanina, 1977, pl. 19, fig. 13 as *Hypagnostus brevifrons*).

Explanation of Plate 11

Aspidagnostus, Clavagnostus, Glaberagnostus, and Dividuagnostus

Figs. 1 and 2. *Aspidagnostus lunulosus* (Krys'kov, 1963): (1) holotype TsNIGR, no. 10/8378, cephalon, 2.5 mm long; (2) TsNIGR, no. 11/8378, pygidium, 1.7 mm long (Borovikov and Krys'kov, 1963, pl. 1, figs. 16, 17, respectively); Kazakhstan, Kendyktas Mountains, loc. 503.

Fig. 3. *Clavagnostus sulcatus* Westergård, 1946, TsSGM, no. 80/724, pygidium, 1.9 mm long (Romanenko and Romanenko, 1967, pl. 1, fig. 17 as the holotype of *Clavagnostus cuneatus*); Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River.

Figs. 4 and 5. *Glaberagnostus altaicus* E. Romanenko, 1985: (4) holotype LFGI, no. 1595/239, dorsal shield, 6.5 mm long (Romanenko, 1985, pl. V, fig. 5); (5) TsSGM, no. 17/723, pygidium with a clearly visible incision, 3.5 mm long (Romanenko, 1977, pl. 23, fig. 17 as gen. et sp. indet.; Romanenko, 1985, pl. 5, fig. 7 as *Glaberagnostus altaicus*); Altai-Sayany Folded Belt, Altai Mountains, Ishpa River, loc. 79.

Fig. 6. *Dividuagnostus noduliferrus* (E. Romanenko, 1967); holotype TsSGM, no. 83/724, cephalon, 2.0 mm long (Romanenko and Romanenko, 1967, pl. 1, fig. 20); Altai-Sayany Folded Belt, Altai Mountains, Tagaza River. loc. 216.

Family Unassigned

For the discussion of familial assignment see Peng and Robison, 2000, pp. 11, 86.

Subfamily Glyptagnostinae Whitehouse, 1936

Diagnosis. Median preglabellar furrow well developed; glabellar posterior lobe with very well-developed F2 furrow; pygidium with triangular axis, secondary node developed in association with well-developed transverse depression occurring in rear of posterior lobe; median postaxial furrow well developed.

Genus *Glyptagnostus* Whitehouse, 1936

Glyptagnostus: Westergård, 1947, p. 5; Moore, 1959, p. O178; Öpik, 1961b, p. 428; 1967, p. 167; Palmer, 1962, p. 15; Shergold et al., 1990, p. 37; Pratt, 1992, p. 41; Choi and Lee, 1995, p. 593; Shergold and Laurie, 1997, p. 347; Peng and Robison, 2000, p. 87; Ergaliev and Ergaliev, 2008, p. 87; Westrop and Eoff, 2012, p. 235.

Type species. *Agnostus toreuma* Whitehouse, 1936 (=*Agnostus reticulatus* Angelin, 1851; see Shergold and Laurie, 1997 for the explanation of nomenclature).

Diagnosis. From Shergold and Laurie, 1997, p. 347 "Of low convexity; both cephalon and pygidium strongly scrobiculate. Glabella with anterior lobe subpentagonal to subquadrate; commonly with median sulcus; F3 bent forwards or straight; posterior lobe with very well-developed F2 furrow and with lateral portions of M2 separating midmost glabella by longitudinal (exsagittal) furrows. Glabellar node located from midway between F1 and F2 to level of F2. Basal lobes large. Pygidial axis constricted across M2; M1 trilobate, F1 bent forward; M2 trilobate, axial node extending well onto posterior lobe."

Species found in Russia. *G. reticulatus* (Angelin, 1851)—Siberian Platform: Olenek River, Sakian Stage, *Glyptagnostus reticulatus* Zone (Pokrovskaya, 1960); Chopko River, Sakian Stage, *Glyptagnostus reticulatus* Zone (Rosova, 1977; Varlamov et al., 2005; Varlamov and Rosova, 2009); Khos-Nelege River, Sakian Stage, *Glyptagnostus reticulatus* Zone (Pegel, 2000; Lazarenko et al., 2008a).

G. reticulatus nodulosus Westergård, 1947—northwestern Siberian Platform: Chopko River, Sakian Stage, *Glyptagnostus reticulatus* Zone (uppermost part) (Varlamov and Rosova, 2009 as *Glyptagnostus nodulosus*).

G. stolidotus—Siberian Platform: Khos-Nelege River, Ayusokkanian Stage, *Glyptagnostus stolidotus* Zone (Pegel, 2000; Lazarenko et al., 2008a).

Family Phalacromidae Hawle et Corda, 1847

Diagnosis. Cephalon mostly effaced; pygidium with long and expanded axis without F1 and F2, pygidial axial node positioned more or less in middle of axis.

Remarks. Distinguishing between effaced genera and species represents very difficult task, and no meaningful phylogeny for this bunch of genera was suggested so far. For this reason the supergeneric taxonomy for effaced forms seems unresolved to a great extent. Here we use the formal morphology to diagnose the genera. The main characters are the shape of cephalic and pygidial borders and the position and shape of median nodes on the cephalon and pygidium. The degree of effacement of axial furrows seems to be less important, because it depends on the mode of preservation. The following genera bear cephalic border—*Agnostogonus*, *Valenagnostus*, *Pseudophalacroma*, *Peratagnostus,* and *Lisogoragnostus* (two latter are within Spinagnostidae, *Lisogoragnostus* in some cases lacks this border). Among them, *Peratagnostus* and *Pseudophalacroma* have the narrowest border; sometimes, it is indiscernible. *Peratagnostus* also has a relic relief of the glabella. Four genera are distinguished by pygidial morphology: *Pseudophalacroma* has a border widened at the rear, but the axial furrow is almost fully effaced. *Peratagnostus* has vestigial axial furrows, which define a narrow axis. *Agnostogonus* has a convex narrow border, median node of moderate size. *Valenagnostus* has a posteriorly widened flat border, but with a long axis indicated by axial relief or/and by a terminal node.

Ciceragnostus was established by Kobayashi in 1937 based on the type species *Agnostus barlowi* Belt, 1868. It possesses a cephalon without border structures, with a faint relief of the glabella outlined posteriorly; the pygidium has a flat border and border furrow, bearing a small median node, axial furrow outlining M1, and it is possibly deuterolobate (Shergold and Laurie, 1997, p. 377). Providing a revision of the type material, Lake (1906) noted that *Agnostus barlowi* Belt, 1868 and *A. cicer* Tullberg, 1880 were synonyms and that Belt had erroneously defined the stratigraphic interval for his species as Tremadocian. Lake considered this species as a Middle Cambrian representative. But to date, the holotype shield of *C. barlowi* is still referred to the Tremadocian and has not been associated with *A. cicer*. Therefore, *A. cicer* may be compared to other Cambrian effaced genera, i.e., *Grandagnostus* (Rushton, 1978), *Toragnostus, Glaberagnostus* (Peng and Robison, 2000), or *Phaldagnostu*s. In other words, *Ciceragnostus* should not be confused with Mid–Upper Cambrian effaced genera.

Grandagnostus Howell, 1935 was defined by a very poorly preserved cephalon and no pygidia accompany this specimen. Therefore, this genus is quite indefinite to discuss its affinities and generic composition. We cannot follow Rushton (1978) in placing *Grandagnostus* at the end of the phyletic lineage from *Peronopsis* to *Cotalagnostus* and *Peratagnostus* due to unreliable

pygidial morphology. In addition, the absence of pygidia does not allow reserving this genus as a basket for effaced forms with cephala without borders and pygidia with border structures, as was suggested by Rushton (1978).

Phaldagnostus Ivshin, 1960 was originally diagnosed with the same characters as *Ciceragnostus*. The image of the type species *Phaldagnostus orbiformis* Ivshin, 1960 was represented with one schematic drawing. The only difference between the two genera seems to be important, that is, the absence of a cephalic border in *Phaldagnostus*. Since the 1960s, no one good image or description of the material of *Phaldagnostus* has been appeared in the literature. Romanenko (1977) published one very poor image without a description. The generic morphology remained rather obscure until Petrunina and Gabova (2008) published a number of images of two species assigned to this genus (without descriptions unfortunately). The images show presence of a scarcely distinguishable cephalic border in *Phaldagnostus* (Petrunina and Gabova, 2008, pl. 4, figs. 4, 6). A revision of the material from this collection (the collection originating from the same locality as the type specimens of *P. orbiformis*) has shown that this species lacks a cephalic border furrow (here Pl. 13, fig. 2); probably the presence of cephalic border structures was confused by shadows. Therefore, *Phaldagnostus* becomes close in morphology to the next group of genera, which lacks border structures on the cephalon.

The group without cephalic border structures includes *Megagnostus*, *Toragnostus*, *Phalagnostus*, *Phalacroma, Glaberagnostus, Sphaeragnostus,* and *Phaldagnostus*. They differ from each other in the shape and expression of pygidial furrows, although not yet clearly. Peng and Robison (2000) suggested combining *Toragnostus* and *Glaberagnostus* as the former may represent a more effaced version of the latter. In my opinion, there is an important character which was not considered in the revision – the indentation at rear of the pygidium in *Glaberagnostus* occupied both border and border furrow and the posterior of the acrolobe. The same structures developed convergently within the Aspidagnostidae. Given this difference, we separate these two genera.

The only feature that distinguishes *Toragnostus* and *Phaldagnostus* is the long pygidial carinated tubercle. Cephalons of the two genera are quite similar. *Toragnostus* was established by Robison (1994) for effaced species with the cephalic doublure turned up. But later, Robison (Peng and Robison, 2000) rejected this feature as it appeared to vary and depend on the mode of preservation. Therefore, the difference between these two genera became inconsiderable and *Toragnostus* and *Phaldagnostus* should be regarded as synonyms with the suppression of the former one. Here we synonymize them and it delineates the taxonomic space for effaced genera with cephala lacking border structures and pygidia with them; nodes on the cephalon and pygidium are present; vestigial axial furrows may present around the rear of glabella and anteroaxis.

Phalagnostus is an exceptional genus lacking the pygidial border (Robison, 1994, p. 69). Another example of a genus lacking a pygidial border is *Lisogoragnostus* (but the latter has both the median and terminal axial nodes). Instead, their pygidial axis expanded and lost both transaxial furrows F1 and F2. In the absence of a pygidial border, the pygidial axis itself resembles an entire acrolobe, while the narrowed pleurae become superficially similar to a border, and the axial furrow, to a border furrow. Therefore, the main differential character of the genus is the distinct pseudoacrolobe usually widened in the rear part. Such pygidial morphology can be accompanied by a slightly different cephalic morphology with fully or partly effaced axial furrows at M1 and M2.

Like *Phalagnostus,* the genus *Sphaeragnostus* also has an expanded round axis with no sign of F1 and F2, but bears a well-expressed border and border furrow. *Phalacroma* with the type species *Battus bibullatus* Barrande, 1846 is characterized by narrow border in pygidium, residual axial furrows around M1 and M2 of a very wide axis. Another character indicated in the generic diagnosis (and sometimes in the diagnosis of the family Phalacromidae, as in Shergold and Laurie (1997, p. 381), is the presence of a transverse pygidial depression or groove behind the axial node.

Family *Phalacromidae,* along with the transverse depression, is defined by (1) variably effaced cephalon; (2) pygidium with long and expanded axis; (3) pygidial axial node is located more or less in the middle of the acrolobe; (4) variable border morphology and spinosity. Three genera were previously included in this family: *Phalacroma*, *Dignagnostus*, and *Lisogoragnostus*. *Lisogoragnostus* was transferred to Spinagnostidae due to clear familial characters in meraspids and early holaspids of *Lisogoragnostus* (Peng and Robison, 2000, p. 64). Therefore, only two genera are left in the Phalacromidae. One of them, *Dignagnostus,* is known only from a pygidium and its spiny border differs strongly from all other effaced genera. For this reason, *Dignagnostus* was placed with caution into Phalacromidae. Probably, the only reason for such taxonomic decision was the similar shape of the pygidial axis in *Dignagnostus* and *Phalacroma*. But in our opinion, this feature is not convincing reason to connect these two taxa. Thus, the family Phalacromidae contains with certainty only one genus, *Phalacroma*.

The genus *Megagnostus* Robison, 1994 was established for large (on the agnostid scale) effaced species with the pygidial border turned anterolaterally more or

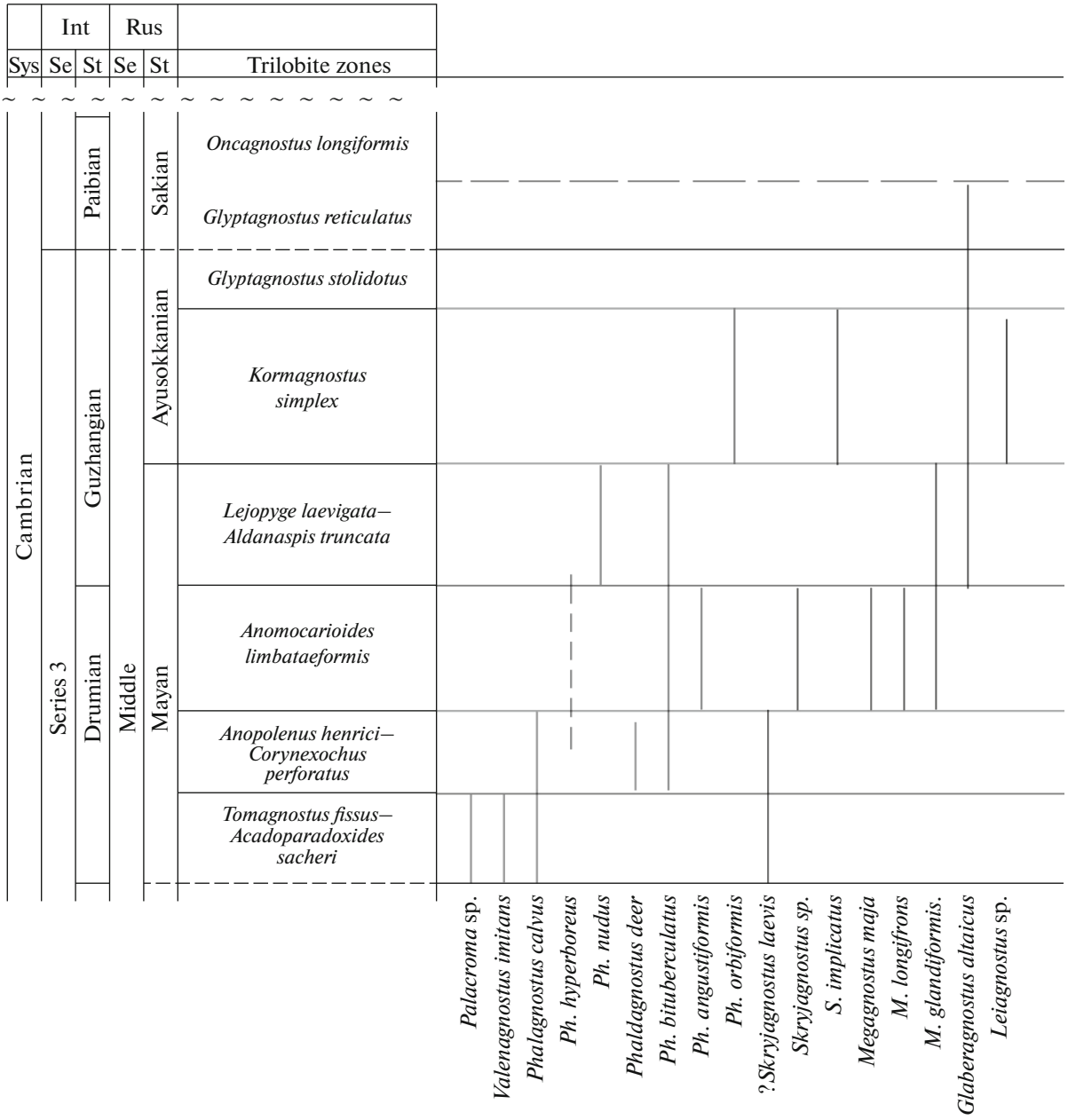


Fig. 11. Stratigraphic distribution of effaced species known from Russia.

less upward, although the latter character Robison did not include in the diagnosis. The original diagnosis indicated vestigial cephalic border, pygidial border flat, and sometimes turned up, effaced pygidial axis with the only median node, which is weak and small. Robison placed some Siberian species in this genus and here we follow his decision with one exception.

Leiagnostus Jaekel, 1909 also has a flat pygidial border rim and no cephalic border. It completely lacks cephalic or pygidial furrows as well as nodes or spines on the borders. In this aspect it resembles *Skryjagnostus,* but differs in the ovate shape of both acrolobes.

Stratigraphic distribution of effaced agnostoid species from different taxonomic groups known from Russia is shown in Fig. 11.

Genus *Phalacroma* Hawle et Corda, 1847

Phalacroma: Pokrovskaya, 1958, p. 42 (see synonymy list, except *Grandagnostus*); Shergold et al., 1990, p. 58; Shergold and Laurie, 1997, p. 381.

Type species. *Battus bibullatus* Barrande, 1846.

Diagnosis. Cephalon totally effaced; no border in cephalon, narrow border in pygidium, pygidial bor-

der furrow almost totally indistinct, pygidial axis wide, expanded, almost reaching border structures; median node at middle of axis, axis with weak transverse depression.

Remarks. Given the lack of the diagnostic transverse axial depression *Phalacroma calva* Pokrovskaya, 1958 should be reassigned to another genus (here to *Phalagnostus*). *Phalacroma laevis* Pokrovskaya, 1958 is an exceptional form among other smooth species, as it possesses borders neither on cephalon nor on pygidium. Moreover, this species lacks cephalic or pygidial furrows. According to the lack of any hints of its generic affinity, we questionably place this species within *Skryjagnostus,* as Fatka et al. (2004) suggested.

Species found in Russia. *Phalacroma* sp.—Siberian Platform: Yudoma River, lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone (Egorova et al., 1982, only pl. 4, fig. 12 as *Phalacroma calva*).

Genus *Skryjagnostus* Šnajdr, 1957

Plate 12, fig. 4

Skryjagnostus: Šnajdr, 1957, p. 236; Shergold et al., 1990, p. 57; Shergold and Laurie, 1997, p. 380; Fatka et al., 2004, p. 77.

Type species. Skryjagnostus pompeckji Šnajdr, 1957.

Diagnosis. Cephalon and pygidium semicircular, cephalon totally effaced, except for hint of axial furrow around rear of basal lobes, border may be visible, but extremely narrow. Pygidium totally effaced, except very narrow border slightly wider at rear.

Remarks. Fatka et al. (2004, p. 77) supposed that *Phalacroma laevis* is conspecific with *Skryjagnostus pompeckji,* but they did not explain their view. In fact, *P. laevis* differs from the type species and does not possess diagnostic characters of *Phalacroma* pygidium. Here we follow the opinion of Czech authors and reassign this species to *Skryjagnostus*, but as a separate species due to the small size of *P. laevis*.

The holotype and paratypes of *P. laevis* with other material to the manuscript of Pokrovskaya (1958) have not been found.

Species found in Russia. *S. implicatus* Lazarenko, 1968—Siberian Platform: Kulyumbe River, Ayusokkanian Stage, lower *Pedinocephalina–Toxotis* Zone (Lazarenko and Nikiforov, 1968).

Skryjagnostus sp.—Siberian Platform: Lena River (middle reaches), Mayan Stage, *Anomocarioides? curtus* Zone (Egorova et al., 1982, pl. 62, fig. 4 as *Phalacroma maja*).

?Skryjagnostus laevis (Pokrovskaya, 1958)—Siberian Platform: Maya River, Mayan Stage, *Anopolenus henrici* Zone (Pokrovskaya, 1958; Egorova et al., 1982 as *Phalacroma laevis*); Botoma and Lena rivers, Mayan Stage, upper *Tomagnostus fissus–Paradoxides hicksi* Zone and lower *Anopolenus henrici–Liostracus jakutensis* Zone (Pokrovskaya, 1958).

Family Uncertain

Genus *Phalagnostus* Howell, 1955

Phalagnostus: Peng and Robison, 2000, p. 95 (see synonymy).

Type species. *Battus nudus* Beyrich, 1845.

Diagnosis. Almost totally effaced, without median node in cephalon and pygidium; no border in cephalon. Pygidial border absent or fused with acrolobe, axis circular or ovate, expanded and, thus, occupying two–thirds of pygidium, making it similar to ordinary effaced acrolobe, but origination of that false acrolobe becoming clear from ontogenesis; "false border" in pygidium widened at rear, but sometime remaining constant in width.

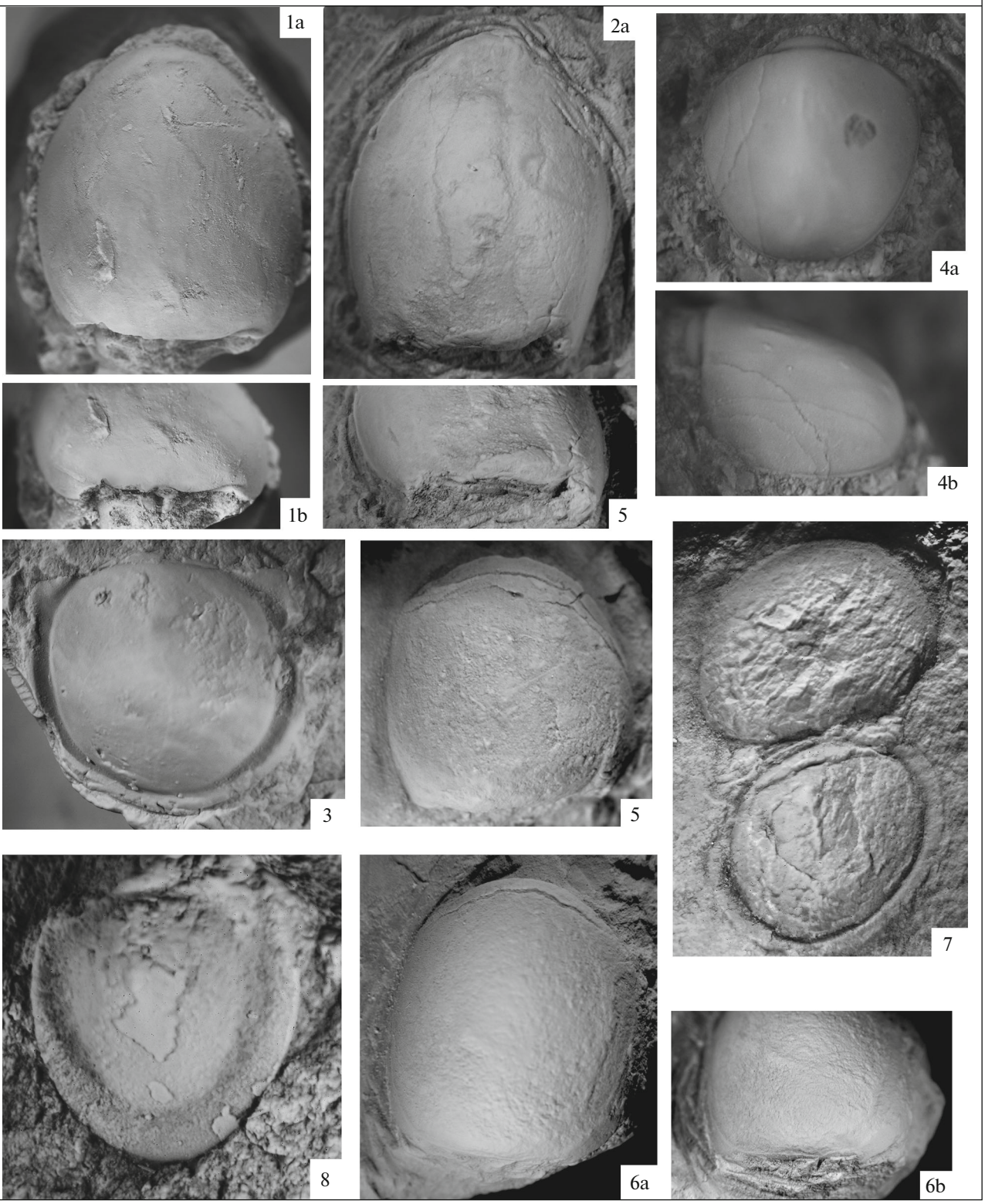
Remarks. The subspecies *Agnostus nudus hyperboreus* was described by Holm and Westergård (1930, p. 12) from Bennett Island; later, Lermontova (1940) ranked it species. Holm and Westergård defined *hyperboreus* as a form with a uniform rim in the pygidium in comparison with *Agnostus nudus*. In addition, they indicated the fairly truncated front of the cephalic acrolobe to separate the subspecies from *Agnostus glandiformis*. But one specimen of Holm and Westergård's collection (1930, pl. 1, fig. 9, refigured in Lermontova, 1940, pl. 36, fig. 9b) shows a nonuniform pygidial rim; and another (Holm and Westergård, 1930, pl. 1, fig. 6) lacks a truncate front, but has very convex cephalic acrolobe, which mimics the truncation. Lermontova repeated the image of this enrolled specimen from Bennett Island, *P. forchhammeri* Zone (Lermontova, 1940, pl. 36, figs. 9c–9f). Another specimen (cephalon) from the Anabar Region was erroneously chosen by Lermotova to illustrate the species. It has different outline and height, thus, belongs to a different species (*Megagnostus maja*). *P. hyperboreus* probably includes representatives from the Abbey shale, *T. fissus* Zone (*Phalagnostus* sp. in Rushton, 1979, fig. 9C).

Siberian specimen of *P. nudus* (pygidium) lacks a median node mentioned in the species description; it may be a preservational bias, but we assigned the Siberian form to this species with a question.

Species found in Russia. *P. ?nudus* (Egorova et al., 1982, pl. 49, fig. 1 as *Phalacroma glandiforme*); *P. calvus* (Pokrovskaya, 1958) (Egorova et al., 1982); *P. hyperboreus* (Holm and Westergård, 1930) (Holm and Westergård, 1930; Lermontova, 1940, pl. 36, figs. 9c–9f as *Phalacroma hyperborea*).

Occurrences. *Phalagnostus nudus* (Beyrich, 1845)—Siberian Platform: Aldan River, upper Mayan Stage, *Anopolenus henrici* Zone (Egorova et al., 1982, pl. 49, fig. 1 as *Phalacroma glandiforme*).

Plate 12



P. calvus (Pokrovskaya, 1958)—Siberian Platform: Yudoma River, Amgan Stage; Maya River, lowermost Mayan Stage, *Tomagnostus fissus–Paradoxides hicksi* Zone (Pokrovskaya, 1958 as *Phalacroma calva*; Egorova et al., 1982 as *Phalacroma calva*, except pl. 2, fig. 3, pl. 4, fig. 12); Maya River, Mayan Stage, *Anopolenus henrici* Zone, Lena River (middle reaches), Mayan Stage, *Tomagnostus fissus* and *Liostracus allachjunensis* zones, *Anopolenus henrici* Subzone (Egorova et al., 1982).

P. hyperboreus—Bennett Island, middle Middle Cambrian (Holm and Westergård, 1930; Lermontova, 1940, pl. 36, figs. 9c–9f as *Phalacroma hyperborea*).

Genus *Phaldagnostus* Ivshin, 1960

Plate 12, fig. 7

Phaldagnostus: Egorova et al., 1960, p. 168; Romanenko, 1977, p. 168; Ergaliev, 1980, p. 81; Shergold et al., 1990, p. 56; Shergold and Laurie, 1997, p. 380; Ergaliev and Ergaliev, 2008, p. 222; Petrunina and Gabova, 2008, p. 32.

Toragnostus: Robison, 1988, p. 52; 1994, p. 72; Shergold et al., 1990, p. 57; Shergold and Laurie, 1997, p. 381; Ergaliev and Ergaliev, 2008, p. 224.

Type species. *Phaldagnostus orbiformis* Ivshin, 1960.

Diagnosis. Agnostoids with advanced effacement of axial furrows. Cephalon retaining vestigial basal lobes and most rear part of axial furrow, but lacking other glabellar furrows as well as border structures. Median glabellar node faint, in position near or advanced from cephalic midpoint. Pygidial axis wide at its front as indicated by anterior vestiges of axial furrow; median node weak, elongate, border moderately wide, nonspinous, and without rear notch, border furrow expressed.

Remarks. We synonymize *Phaldagnostus* and *Toragnostus,* since the difference between them seems insufficient for generic rank. These differences are the carinated, elongate pygidial median node in *Phaldagnostus*, pygidial doublure upturned in *Toragnostus*. But these characters are variable and the carinate node in *Phaldagnostus* expresses only on exfoliated specimens.

Phaldagnostus orbiformis and *P. oviformis* Ivshin, 1960 differ in the shape of acrolobes, which are ovate in the latter and rounded in the type species. The revision of the type collection revealed intermediate forms between them, thus, these species may be synonyms.

Agnostus cicer Tullberg, 1880 is assigned to *Phaldagnostus*, although Peng and Robison (2000, p. 91) assigned this species to *Glaberagnostus*. *Phaldagnostus cicer* from Siberia was illustrated by two varieties. One of them we identified as true *P. cicer* identical to the holotype (Tullberg, 1880, pl. 2, fig. 16). The second variety (Egorova et al., 1982, pl. 18, fig. 1, pl. 19, fig. 4, pl. 23, fig. 3) differs from typical *P. cicer* in several characteristics of the pygidium: the narrow convex border, the axis constricted across M2 with expanded posteroaxis, vestigial F1 and F2 visible on sides. All this characters allowed us to associate this variety with *Cotalagnostus*.

Species found in Russia. *Phaldagnostus bituberculatus* (Angelin, 1851)—Siberian Platform: Anabar and Aldan regions, Mayan Stage, *Paradoxides forchhammeri* Zone (Lermontova, 1940 as *Phoidagnostus bituberculatus*); Maya, Lena, Olenek, and Kulyumbe rivers, *Centropleura oriens* Zone (Pokrovskaya, 1958, 1960 both as *Phoidagnostus bituberculatus*); Kulyumbe River, middle Cambrian, Nenetsky Horizon (Rosova, 1964 as *Phoidagnostus bituberculatus*); Maya River, Mayan Stage, *Anopolenus henrici* and *Anomocarioides limbataeformis* zones, lowermost *Aldanaspis truncata* Zone (Egorova et al., 1982, pl. 22, fig. 6 as *Phoidagnostus angustiformis*, pl. 23, fig. 5 as *Phalacroma glandiforme*). Altai-Sayany Folded Belt: Salair Ridge, Orlinaya Mountain, upper Middle Cambrian (Lermontova, 1940 as *Phoidagnostus bituberculatus*); Altai Mountains, Bol'shaya Isha River, upper Mayan Stage (Romanenko, 1977 as *Phoidagnostus bituberculatus*).

P. angustiformis (Pokrovskaya, 1958)—Siberian Platform: Maya River Mayan Stage, *Prohedinia–Forchhammeria–Anomocarioides limbataeformis* Zone (Pokrovskaya, 1958 as *Phoidagnostus angustiformis*); Altai-Sayany Folded Belt, Salair Ridge, Orlinaya

Explanation of Plate 12

Phalacromidae and effaced species.

Figs. 1–3. *Megagnostus longifrons* (Lermontova, 1940), lectotype TsNIGR, no. 88/9182, cephalon, 14 mm long (Lermontova, 1940, pl. 36, fig. 8): (1a) plan and (1b) rear views; (2a) TsNIGR, no. 91/9182, cephalon, 15 mm long (Lermontova, 1940, pl. 36, fig. 8d): (2a) plan and (2b) rear views; (3) TsNIGR, no. 89/9182a, pygidium, 9.8 mm long (Lermontova, 1940, pl. 36, fig. 8a); Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain.

Fig. 4. *Skryjagnostus implicatus* Lazarenko, 1968, holotype (TsNIGR, no. 17/9969, pygidium, 2.9 mm long; (4a) plan and (4b) lateral views (Lazarenko and Nikiforov, 1968, pl. 1, figs. 14, 15); northwestern Siberian Platform, Kulyumbe River, loc. 23–d[1].

Figs. 5 and 6. *Megagnostus maja* (Pokrovskaya, 1958): (5) TsNIGR, no. 84/9182a, pygidium, 7 mm long; (6) TsNIGR, no. 84/9182b (same slab as previous), pygidium, 10 mm long: (6a) plan and (6b) rear views; Siberian Platform, Anabar Region.

Fig. 7. *Phaldagnostus orbiformis* Ivshin, 1960, LFGI, no. 1595/136, dorsal shield, 9.8 mm long; Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River, loc. 2633.

Fig. 8. *?Leiagnostus* sp., LFGI, no. 61/1595, pygidium, 3.1 mm long; Altai-Sayany Folded Belt, Altai Mountains, Bol'shaya Isha River, loc. 87.

Mountain, Mayan Stage, Altyrgainsky Horizon (=*Goniagnostus nathorsti* Zone) (Fedjanina, 1977 as *Phoidagnostus angustiformis*).

P. orbiformis Ivshin, 1960—Altai-Sayany Folded Belt: northwestern Kuznetsky Alatau, Kazennaya Vasil'evka River, lower Upper Cambrian, Ust'-Kul'bich Horizon (Petrunina and Gabova, 2008 as *Phaldagnostus oviformis*); Gornyi Altai, Kul'bich and Bol'shaya Isha rivers, Ust'-Kul'bich Horizon (Egorova et al., 1960 as *Phaldagnostus oviformis*; Romanenko, 1977).

P. cicer (Tullberg, 1880)—Siberian Platform: Lena River, (middle reaches), Mayan Stage, *Liostracus allachjunensis* Zone, *Anopolenus henrici* Subzone (Egorova et al., 1982, pl. 54, fig. 8, pl. 61, figs. 3, 4 as *Ciceragnostus cicer*); Yudoma River, Middle Cambrian (Pokrovskaya, 1960 as *Ciceragnostus cicer*).

Genus *Glaberagnostus* Romanenko, 1985

Plate 11, figs. 4 and 5

Glaberagnostus: Romanenko, 1985, p. 57; Shergold et al., 1990, p. 55; Shergold and Laurie, 1997, p. 377; Peng and Robison, 2000, p. 90; Ergaliev and Ergaliev, 2008, p. 218.

Type species. *Glaberagnostus altaicus* Romanenko, 1985.

Diagnosis. Cephalon smooth, lacking border, and mostly effaced, with glabella and small basal lobes outlined only posteriorly, median node weak elongate and in position at cephalic midpoint. Pygidium smaller than cephalon, border narrow, convex, indented by deep notch at rear, border furrow moderate to deliquiate widened at rear with acrolobe having recession at rear; axial furrows effaced in posterior part, F1, F2 effaced, but may be seen on exfoliated surface, median node weak, elongate.

Species found in Russia. *Glaberagnostus altaicus* E. Romanenko, 1985 – Altai-Sayany Folded Belt: Altai Mountains, Isha and Bol'shaya Isha rivers, Mayan Stage (*Anopolenus henrici* Zone), Ayusokkanian Stage and Sakian Stage (*Glyptagnostus reticulatus* Zone) (Romanenko, 1977, pl. 23, figs. 17–19 as gen. et sp. indet.; Romanenko, 1985).

Genus *Megagnostus* Robison, 1994

Plate 12, figs. 1–3, 5, and 6

Megagnostus: Robison, 1994, p. 61; Westrop et al., 1996, p. 825; Ergaliev and Ergaliev, 2008, p. 227.

Type species. *Agnostus glandiformis* Angelin, 1951.

Diagnosis. From Robison, 1994, pp. 60–61: Large agnostids, with "cephalon mostly effaced, retaining only vestiges of posterior border furrows; convexity low to moderate; cephalic doublure narrow. Pygidium with doublure curved inward and downward, forming ventrally projecting flange; pygidium smaller than cephalon, with acrolobe effaced, except for weak median node; convexity low; border furrow of pygidium well developed or may become effaced posteriorly on large holaspids."

Remarks. We considered *Phalacroma longifrons* Lermontova, 1940 to be a species of this genus. There is no holotype chosen by Lermontova for the *P. longifrons*, but there are a number of specimens (both cephala and pygidia) from the same locality in the type collection. The cephala expose visible outline of the cephalothoracic foramen and residue of the axial furrow defined the very rear of the glabella. Pygidia possess border structures, which are specific for *Megagnostus;* the border is flattened in the posterior and turns up on sides; the border furrow deepens on sides. As no complete shields have been found so far, the cephala and pygidia of this species are combined together with a certain doubt. Pygidia of *Phalacroma longifrons* closely resemble those of *M. maja* Pokrovskaya, 1958 and they are difficult to distinguish.

Phalacroma cuneatus Rosova, 1964 is possibly referred to as a junior synonym of *M. longifrons. P. cuneatus* is based on two specimens: the holotype pygidium and cephalon. The holotype pygidium lacks an anterior part and, therefore, we cannot distinguish it from the cephalon. Its cephalon is also broken and either lacks articulating devices. The shape of the acrolobe and specific anteriorly elongated margin do not differ from the cephala of *M. longifrons*.

Megagnostus maja (Pokrovskaya, 1958) can be separated from *M. glandiformis* by the more rounded cephalic outline and higher cephalic acrolobe with rather steep sides, and by the absence of even a slight trace of the median node on the acrolobe; their pygidia look the same. Given the differences in cephalic characters, we do not follow the synonymy suggested by Robison (1994) and consider this species valid. *M. maja* should be synonymized with *Phalacroma antiqua* Pokrovskaya, 1958, for which only cephala were known. Although the type collection with these species was not found, some other representatives from the Anabar Region were identified from Lermontova's collection. These specimens (cephala) were on the same slab; one of them displayed the indicated differential characters of *M. maja*, and another, those of *P. antiqua* (here Pl. 2, figs. 5, 6): the different shape of cephalic rear and width-to-length ratio.

M. maja, M. glandiformis, and *M. longifrons* demonstrate gradually elongating cephala, the flange of which is rounded in the first and long (exag.) and flat in the third.

Species found in Russia. *M. glandiformis* (Angelin, 1851)—Bennett Island, Mayan Stage, *Paradoxides forchhammeri* Zone (Lermontova, 1940 as

Grandagnostus glandiformis; Pokrovskaya, 1958 as *Phalacroma glandiforme*); Siberian Platform: Maya, Chabda, and Aldan rivers, Mayan Stage, *Anomocarioides limbataeformis* and *Anopolenus henrici* zones (Lermontova, 1940; Pokrovskaya, 1958; Egorova et al., 1982 pl. 55, figs. 12, 13, pl. 59, fig. 5, pl. 62, fig. 9 as *Phalacroma glandiforme*, pl. 19, fig. 2, pl. 25, fig. 3, pl. 47, figs. 2, 3, pl. 59, fig. 4 as *Phalacroma maja*; Pegel, 2000); Lena River, Mayan Stage, *Liostracus allachjunensis* and *Anomocarioides? curtus* zones (Pokrovskaya, 1958; Egorova et al., 1982); Yudoma, Botoma, and Olenek rivers, Mayan Stage, *Anomocarioides limbataeformis* and *Centropleura oriens* zones (Pokrovskaya, 1958, 1960); Kulyumbe River, upper Sel'kupsky Horizon (Rosova, 1964 pl. 2, figs. 14, 15 as *Phalagnostus glandiformis*).

M. longifrons (Lermontova, 1940)—Siberian Platform: Maya, Olenek, Botoma, and Lena rivers, Mayan Stage, *Prohedinia–Anomocarioides limbataeformis* Zone (Lermontova, 1940 *Grandagnostus longifrons*; Pokrovskaya, 1958; Egorova et al., 1982 both as *Plalacroma longifrons*); Kulyumbe River, Mayan Stage, Sel'kupsky and Nenezky Horizons (Rosova, 1964 as *Phalagnostus cuneatus;* Rosova, 1964). Altai-Sayany Folded Belt, Salair Ridge, Orlinaya Mountain, Mayan Stage, *Paradoxides forchhammeri* Zone (Lermontova, 1940).

M. maja—Siberian Platform: Maya and Lena rivers, Mayan Stage, *Centropleura oriens*, *Prohedinia–Forchhammeria–Anomocarioides limbataeformis* zones (Pokrovskaya, 1958 as *Phalacroma maja* and *P. antiqua*); Anabar Region, Mayan Stage (from Lermontova, 1940, pl. 36, fig. 9b as *Phalacroma hyperborea*).

Genus *Leiagnostus* Jaekel, 1909

Plate 12, fig. 8

Leiagnostus: Jaekel, 1909, p. 401; Troedsson, 1937, p. 31; Harrington and Leanza, 1957, p. 76; Lisogor, 1971, p. 181; Ahlberg, 1988, p. 364; 1992, p. 567; Shergold et al., 1990, p. 56; Shergold and Laurie, 1997, p. 380; Nielsen, 1997, p. 490; Tortello, 1998, p. 97; Bao and Jago, 2000, p. 887.

Phoidagnostoides: Pillet in Capera et al., 1978, p. 78.

Type species. *Leiagnostus erraticus* Jaekel, 1909.

Diagnosis. Cephalon and pygidium ovoid, effaced, lacking axial and transaxial furrows, axial nodes very weak or absent; cephalic border absent, pygidial border nonspinose, flat or convex, border furrow leveled with border; thoracic segments relatively narrow.

Remarks. Only one specimen (pygidium) of this genus was found among the Russian material. This specimen originates from the Altai Region and has been stored in Novokuznetsk (LZGU, undescribed). We refer it to *Leiagnostus* sp., but more reliable identification would be possible with additional specimens in hand. This specimen fits the generic diagnosis; but it should be noted that there are neither discernible axial node nor axial furrows on the acrolobe, although it needs to be mentions that its preservation is rather poor. A similar form was mentioned in the upper Upper Cambrian Yinchupu Formation (Lu and Lin, 1984, *Leiagnostus* sp. 3). We imaged the specimen from Altai, since this is the only representative of the genus known from Russia. The second specimen from the same locality looks more or less the same, but with a definitely upturned pygidial border. We do not know if this difference reflects the intraspecific or preservational variability or the intraspecific or intrageneric characters. In the case of the intraspecific variability, this species should be assigned to *Phaldagnostus* (or *Toragnostus*), which also agrees better with its relatively low stratigraphic position for *Leiagnostus.*

Species found in Russia. *Leiagnostus* sp.—Altai Folded Belt: Altai Mountains, Bol'shaya Isha River, loc. 87 (probably Ausokkanian Stage) (Romanenko, 1977, p. 163, fig. 17).

Genus *Valenagnostus* Jago, 1976

Valenagnostus: Jago, 1976, p. 142; Shergold et al., 1990, p. 57; Shergold and Laurie, 1997, p. 381; Peng and Robison, 2000, p. 95; Peng et al., 2009, p. 24.

Type species. *Agnostus nudus* var. *marginata* Brögger, 1878.

Diagnosis. Cephalon with narrow border and border furrow, axial furrows effaced, except rear of basal lobes; glabellar relief may be discernible, median node usually present. Pygidium with deliquate border furrow and border widened posteriorly, axial furrows effaced or very weak, axis reaching border furrow, median node is present and also terminal node may appear.

Remarks. The Siberian form is most similar to the Australian species *V. imitans* (Öpik, 1961). These two are similar in the pygidial outline, border and border furrow morphology, in the position of median and terminal nodes (the latter is not well expressed), and in the shape of vestigial M1. They differ in the presence of a low crest extended from the median to the terminal node in *V. imitans*. This feature may result from a preservational bias; if this is the case, the Siberian form should be referred to *V. imitans*.

Species found in Russia. *V. imitans* (Öpik, 1961)—Siberian Platform: Yudoma River, *T. fissus* Zone (Egorova et al., 1982 as *Cotalagnostus* sp. 1).

Family Metagnostidae Jaekel, 1909

Diagnosis. Shergold and Laurie, 1997, p. 373: "Usually en grand tenue; cephalon nonspinose; median preglabellar furrow absent; glabella with semiovate anterior lobe, transglabellar F3 variably chevron or concave forward, glabellar node advanced

at F3. Pygidium usually bispinose, postaxial furrow absent; axis short, not reaching border furrow; F1 impressed laterally, curving forward to articulating furrow, isolating anterolateral lobes; F2 straight or deflected by axial node; posterior lobe short, commonly with secondary node."

Genus *Dividuagnostus* Koroleva, 1982

Plate 11, fig. 6

Dividuagnostus: Koroleva, 1982, p. 21; Zhou, 1987, p. 659; Shergold et al., 1990, p. 54; Nielsen, 1997, p. 479; Shergold and Laurie, 1997, p. 375.

Peziziopsis Lu; Qiu et al., 1983, p. 29.

Type species. *Dividuagnostus minus* Koroleva, 1982.

Diagnosis. Glabella with bulbous, subcircular anterior lobe, F3 strong, chevron-like, posterior lobe subcircular lacking F2; glabellar node immediately behind F3; pygidial axis short, constricted across M2. Posteroaxis equidimensional, semiovate to subrectangular, without terminal node.

Species found in Russia. *Dividuagnostus noduliferrus* (E. Romanenko, 1967)—Altai-Sayany Folded Belt: Altai Mountains, Tagaza River, ?Upper Cambrian (Koroleva, 1982 as *Geragnostus noduliferrus*).

CONCLUSIONS

(1) A revision of the Cambrian Agnostina found in Russia is provided. After the revision, the inventory of the museum collections includes 16 families, 70 genera, and 207 species. From these, 11 genera and 53 species were established by Russian authors; 37 were described in open nomenclature, 117 were originally described from other regions.

(2) New images of the holotypes of species housed in Russian museums are presented. Two collections were not found: one is from Pokrovskaya (1958), which was indicated to have been deposited in the Geological Museum in Moscow; the second had been assigned to Tomsk State University.

(3) Forty species and forms which had been described in the open nomenclature are reassigned to different genera; six species which were described from other regions appeared to be synonyms of Siberian species.

(4) The revised set of species shows a closer affinity of the Siberian agnostid fauna to Chinese and Australian faunas in the Middle Cambrian (Cambrian Series 3) and to Australian and Kazakhstan faunas in the Upper Cambrian (Cambrian Series 4).

(5) New taxonomy is suggested for the Ptychagnostidae and Agnostidae. This is based on the assumption that all morphological characters considered in the generic diagnoses are of equal rank. Therefore, the new systematics accurately sorted possible combinations of the diagnostic characters without any confused morphological ranking.

PLATE CAPTIONS

The Catalogue includes images of the type specimens for species described from Russia. Unfortunately, some collections have not been found. These are (i) the collection supplemented for Pokrovskaya (1958), which was stored in the Geological Institute in Moscow, (ii) the material for the work of Rosova (1960), which was stored in the Tomsk Polytechnic Institute. Other specimens are stored in different organizations and available for restudy. Abbreviations for these organizations in the plate captions are: (Novokuznetsk, LFGI) Local Foundation of Geological Information on the Kemerovo Region; (St. Petersburg, TsNIGR) Central Scientific Research Geological Exploration Museum (Chernyshev Museum); (Novosibirsk, TsSGM) Central Siberian Geological Museum; (Novosibirsk, SNIIGGiMS) Siberian Research Institute of Geology, Geophysics, and Mineral Resources.

We provided measurements of the length for every specimen in the plate captions instead of scaling bars. This way of representing size seems to be more convenient, as allows double bias in recalculating the scale to be avoid. The length omitted the articulating ring from the measurement, as it is rarely preserved and has a very complicated shape.

REFERENCES

Ahlberg, P., A revision of the Ordovician agnostid trilobite Leiagnostus Jaekel 1909, *GFF*, 1988, vol. 110, no. 4, pp. 363–370.

Ahlberg, P., Agnostid trilobites from the Lower Ordovician of southern Sweden, *Trans. Royal Soc. Edinburgh: Earth Sci.,* 1992, vol. 83, pp. 539–570.

Ahlberg, P. and Ahlgren, J., Agnostids from the Upper Cambrian of Västergötland, Sweden, *GFF,* 1996, vol. 118, part 3, pp.129–140.

Ahlberg, P. and Terfelt, F., Furongian (Cambrian) agnostoids of Scandinavia and their implications for intercontinental correlation, *Geol. Mag.*, 2012, vol. 149, pp. 1001–1012.

Allen, P.M., Jackson, A.A., and Rushton, A.W.A., The stratigraphy of the Mawddach group in the Cambrian succession of North Wales, *Proc. Yorkshire Geol. Soc.,* 1981, vol. 43, part 3, no. 16, p. 295–329.

Alonso, E.N., Malanca, S., and Sureda, R.J., Consideraciones sobre el Ordovicico de la sierra de Aguilar, Jujuy, Argentina, *Rev. Inst. Ciencias Geol. Univ. Nac. Jujuy,* 1982, vol. 5, pp. 15–37.

Astashkin, V.A., Pegel, T.V., Shabanov, Yu.Ya., Sukhov, S.S., Sundukov, V.M., Repina, L.N., Rozanov, A.Yu., and Zhuravlev, A.Yu., The Cambrian System of the Siberian Plat-

form: Correlation chart and explanatory notes, *Int. Union Geol. Sci. Publ.,* 1991, no. 27, pp. 1–133.

Astashkin, V.A., Pegel, T.V., Repina, L.N., Belyaeva, G.V., Esakova, N.V., Rozanov, A.Yu., Zhuravlev, A.Yu., Osadchaya, D.V., and Pakhomov, N.N., The Cambrian System of the Foldbelts of Russia and Mongolia: Correlation Chart and Explanatory Notes, *Int. Union Geol. Sci Publ.,,* 1995, no. 32, pp. 1–132.

Balashova, E.A., The first find of the upper Cambrian trilobites in the Russian Platform, *Vest. Len. Gos. Univ. Ser. Geol. Geogr.*, 1963, no 12, pp. 126–128.

Bao, J.-S. and Jago, J.B., Late Cambrian trilobites from near Birch Inler, South–western Tasmania, *Paleontology,* 2000, vol. 43, no. 5, pp. 881–917.

Blaker, M.R. and Peel, J.S., Lower Cambrian trilobites from North Greenland, *Meddel. Grønl., Geosci.*, 1997, vol. 35, pp. 1–145.

Bognibova, R.T., Middle Cambrian trilobites from the area of Dolgii Mys Mountain (Batenevsky Mountain Range), *Tr. Sib. Nauchno–Issled. Inst. Geol. Geofiz. Mineral. Syr.,* 1965, vol. 34 (Data on the Geology, Geophysics, and Minerals of Siberia: Part 1), pp. 59–74.

Bognibova, R.T., Koptev, I.I., Mikhailova, L.M., Poletaeva, O.K., Romanenko, E.V., Romanenko, M.F., Semashko, A.K., Tomashpol'skaya, V.D., Fedjanina, E.S., and Chernysheva, N.E., Trilobites of the Amgan Age of the Altai-Sayany Region, in *Amginskii yarus Altae-Sayanskoi oblasti (Amgan Stage of the Altai-Sayany Region)*, Novosibirsk: Zap.-Sib. Knizh. Izd., 1971, pp. 82–263.

Borovikov, L.I. and Krys'kov, L.N., *Cambrian depositions in the Kendyktas Mountains (southern Kazakhstan), Tr. Vsesoyuz. Nauchno-Issled. Geol. Inst. Nov. Ser.,* 1963, vol. 94 (Data on Geology and Minerals of the Altai and Kazakhstan), pp. 266–280.

Buchholz, A., Agnostida (Trilobita) aus oberkambrischen Geschieben Mecklenburg/Vorpommenrs (Norddeutschland), *Greifswal. Geowissensch. Beitr.,* 1999, vol. 6, pp. 237–259.

Buchholz, A., Ein Geschiebe der *Hypagnostus parvifrons*–zone, (B3 Mittel–kambrium), mit feinstratigraphischer Schichtung und seltenen sowie neuen Trilobiten, *Arch. Geschieb.,* 2004a, vol. 3, no. 8/12, pp. 501–524.

Buchholz, A., *Homagnostus* Howell, 1935 und ähnliche Gattungen der Agnostinae (Trilobita) in oberkambrischen Geschieben aus Mecklenburg und Vorpommern (Norddeutschland), *Arch. Geschieb.*, 2004b, vol. 3, no. 8/12, pp. 537–556.

Capèra, J.C., Courtessole, R., and Pillet, J., Contribution à l'étude de l'Ordovicien inférieur de la Montagne noire: Biostratigraphie et révision des Agnostida, *Ann. Soc. Geol. Nord.*, 1978, vol. 98, pp. 67–88.

Chernysheva, N.E., Cambrian stratigraphy of the Aldan Anteclise and Paleontological Foundation for the Recognition of the Amgan Stage, *Tr. Vsesoyuz. Nauchno-Issled. Inst. Geol. Inst. Nov. Ser.,* 1961, vol. 49, pp. 1–347.

Choi, D.K. and Lee, J.G.L., Occurrence of *Glyptagnostus stolidotus* Öpik, 1961 (Trilobita, Late Cambrian) in the Machari Formation of Korea, *J. Paleontol.*, 1995, vol. 69, pp. 590–594.

Choi, D.K., Lee, J.G., and Sheen, B.C., Upper Cambrian agnostid trilobites from the Machari Formation, Yongwol, Korea, *Geobios,* 2004, vol. 37, pp. 159–189.

Clark, T.H., A group of new species of *Agnostus* from Levis, Quebec, *Can. Field–Natur.,* 1923, vol. 37, no. 7, pp. 121–125.

Cooper, R.A., Jago, J.B., and Begg, J.G., Cambrian trilobites from Northern Victoria Land, Antarctica, and their stratigraphic implications, *New Zealand J. Geol. Geophys.,* 1996, vol. 39, no. 3, pp. 363–387.

Daily, B. and Jago, J.B., The trilobite *Lejopyge* Hawle and Corda and the Middle–Upper Cambrian boundary, *Palaeontology*, 1975, vol. 18, no, 3, pp. 527–550.

Danukalova, M.K., Kuz'michev, A.B., and Korovnikov, I.V., The Cambrian of Bennett Island (New Siberian Islands), *Stratigr. Geol. Correlation,* 2014, vol. 22, no. 4, pp. 347–369.

Datsenko, V.A., Zhurazleva, I.T., Lazarenko, N.P., et al., *Biostratigraphiya i fauna kembriiskikh otlozhenii severo-zapada Sibirskoi platformy (Biostratigraphy and Fauna of the Cambrian of Northwestern Siberian Platform)*, Leningrad: Nedra, 1968.

Dragunov, V.I., Smirnov, A.L., and Chernysheva, N.E., Lower Paleozoic deposits at the base of the eastern part of the West Siberian Lowland (Eloguiskaya test well), *Dokl. Akad. Nauk SSSR,* 1967, vol. 172, no. 2, pp. 420–422.

Egorova, L.I., Hsiang, L.W., Lee, S.C., Nan, J.S., and Kuo, C.M., *The Cambrian trilobite faunas of Kueichou and western Hunan*, *Spec. Pap. Inst. Geol. Miner. Res. Stratigr. Palaeontol.,* 1963, pp. 1–117.

Egorova, L.I., Ivshin, N.K., Pokrovskaya, N.V., Poletaeva, O.K., Repina, L.N., Rosova, A.V., Romanenko, E.V., Sivov, A.G., Tomashpol'skaya, V.D., Fedjanina, E.S., and Chernysheva, N.E., Cambrian System: Description of the index fossils: Phylum Artropoda, *Tr. Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral. Syr.,* 1960, vol. 19 (Paleozoic Biostratigraphy of the Sayany-Altai Region: Part 1. Lower Paleozoic), pp. 152–253.

Egorova, L.I., Lomovitskaya, M.P., Poletaeva, O.K., and Sivov, A.G., Cambrian System: Trilobita, in *Atlas rukovodyashchikh form iskopaemykh fauny i flory Zapadnoi Sibiri* (Atlas of the Plant and Animal Index Fossils of Western Siberia), Moscow: Gosgeoltekhizdat, 1955, vol. 1, pp. 102–145.

Egorova, L.I. and Pegel, T.V., New data on the biostratigraphy of reefogenic rocks of Middle Cambrian Mayan Stage in the southeastern Siberian Platform, *Tr. Sib. Nauchno–Issled. Inst. Geol. Geofiz. Mineral. Syr.,* 1979, vol. 270, pp. 72–90.

Egorova, L.I. and Romanenko, E.V., Boundary beds of the Middle and Upper Cambrian of the northeastern Altai, in *Granitsy krupnykh podrazdelenii fanerozoya Sibiri* (Boundaries of the Large Phanerozoic Divisions in Siberia), Novosibirsk: Tr. Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral. Syr., 1982, pp. 56–70.

Egorova, L.I. and Savitzkiy, V.E., Cambrian stratigraphy and biofacies of the Siberian Platform, western Prianabar Region, *Tr. Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral. Syr.,* 1969, vol. 43, pp. 1–408.

Egorova, L.I., Shabanov, Yu.Ya., Pegel, T.V, Savitzkiy, V.E., Sukhov, S.S., and Chernysheva, N.E., *Maiskii yarus strato-*

tipicheskoi mestnosti (srednii kembrii yugo-vostoka Sibirskoi platformy) (Mayan Stage of the Stratotypic Region: Middle Cambrian of the Southeastern Siberian Platform), Moscow: Nauka, 1982.

Egorova, L.I., Shabanov, Yu.Ya., Rozanov, A.Yu., Savitzkiy, V.E., Chernysheva, N.E., and Shishkin, B.B., Elansky and Kuonamka faciostratotypes of the lower boundary of the Middle Cambrian of Siberia, *Tr. Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral Syr.,* 1976, vol. 211, pp. 1–228.

Ergaliev, G.Kh., *Trilobity srednego i verkhnego kembriya Malogo Karatau* (Trilobites from the Middle and Upper Cambrian of the Lesser Kara-Tau), Almaty: Nauka, 1980.

Ergaliev, G.Kh. and Ergaliev, F.G., *Agnostidy srednego i verkhnego kembriya Aksaiskogo gosudarstvennogo geologicheskogo zakaznika v Yuzhnom Kazakhstane* (Agnostids from the Middle and Upper Cambrian of the Aksai State Geological Reserve in Southern Kazakhstan), Almaty: Gylym, 2008, part 1.

Fatka, O., Kordule, V., and Szabad, M., Stratigraphical distribution of Cambrian fossils in the Příbram–Jince Basin (Barrandian area, Czech Republic), *Senckenberg. Leth.,* 2004, vol. 84, nos. 1/2, pp. 367–389.

Fedjanina, E.S., *Trilobites of Orlinogorskaya Formation, Orlinaya Mountain, northeastern Salair, Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR,* 1977, vol. 313 (Biostratigraphy and Fauna of the Upper Cambrian and Its Boundary Beds), pp. 145–152.

Fedoseev, A.V., Features of distribution of ptychagnostids (trilobites) in the Amydaiskii section of the Amgan Age, *Geol. Geofiz.,* 1999, vol. 40, no. 10, pp. 1411–1424.

Fletcher, T.P., *Ovatoryctocara granulata,* the key to a global Cambrian stage boundary and the correlation of the Olenellid, Redlichiid and Paradoxidid realms, *Spec. Pap. Palaeontol.,* 2003, vol. 70, pp. 73–102.

Fletcher, T.P., Theokritoff, G., Lord, G.S., and Zeoli, G., The early Paradoxidid harlani trilobite fauna of Massachusetts and its correlatives in Newfoundland, Morocco, and Spain, *J. Paleontol.,* 2005, vol. 79, no. 2, pp. 312–336.

Fortey, R.A., *The Ordovician trilobites of Spitsbergen: Ill. Remaining trilobites of the Valhallfonna Formation. Skrifter Nr. 171*, Oslo: Norsk Polarinstitutt, 1980.

Gogin, I.Ya. and Pegel, T.V., Trilobites of the Middle and Upper Cambrian of the western Sette–Daban, in *Atlas zonal'nykh kompleksov vedushchikh grupp rannepaleozoiskoi fauny severa Rossii* (Atlas of Zonal Assemblages of Key Groups of Early Paleozoic Fauna of Northern Russia), St. Petersburg: Vseross. Nauchno-Issled. Geol. Inst., 1997, pp. 100–132.

Harrington, H.J., Sobre las faunas del Ordoviciano Inferior del Norte Argentino, *Rev. Mus. Plata (Nueva Ser.), Sec. Paleontol.*, 1938, no. 1, pp. 209–289.

Harrington, H.J. and Leanza, A.F., Ordovician trilobites of Argentina, *Spec. Publ. Univ. Kansas, Dept. Geol.,* 1957, part 1, pp. 1–276.

Hawle, I. and Corda, A.J.C., *Monographie der böhmischen Trilobiten,* Prague, 1847, 176 p.

Hinz–Schallreuter, I. and Buchholz, A., Mittelkambrische Agnostiden von Bornholm, *Arch. Geschieb.,* 2004, vol. 3, nos. 8/12, pp. 525–536.

Holm, G. and Westergård, A.H., A Middle Cambrian fauna from Bennet Island, *Mem. de l'Acad. Sci. l'URSS, Clas. Phys.-Matem.,* 1930, vol. 21, no. 8, pp. 5–25.

Hong, P.S., Lee, J.G., and Choi, D.K., Trilobites from the *Lejopyge armata* Zone (Upper Middle Cambrian) of the Machari Formation, Yongwol Group, Korea, *J. Paleontol.,* 2003, vol. 77, no. 5, pp. 895–907.

Howell, B.F., New Middle Cambrian agnostian trilobites from Vermont, *J. Paleontol.,* 1935a, vol. 9, no. 3, pp. 218–220.

Howell, B.F., Some New Brunswick Cambrian agnostians, *Bull. Wagner Inst. Sci.,* 1935b, vol. 10, no. 2, pp. 13–17.

Howell, B.F., Cambrian and Ordovician trilobites from Herault, southern France, *J. Paleontol.,* 1935c, vol. 9, no. 3, pp. 222–238.

Howell, B.F., Cambrian *Centropleura vermontensis* fauna of Northern Vermont, *Bull. Geol. Soc. Am.,* 1937, vol. 48, no. 8, pp. 1147–1209.

Huang, Y.-z., Yuan, J.-l., *Peronopsis* of Early–Middle Cambrian Kaili Area, Guizhou, *Acta Paleontol. Sin.,* 1994, vol. 33, no. 3, pp. 295–304.

Hupé, P., Contribution à l'étude du Cambrien inférieur et du Précambrian III de l'Anti–Atlas Marocain: Direction de la Production Industrielle et des Mines, Division des Mines et de la Géologie, Service Géologique, *Notes Mém.*, 1953, vol. 103, pp. 1–402.

Hutchinson, R.D., Cambrian stratigraphy and trilobite faunas of southern Newfoundland, *Geol. Surv. Can.,* 1962, bull. 88, pp. 1–156.

International Code of Zoological Nomenclature, London: Intern. Trust Zool. Nomencl., 1999.

Ivshin, N.K., *Srednekembriiskie trilobity Kazakhstana (Middle Cambrian Trilobites of Kazakhstan), part 1: Boshchekul'skii faunisticheskii gorizont* (Boshchekul' Faunal Regional Stage), 1953, Almaty: Akad. Nauk Kaz. SSR, 226 p.

Ivshin, N.K., *Verkhnekembriyskie trilobity Kazakhstana* (Upper Cambrian Trilobites of Kazakhstan)*, part 1: Kuyandinskii faunisticheskii gorizont mezhdurech'ya Olenty–Shiderty* (Kuyandinskii Faunal Regional Stage in the Olenty–Shiderty Area), Almaty: Akad. Nauk Kaz. SSR, 1956, 97 p.

Jaekel, O., Uber dei Agnostiden, *Zeitschdeutsch. Geol. Gesellsch.,* 1909, vol. 61, pp. 380–401.

Jago, J.B., Late Middle Cambrian agnostid trilobites from north–western Tasmania, *Palaeontology,* 1976, vol. 19, part 1, pp.133–172.

Jago, J.B. and Brown, A.V., Late Middle Cambrian trilobites from Trial Ridge, southwestern Tasmania, *Pap. Proc. R. Soc. Tasm.,* 2001, vol. 135, pp. 1–14.

Jago, J.B. and Cooper, R.A., A *Glyptagnostus stolidotus* trilobite fauna from the Cambrian of northern Victoria Land, Antarctica, *New Zealand J. Geol. Geophys.,* 2005, vol. 48, no. 4, pp. 661– 681.

Jell, P.A. and Adrain, J.M., Available generic names for trilobites, *Mem. Queensland Mus.,* 2002, vol. 48, no. 2, pp. 331–553.

Kobayashi, T., The Cambro–Ordovician shelly faunas of South America, *J. Fac. Sci. Tokyo Univ. Sec. 4*, 1937, vol. 4, pp. 369–522.

Kobayashi, T., On the agnostids: Part 1, *J. Fac. Sci. Imp. Univ. Tokyo, Sect. II,* 1939, vol. 5, no. 5, pp. 1–198.

Korobov, M.N. and Yankauskas, T.V., Middle Cambrian trilobite in the ancient rocks of Moscow Syneclise (Yaroslavl Region), *Dokl. Akad. Nauk SSSR, Geol.*, 1980, vol. 262, no. 5, pp. 677–678.

Koroleva, M.N., *Trilobity ordovika severo-vostochnogo Kazahstana* (Ordovician Trilobites of Northeastern Kazakhstan), Moscow: Nedra, 1982, 192 p.

Korovnikov, I.V., Pegel, T.V., and Shabanov, Yu. Ya., New trilobite records from the Middle and Upper Cambrian of the left bank of the Yenisei River (based on materials of well Vostok-1 drilling)), in *Regional'naya geologiya. Stratigrafiya i paleontologiya dokembriiskikh i nizhnepaleozoiskikh otlozhenii Sibiri* (Regional Geology. Stratigraphy and Paleontology of Precambrian and Lower Paleozoic Strata in Siberia), Novosibirsk: Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral. Syr., 2010, pp. 93–110.

Korovnikov, I.V. and Shabanov, Yu.Ya., Trilobites from the boundary beds of the Lower and Middle Cambrian of the stratotypic section on the Molodo River (eastern Siberian Platform), in *Razrezy kembriya Sibirskoi platformy–kandidaty v stratotipy podrazdelenii Mezhdunarodnoi stratigraficheskoi shkaly (stratigrafiya i paleontologiya). Materialy k 13-i Mezhdunarodnoi polevoi konferentsii rabochei gruppy po yarusnomu deleniyu kembriya* (Sections of the Cambrian of the Siberian Platform–Candidates for Stratotypes of Divisions of the International Stratigraphical Chart (Stratigraphy and Paleontology): Materials to the 13th International field conference of the Working Group for the Stage Division of the Cambrian), Novosibirsk: Sib. Otd. Ross. Akad. Nauk, 2008, pp. 71–104.

Lake, P., *A Monograph of the British Cambrian trilobites: Part 1*, *Palaeontogr. Soc*., 1906, pp. 1–28.

Laurie, J.R., Revision of some Australian Ptychagnostinae (Agnostida, Cambrian), *Alcheringa,* 1988, vol. 12, pp. 169–205.

Laurie, J.R., Revision of species of *Goniagnostus* Howell and *Lejopyge* Corda from Australia (Agnostida, Cambrian), *Alcheringa,* 1989, vol. 13, pp. 175–191.

Laurie, J.R., On the Middle Cambrian agnostoid species *Agnostus fallax* Linnarsson, 1869, *Alcheringa,* 1990, vol. 14, pp. 317–324.

Laurie, J.R., Early Middle Cambrian trilobite faunas from NTGS Elkedra 3 corehole, Southern Georgina basin, Northern Territory, *Mem. Assoc. Austral. Paleontol*., 2004, vol. 30, pp. 221–260.

Lazarenko, N.P., Some Upper Cambrian trilobites from the northwestern Siberian Platform, in *Sbornik statey po paleontologii i biostratigrafii* (Collected Works on Paleontology and Biostratigraphy), Leningrad: Nauchno-Issled. Inst. Geol. Ark., 1960, vol. 20, pp. 12–44.

Lazarenko, N.P., Biostratigraphy and certain new trilobites from the Upper Cambrian of the Olenek Uplift and Kharaulakh Mountains, *Uch. Zap. Nauchno-Issled. Inst. Geol. Ark. Paleontol. Biostratigr.,* 1966, vol. 11, pp. 33–78.

Lazarenko, N.P., Gogin, I.Ya., Pegel, T.V., and Abaimova, G.P., The Khos-Nelege River section of the Ogon'or Formation: A potential candidate for the GSSP of Stage 10, Cambrian System, *Bull. Geosci.*, 2011, vol. 86, no. 3, pp. 555–568.

Lazarenko, N.P., Gogin, I.Ya., Pegel, T.V., Sukhov, S.S., Abaimova, G.P., Egorova, L.I., Fedorov, A.B., Raevskaya, E.G., and Ushatinskaya, G.T., Cambrian stratigraphy of the northeastern Siberian Platform and potential stratotypes of lower boundaries of the proposed Upper Cambrian Chekurovkian and Nelegerian stages in the Ogon'or Formation section at the Khos-Nelege River; The boundaries are defined by the FADs of *Agnostotes orientalis* and *Lotagnostus americanus*, in *Cambrian System of the Siberian Platform: Part 2: Northeast of the Siberian Platform*, Moscow–Novosibirsk: Paleontol. Inst. Ross. Akad. Nauk, 2008a, pp. 60–139

Lazarenko, N.P. and Nikiforov, N.I., Trilobite assemblages from the Upper Cambrian deposites, Kulyumbe River (northwestern Siberian Platform), *Uch. Zap. Nauchno-Issled. Inst. Geol. Ark. Paleontol. Biostratigr.,* 1968, vol. 23, pp. 20–80.

Lazarenko, N.P., Pegel, T.V., Sukhov, S.S., Abaimova, G.P., and Gogin, I.Ya., Type section for the Upper Cambrian of the Siberian Platform As a candidate for GSSP (Khos-Nelege River, western Yakutia, Russia), in *Materialy k 13 Mezhdunarodnoy polevoy konferentsii rabochey gruppy po yarusnomu deleniyu kembriya: Razrezy kembriya Sibirskoi platformy – kandidaty na GSSP* (13th International Conference of the Working Group on the Stage Division of the Cambrian: Sections of the Cambrian of the Siberian Platform As Candidates for GSSP), Yakutsk, Novosibirsk: Sib. Otd. Ross. Akad. Nauk, 2008b, pp. 3–58.

Lee, J.G. and Choi, D.K., Late Cambrian trilobites from the Machari Formation, Yeongweol–Machari area, Korea, *J. Paleontol. Soc. Korea,* 1995, vol. 11, no. 1, pp. 1–46.

Lermontova, E.V., Class Trilobita, in *Atlas rukovodyashchikh form iskopaemykh faun SSSR* (Atlas of Index Taxa of Fossil Faunas of the USSR), vol. 1: *Kembrii* (Cambrian), Moscow–Leningrad: Gosgeolizdat, 1940, pp. 112–157.

Lermontova, E.V., *Verkhnekembriiskie trilobity i brakhiopody Boshche–Kulya (severo-vostochnyi Kazakhstan)* (Upper Cambrian Trilobites and Brachiopods of Boshche-Kul'), Moscow: Gosgeolizdat, 1951a.

Lermontova, E.V., *Nizhnekembriiskie trilobity i brakhiopody Vostochnoy Sibiri* (Lower Cambrian Trilobites and Brachiopods of Eastern Siberia), Moscow: Gosgeolizdat,1951b.

Lermontova, E.V., *Srednekembriiskie trilobity i gastropody Shody–Mira* (Yuzhnaya okraina Ferganskoy kotloviny) (Middle Cambrian Trilobites and Gastropods of Shody–Mir: Southern Periphery of the Fergana Depression), Moscow: Gosgeolizdat, 1951c.

Liñán, E., Álvaro, I., Gozalo, R., Gámez-Vintaned, J.A., and Palacios, T., El Cámbrico Medio de la Sierra de Córdoba (Ossa–Morena, S de España): Trilobites y paleoichnología: Implicaciones bioestratigráficas y paleoambientales, *Rev. Españ. Paleontol.,* 1995, vol. 10, no. 2, pp. 219–238.

Linnarsson, J.G.O., Om Vestergotlands Cambriska och Siluriska aflagringar, Kongl. Sven, *Vetenskaps–Acad. Handlingar.,* 1869, vol. 8, no. 2, pp. 1–89.

Lisogor, K.A., *Trilobites from the Tremadocian beds of the Kyrgyz Mountain Range, Nauch. Tr. Kaz. Politekh. Inst.,* 1971, pp. 179–185.

Lisogor, K.A., Biostratigraphy and trilobites from the Upper Cambrian and Tremadocian of the Malyi Karatau (southern Kazakhstan), *Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR,* 1977, vol. 313 (Biostratigraphy and Fauna from the Upper Cambrian and Boundary Strata: New Data from the Asiatic Part of the USSR), pp. 197–265.

Lisogor, K.A., Rosov, S.N., and Rosova, A.V., Correlation of Middle Cambrian deposits of the Lesser Karatau and Siberian Platform based on trilobites, *Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR,* 1988, vol. 720 (Cambrian of Siberia and Central Asia), pp. 54–82.

Liu, Y-r., Trilobita, in *Paleontological Atlas of Hunan*, Beijing: Geol. Pabl. House, 1982, pp. 290–346

Lochman, C. and Duncan, D., Early Upper Cambrian faunas of central Montana, *Geol. Soc. Am. Spec. Papers,* 1944, vol. 54, pp. 1–181.

Lu, Y., Cambrian trilobites, in *Handbook of Index Fossils of South China,* Wang, Y., Ed., Beijing: Sci. Press, 1964, pp. 26–39.

Lu, Y. and Lin, H., Late Cambrian and earliest Ordovician trilobites of Jiangshan–Changshan area, Zhejiang, in *Stratigraphy and Palaeontology of Systematic Boundaries in China, Cambrian–Ordovician Boundary*, Hefei: Anhui Sci. Techn. Publ. House, 1984, vol. 1, pp. 45–164.

Lu, Y. and Lin, H., Late Late Cambrian and earliest Ordovician trilobites of Jiangshan–Changshan area, Zhejiang, in *Stratigraphy and Palaeontology of Systematic Boundaries in China, Cambrian–Ordovician Boundary,* Hefei: Anhui Sci. Techn. Publ. House, 1989, vol. 1, pp. 45–143

Lu, Y., Zhang, W., Zhu, Z., Qian, Y., and Xiang, L., *Trilobites of China,* Beijing: Sci. Press, 1965.

Lu, Y., Zhang, W., Qian, Y., Zhu, Z., Lin. H., Zhou, Z., Zhang, S., and Yuan J., Cambrian trilobites, in *Handbook of Stratigraphy and Palaeontology*, Beijing: Southwest China Sci. Press, 1974, pp. 82–107.

Ludvigsen, R., *Upper Cambrian and Lower Ordovician trilobite biostratigraphy of the Rabbitkettle Formation, western district of Mackenzie*, *Life Sci. Contrib., Roy. Ontario Mus.*, 1982, pp. 1–134.

Ludvigsen, R., Westrop, S.R., and Kindle, C.H., Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada, *Palaeontogr. Can.,* 1989, vol. 6, pp. 1–175.

Moore, R.C., Ed., Systematic descriptions of Trilobita, in *Treatise on Invertebrate Paleontology: Part. O. Arthropoda 1*, Lawrence: Univ. Kansas Press, 1959, pp. O170–O526.

Müller, K. and Walossek, D., Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden, *Foss. Strata*, 1987, vol. 19, pp. 1–123.

Naimark, E., Ontogeny of Agnostida, *Palaeoworld,* 2006, vol. 261, no. 15, pp. 315–327.

Naimark, E., Comparative ontogeny of different species of agnostina, *Paleontol. J.,* 2007, vol. 41, no. 1, pp. 69–78.

Naimark, E., Morphogenesis in the genus *Peronopsis* Hawle et Corda (Agnostina), *Paleontol. J.*, 2008, vol. 42, no. 4, pp. 389–400.

Naimark, E., Hundred species of the genus *Peronopsis* Hawle et Corda, 1847, *Paleontol. J.,* 2012, vol. 46, no. 9, pp. 945–1057.

Naimark, E., Revision of *Eurudagnostus* Lermontova (Agnostida, ?Trilobita), *Paleontol. J.*, 2014, vol. 48, no. 2. pp. 166–176.

Naimark, E., Revision of *Rseudorhaptagnostus* Lermontova (Agnostida, ?Trilobita), *Paleontol. J.*, 2016, vol. 50, no. 1, pp. 54–68.

Nielsen, A.T., A review of Ordovician agnostid genera (Trilobita), *Transact. Roy. Soc. Edinburgh Erath Sci.,* 1997, vol. 87, pp. 463–501.

Ogienko, L.V. and Garina, S.Yu., *Stratigrafiya i trilobity kembriya Sibirskoi platformy* (Cambrian Stratigraphy and Trilobites of the Siberian Platform), Moscow: Nauch. Mir, 2001.

Öpik, A.A., The geology and palaeontology of the headwaters of the Burke River, Queensland, *Bull. Bur. Miner. Res. Austral., Geol. Geophys.,* 1961a, vol. 53, pp. 1–249.

Öpik, A.A., Alimentary Caeca of Agnostids and other Trilobites, *Paleontology,* 1961b, vol. 3, pp. 410–438.

Öpik, A.A., Early Upper Cambrian fossils from Queensland, *Bull. Bur. of Min. Res. Australia, Geol. Geophys.,* 1963, vol. 64, pp. 1–133.

Öpik, A.A., The Myndyallan Fauna of North-Western Queensland, *Bull. Bur. of Min. Res., Geol. Geophys.,* 1967, vol. 74, pp. 1–399.

Öpik, A.A., Middle Cambrian agnostids: Systematics and biostratigraphy, *Bull. Bur. of Min. Res. Australia, Geol. Geophys.,* 1979, vol. 172, pp. 1–187.

Palmer, A.R., An appraisal of the Great Basin Middle Cambriam trilobites, described before 1900, *US Geol. Surv. Prof. Pap.*, 1954, vol. 264–D, pp. 1–86.

Palmer, A.R., Trilobites of the Upper Cambrian Dunderberg Shale, Eureka District, Nevada, *US Geol. Surv. Prof. Pap.*, 1960, vol. 334–C, pp. 1–109.

Palmer, A.R., *Glyptagnostus* and associated trilobites in the United States, *US Geol. Surv. Prof. Pap*, 1962, vol. 374–F, pp. 1–63.

Palmer, A.R., Cambrian trilobites of East–central Alaska, *US Geol. Survey Prof. Pap.*, 1968, vol. 559–B, pp. 1–115.

Palmer, A.R. and Gatehause, C.G., *US Geol. Survey Prof. Pap.,* 1972, vol. 456–D, pp. 1–37.

Pegel, T.V., *New species of the Middle Cambrian trilobites from South Yakutia, Tr. Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral. Syr.,* 1978, vol. 260 (New Data on the Stratigraphy and Paleontology of Siberia), pp. 84–90.

Pegel, T.V., Evolution of trilobite biofacies in Cambrian Basins of the Siberian Platform, *J. Paleontol.,* 2000, vol. 74, no. 6, pp. 1000–1019.

Pegel, T.V., The correlation of the different facies type sections of late Middle Cambrian in the Siberian Platform, in *Regional'naya geologiya. stratigraphya i paleontologiya dokembriya i nizhnego paleozoya Sibiri* (Regional Geology, Stratigraphy and Paleontology of the Precambrian and Lower Paleozoic of Siberian, Novosibirsk: Tr. Sib.

Nauchno–Issled. Inst. Geol. Geofiz. Mineral. Syr., 2010, pp. 110–123.

Pegel, T.V., Biofacies and age of Cambrian trilobite associations of the Diringde reef complex (northern Siberian Platform, Russia), *Bull. Geosci.,* 2014, vol. 89, no. 2. pp. 335–345.

Pegel, T.V., Egorova, L.I., Shabanov, Yu.,Ya., Korovnikov, I.V., Luchinina, V.A., Salikhova, A.K., Sundukov, V.M., Fedorov, A.B., Zhuravlev, A.Yu., Parkhaev, P.Yu., and Demidenko, Yu.E. *Stratigrafiya neftegazonosnykh basseinov Sibiri (v devyati knigakh) : kembrii Sibirskoi platformy* (Stratigraphy of oil and gas basins of Siberia) (in nine books): Cambrian of Siberian Platform, vol. 2: *Paleontologiya* (Paleontology), Kontorovich, A.E., Ed., Novosibirsk: Inst. Neftegaz. Geol. Geofiz. Sib. Otd. Ross. Akad. Nauk, 2016.

Pegel, T.V. and Sukhov, S.S., Cambrian biostratigraphy and sedimentary evolution of the Siberian Platform, in *Proceedings of the 3rd IGCP 591 Annual Meeting, Lund, 9–19 June 2013*, 2013, pp. 260–261.

Pek, I. and Vanek, J., Revision of the genera *Peronopsis* Hawle et Corda, 1847 and *Diplorrhina* Hawle et Corda, 1847 (Trilobita) from the Middle Cambrian of Bohemia, *Vest. Usrted. Ustavu Geol.*, 1971, vol. 46, no. 5, pp. 269–275

Peng, S.C., Upper Cambrian biostratigraphy and trilobite faunas of the Cili Taoyuan area, north–western Hunan, China, *Assoc. Australas. Palaeontol. Mem.,* 1992, vol. 13, pp. 1–119.

Peng, S.C. and Babcock, L.E., Two Cambrian agnostoid trilobites, *Agnostotes orientalis* (Kobayashi, 1935) and *Lotagnostus americanus* (Billings, 1860): Key species for defining global stages of the Cambrian System, *Geosci. J.,* 2005, vol. 9, pp. 107–115.

Peng, S., Hughes, N.C., Heim, N.A., Sell, B.K., Zhu, X.-J., Myrow, P.M., and Parcha, S.K., Cambrian trilobites from the Parahio and Zanskar valleys, Indian Himalaya, *Paleontol. Soc. Mem*., 2009, vol. 71, pp. 1–95.

Peng, S. and Robison, R.A., Agnostid biostratigraphy across the Middle–Upper Cambrian boundary in Unan, China, *Paleontol. Soc. Mem.,* 2000, vol. 53, pp. 1–104.

Petrunina, Z.E. and Gabova, M.F., Trilobites of the Upper Cambrian from Kuznetsk Alatau and Salair (Ust'-Kul'bichskii Regional Stage), in *Paleontologiya Kuzbassa* (Paleontology of the Kuzbass), 2008, vol. 1, pp. 1–114.

Pokrovskaya, N.V., *Agnostidy srednego kembriya Yakutii* (Agnostida from the Middle Cambrian of Yakutia), Moscow: Akad. Nauk SSSR, 1958.

Pokrovskaya, N.V., Class Trilobita: order Miomera, in *Osnovy paleontologii (Fundamentals of Paleontology)*, Chernysheva, N.E., Ed., Moscow: Gosnauchtekhizdat, 1960, pp. 54–61.

Poletaeva, O.K. and Romanenko, E.V., Some trilobites from the Middle and Late Cambrian of Altai, *Paleontol. J.,* 1970, no. 2, pp. 72–83.

Poulsen, Ch., Fossils from the Late Middle Cambrian *Bolaspidella* Zone of Mendoza, Argentina, *Mat. Fys. Medd. Dan. Vid. Selsk.,* 1960, vol. 32, no. 11, pp. 1–42.

Pratt, B.R., Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabibitkettle Formation, southern Mackenzie Mountains, northwest Canada, *Paleontogr. Can.,* 1992, no. 9, pp. 1–179.

Qiu, H., Lu, Y., Zhu, Z., Bi, D., Lin, T., Zhang, Q., Qian, Y., Ju, T., Han, N., and Wei, X., Trilobita, in *Palaeontological Atlas of East China, part 1: Early Paleozoic,* Beijing: Geol. Publ. House, 1983, pp. 28–254.

Rasetti, F., Middle Cambrian trilobites from the conglomerates of the Quebec (exclusive of the Ptychopariidea), *J. Paleontol.,* 1948, vol. 22, no. 3, pp. 45–52.

Rasetti, F., Middle Cambrian Stratigraphy and Faunas of the Canadian Rocky Mountains, *Smithson. Misc. Coll.,* 1951, vol. 116, no, 5, pp. 3–276.

Rasetti, F. and Teokritoff, G., Lower Cambrian agnostid trilobites of North America, *J. Paleontol.,* 1967, vol. 41, no. 1, pp. 188–196.

Repina, L.N., Biofacies of trilobites in Early Cambrian of the Siberian Platform, in *Sreda i zhizn' v geologicheskom proshlom. Paleobiogeografiya i paleoekologiya* (Life and Environments in the Geological Past: Paleobiogeography and Paleoecology), Novosibirsk: Nauka, 1983, pp. 54–76.

Repina, L.N., Types of trilobite associations and their relationships with landscapes in the Early Cambrian sea of the Siberian Platform, in *Sreda i zhizn' v geologicheskom proshlom. Paleolandshafty morei i kontinentov* (Life and Environments in the Geological Past: Paleolanscapes of Oceans and Continents), Novosibirsk: Nauka, 1987, pp. 13–26.

Repina, L.N., Petrunina, Z.E., and Hairullina, T.I., Trilobites, in *Stratigrafiya i fauna nizhnego paleozoya severnykh predgorii Turkestanskogo i Alaiskogo khrebtov (yuzhniy Tyan'–Shan')* (Stratigraphy and Fauna of the Lower Paleozoic of the Northern Foothills of Turkestan and Alai Mountain Ranges (Southern Tien Shan)), Novosibirsk: Nauka, Sib. Otd., 1975, pp. 100–233.

Resheniya Vsesoyuznogo stratigraficheskogo soveshchaniya po dokembriyu, paleozoyu i chetvertichnoi sisteme Srednei Sibiri, chast' 1 (verkhnii proterozoi i nizhnii paleozoi) (Resolution of All–Union Stratigraphical Meeting on the Precambrian, Paleozoic, and Quaternary System of Middle Siberia: Part 1. Upper Proterozoic and Lower Paleozoic), Novosibirsk: Sib. Nauchno–Issled. Inst. Geol. Geofiz. Mineral. Syr., 1983.

Resser, Ch.E., Middle Cambrian fossils from Pend Oreille Lake, Idaho, *Smithson. Miscell. Coll.,* 1938, vol. 97, no 3, pp. 1–12.

Resser, C.E. and Howell, B.F., Lower Cambrian *Olenellus* Zone of the Appalachians, *Geol. Soc. Am.,* 1938, vol. 49, pp. 195–248.

Robison, R.A., Middle Cambrian faunas from Western Utah, *J. Paleontol.,* 1964, vol. 38, no. 3, pp. 79–92.

Robison, R.A., Some Middle Cambrian agnostoid trilobites from western North America, *J. Paleontol.*, 1982, vol. 56, pp. 132–160.

Robison, R.A., Cambrian Agnostida of North America and Greenland: Part 1. Ptychagnostidae, *Univ. Kansas Paleontol. Contrib.*, 1984, vol. 109, pp. 1–59.

Robison, R.A., Triloibites of the Holm Dal Formation (Late Middle Cambrian), central North Greenland, *Meddr. Grønland, Geosci.,* 1988, vol. 20, pp. 23–103.

Robison, R.A., Agnostoid trilobites from the Henson Gletcher and Kap Stanton formations (Middle Cambrian), North Greenland, *Bull. Grønland. Geol. Unders.,* 1994, vol. 169, pp. 25–77.

Robison, R.A., Revision of the Middle Cambrian trilobite *Agnostus acadicus* Hartt, *J. Paleontol.,* 1995, vol. 69, no. 1, pp. 302–306.

Romanenko, E.V., *Cambrian trilobites from the Bol'shaya Isha River section (northeastern Altai), Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR,* 1977, vol. 313 (Biostratigraphy and Fauna of the Upper Cambrian and Its Boundary Beds), pp. 161–183.

Romanenko, E.V., Trilobites of the Middle/Upper Cambrian boundary in Altai, *Paleontol. J.,* 1985, no. 4, pp. 54–63.

Romanenko, E.V., New trilobites from the Cambrian phosphatic deposits in Altai, *Paleontol. J.,* 1988, no. 2, pp. 43–53.

Romanenko, M.F. and Romanenko, E.V., Some aspects of paleogeography and trilobites of the Cambrian from Gornyi Altai, *Izv. Altai. Otd. Geogr. Obshch. SSSR,* 1967, vol. 8, pp. 62–96.

Rosova, A.V., Upper Cambrian trilobites of Salair (Tolstochikhinskaya Formation), *Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR,* 1960, vol. 5, pp. 1–116.

Rosova, A.V., Biostratigraphic scheme for the upper Middle Cambian and Upper Cambrian, and new Upper Cambrian trilobites, *Geol. Geophys.,* 1963, no. 9, pp. 3–19.

Rosova, A.V., *Biostratigraphiya i opisanie trilobitov srednego i verkhnego kembriya severo-zapada Sibirskoy platformy* (Middle and Upper Cambrian Biostratigraphy and Descriptions of Trilobites from the Northwestern Siberian Platform), Moscow: Nauka, 1964, pp. 3–148.

Rosova, A.V., Upper Cambrian and Lower Ordovician biostratigraphy and trilobites of the northwestern Siberian Platform, *Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR,* 1968, vol. 36, pp. 1–196.

Rosova, A.V., *Some Upper Cambrian and Lower Ordovician trilobites from the Rybnaya, Khantaika, Kureika, and Letnyaya river basins, Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR,* 1977, vol. 313 (Biostratigraphy and Fauna of the Upper Cambrian and Its Boundary Beds), pp. 54–84.

Rosova, A.V., Upper Cambrian and Lower Ordovician biogeography of the Siberian Platform (based on trilobites), in *Sreda i zhizn' v geologicheskom proshlom. Voprosy ekostratigrafii* (Life and Environments in the Geological Past: Questions of Ecostratigraphy), Novosibirsk: Nauka, 1979, pp. 87–99.

Rusconi, C., Trilobites Cambricos del Cerro Pelado (Mendoza), *Bull. Paleonol. Buenos Aires*, 1951, no. 24, pp. 303–306.

Rushton, A.W.A., *The Cambrian trilobites from the Purley Shales of Warwickshire*, London: Palaeontogr. Soc., 1966.

Rushton, A.W.A., Fossils from the Middle–Upper Cambrian transition in the Nuneaton District, *Palaeontology*, 1978, vol. 21, part 2, pp. 245–283.

Rushton, A.W.A., A review of the Middle Cambrian Agnostida from the Abbey Shales, England, *Alcheringa*, 1979, vol. 3, nos. 1–2, pp. 43–61.

Rushton, A.W.A., Revision of the Furongian agnostoid *Lotagnostus trisectus* (Salter), *Mem. Assoc. Australas. Palaeontol.*, 2009, vol. 37, pp. 273–279.

Rushton, A.W.A. and Weidner, T., The Middle Cambrian paradoxidid trilobite *Hydrocephalus* from Jämtland, central Sweden, *Acta Geol. Polon.*, 2007, vol. 57, no. 4, pp. 391–401.

Savitzkiy, V.E., Evtushenko, V.M., Egorova, L.I., Kontorovich, A.E., and Shabanov, Yu.Ya., Cambrian of the Siberian Platform (Yudoma–Olenek type of section: Kuonamka complex of deposits), *Tr. Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral Syr.,* 1972, vol. 130, pp. 1–198.

Schmidt, F., Ueber einige neue ostibirische Trilobiten und vermandte Thierformen, *Bull. Acad. Imp. Sci. St.-Petersburg*, 1886, vol. 30, no, 4, pp. 501–512.

Shabanov, Yu.Ya., Astashkin, V.A., Pegel, T.V., Egorova, L.I., Zhuravleva, I.T., Pelman, Yu.L., Sundukov, V.M., Stepanova, M.V., Sukhov, S.S., Fedorov, A.B., Shishkin, B.B., Vaganova, N.V., Ermak, V.I., Ryabukha, K.V., Yadrenkina, A.G., Abaimova, G.P., Lopushinskaya, T.V., Sychev, O.V., and Moskalenko, T.A., *Nizhnii paleosoi yugo-zapadnogo sklona Anabarskoi anteklizy (po materialam bureniya)* (Lower Paleozoic of the Southeastern Slope of the Ananbar Anteclyse Based on Drilling Records), Novosibirsk: Sib. Otd. Akad. Nauk SSSR, 1987.

Shabanov, Yu.Ya, Korovnikov, I.V., Pereladov, V.S., and Fefelov, A.F., Excursion 1a: The traditional Lower–Middle Cambrian boundary in the Kuonamka Formation of the Molodo River section (the southeastern slope of the Olenek Uplift of the Siberian Platform) proposed as a candidate for GSSP of the lower boundary of the Middle Cambrian and its basal (Molodian) stage, defined by the FAD of *Ovatoryctocara granulata,* in *The Cambrian System of the Siberian Platform: Part 2. North-East of the Siberian Platform,* Moscow–Novosibirsk: Paleontol. Inst. Ross. Akad. Nauk SSSR, 2008, pp. 8–59.

Shaw, A.B., The palaeontology of northwestern Vermont: 1. New Late Cambrian trilobites, *J. Paleontol.*, 1951, vol. 25, pp. 97–114.

Shergold, J.H., Late Upper Cambrian trilobites from the Gola Beds, Western Queensland, *Austral. Bureau Mineral Res. Geol. Geophys.,* 1971, vol. 112, pp. 1–127.

Shergold, J.H., Late Upper Cambrian trilobites from the Gola Beds, western Queensland, *Austral. Bureau Mineral Res. Geol. Geophys.,* 1972, vol. 112, pp. 1–127.

Shergold, J.H., Late Cambrian and Early Ordovician trilobites from the Burke River Structural Belt, western Queensland, *Austral. Bureau Mineral Res. Geol. Geophys.,* 1975, vol. 153, part 1, pp. 1–246.

Shergold, J.H., Classification of the trilobite *Pseudagnostus, Palaeontology*, 1977, vol. 20, no. 1, pp. 69–100.

Shergold, J.H., Late Cambrian trilobites from the Chatsworth limestone: Western Queensland, *Austral. Bureau Mineral Res. Geol. Geophys.,* 1980, vol. 186, pp. 1–111.

Shergold, J.H., Idamean: Late Cambrian trilobites, Burke River Structural Belt, western Queensland, *Austral. Bureau Mineral Res. Geol. Geophys.,* 1982, vol. 187, pp. 1–69.

Shergold, J.H. and Laurie, J.R., *Ptychagnostus* Jaekel, 1909 and *Glyptagnostus* Whitehouse, 1936 (Trilobita): Proposed conservation of accepted usage, *Bull. Zool. Nomencl.*, 1991, vol. 48, no 3, pp. 200–202.

Shergold, J.H. and Laurie, J.R., Suborder Agnostina Salter, 1864, in *Treatise on Invertebrate Paleontology: Part O: Arthropoda 1: Trilobita 1*, Lawrence: Univ. Kansas Press, 1997, pp. 331–383.

Shergold, J.H., Laurie, J.R., and Sun, X., *Classification and review of the trilobite, Order Agnostida Salter, 1864: An Australian perspective,* Canberra: Austral. Gover. Publ. Serv., 1990.

Shergold, J.H. and Sdzuy, K., Cambrian and Early Ordovician trilobites from Sultan Dag, central Turkey, *Senckenb. Letheae,* 1984, vol. 65, nos. 1/3, pp. 51–135.

Shergold, J.H. and Webers, G.F., Late Dresbachian and other trilobite faunas, *Heritage Range, Mem. Geol. Soc. Am.,* 1992, vol. 170, pp. 125–168.

Shimer, H.W. and Shrock, R.R., *Index Fossils of North America,* New York–London: J. Wiley and Sons–Chapman and Hall, 1944.

Šnajdr, M., O nových trilobitech z èeského kambria (On new trilobites of the Cambrian of Bohemia), *Vìst. Ústr. Úst. Geol.,* 1957, vol. 32, pp. 235–244.

Šnajdr, M., Trilobiti ceskeho stredniho Kambria, *Rozpr. Ustred.o Ustr. Geol.*, 1958, vol. 24, pp. 1–280.

Šnajdr, M., *Bohemian Trilobites,* Praha: Czech Geol. Surv., 1990.

Sobolevskaya, R. and Kaban'kov, V.Ya., *Stratigrafiya kembriiskikh otlozhenii Gornogo Taimyra (Stratigraphy of the Cambrian Deposits of the Taimyr Mountain Region)*, St. Petersburg: Vseross. Nauchno-Issled. Inst. Okean. Geol., 2014.

Sohn, J.W. and Choi, D.K., An uppermost Cambrian trilobite fauna from the Yongwol Group, Trabaeksan Basin, Korea, *Ameghiniana,* 2002, vol. 39, pp. 59–76.

Suárez-Soruco, R., Nuevos trilobites del Tremadociano inferior (Ordovicico) del sur de Bolivia, *Rev. Técn. YPFB, Bolivia,* 1975, vol. 4, no. 3, pp. 129–146.

Sukhov, S.S., Cambrian depositional history of the Siberian craton: Evolution of the carbonate platforms and basins, *Sediment. Fac. Palaeogeogr.,* 1997, vol. 17, no. 5, pp. 27–39.

Sukhov, S.S., Shabanov, Yu.Ya., Pegel, T.V., Saraev, S.V., Philippov, Yu.F., Korovnikov, I.V., Sundukov, V.M., Fedorov, A.B., Varlamov, A.I., Efimov, A.S., Kontorovich, V.A., and Kontorovich, A.E., *Stratigrafiya neftegazonosnykh basseinov Sibiri (v devyati knigakh): kembrii Sibirskoi Platformy* (Stratigraphy of oil and gas basins of Siberia (in nine books): Cambrian of Siberian Platform), vol. 1: *Stratigrafiya* (Stratigraphy), Kontorovich, A.E., Ed., Novosibirsk: Inst. Neftegaz. Geol. Geofiz. Sib. Otd. Ross. Akad. Nauk, 2016.

Sun, X., Cambrian agnostids from the North China Platform, *Palaeontol. Cathayana,* 1989, no. 4, pp. 53–99.

Taylor, K. and Rushton, A.W.A., The pre-Westphalian geology of the Warwickshire Coalfield, *Bull. Geol. Surv. Great Brit.,* 1972, vol. 35, pp. 1–150.

Tortello, M.F., Una nueva especie de *Leiagnostus* (Trilobita, Agnostida) en el Tremadociano superior (Ordovicico Inferior) de Salta, Argentina, *Ameghiniana,* 1998, vol. 35, no. 1, pp. 97–99.

Tortello, M.F., A systematic revision of the late Furongian trilobites from Cerro Pelado, Mendoza, Argentina, *Ameghiniana,* 2014, vol. 51, no. 4, pp. 295–310.

Tortello, M.F. and Acenolaza, G.F., Trilobites agnóstidos del límite Cámbrico–Ordovícico de la Formación Lampazar, Sierra de Cajas, Provincia de Jujuy, Argentina, *Rev. Españ. Paleontol.*, 1993, vol. 8, no. 2, pp. 177–184.

Tortello, M.F. and Esteban, S.B., Trilobites del Cámbrico Tardío de la Formación Lampazar (sierra de Cajas, Jujuy, Argentina): Implicancias bioestratigráficas y paleoambientales, *Ameghiniana*, 2003, vol. 40, no. 3, pp. 323–344.

Tortello, M.F. and Esteban, S.B., Trilobites agnóstidos del Cámbrico Tardío de la Sierra de Famatina (La Rioja, Argentina): Significado bioestratigráfico y paleoambiental, *INSUGEO, Ser. Corr. Geol.*, 2005, vol. 19, pp. 157–168.

Tortello, M.F. and Esteban, S., Early Ordovician trilobites from the Nazareno area, northwestern Argentina, *J. Paleontol.,* 2014, vol. 88, no. 5, pp. 925–947.

Troedsson, G.T., *On the Cambro-Ordovician faunas of Western Quruq tagh, Eastern T'ien-Shan, Palaeontol. Sin. Whole Ser. No 106, New Ser. B, Nanking: Geol.* Surv. China, 1937.

Tullberg, S.A., Om *Agnostus*–arterne i de kambriska aflagringarne vid Andrarum, *Sver. Geol. Unders. Ser. C,* 1880, vol. 42, no. 1, pp. 1–38.

Varlamov, A.I., Pack, K.L., and Rosova, A.V., *Stratigrafiya i trilobity verkhnego kembriya razreza r. Chopko. Noril'skii rayon, severo–zapad Sibirskoi platformy* (Stratigraphy and Trilobites of the Chopko River Section, Norilsk Region, Northwestern Siberian Platform), Novosibirsk: Nauka, 2005.

Varlamov, A.I. and Rosova, A.V., New Upper Cambrian Siberian regional stages (Eveniysk Series), in *Novye dannye po stratigrafii i paleontologii nizhnego paleozoya Sibiri* (New Data on the Stratigraphy and Paleontology of the Lower Paleozoic of Siberia), Novosibirsk: Sib. Nauchno-Issled. Inst. Geol. Geofiz. Mineral. Syr., 2009, pp. 3–61.

Weidner, T. and Nielsen, A.T., *Tomagnostus sibiricus* Pokrovskaya & Egorova, 1972 (Trilobita) from the Middle Cambrian Exsulans Limestone of Scania, Sweden, *GFF*, 2015, vol. 137, no. 1. pp. 9–19.

Westergård, A.H., *Paradoxides oelandicus* beds of Oland: With the account of a diamond boring through the Cambrian at Mossberga, *Sver. Geol. Undersok., Ser. C,* 1936, no. 394, part 30, pp. 1–65.

Westergård, A.H., Agnostidea of the Middle Cambrian of Sweden, *Sver. Geol. Unders., Ser. C,* 1946, no. 477, pp. 1–85.

Westergård, A.H., Supplementary notes on the Upper Cambrian trilobites of Sweden, *Sver. Geol. Unders., Ser. C,* 1947, no. 489, pp. 1–34.

Westrop, S.R., Trilobites of the Upper Cambrian Sunwaptan Stage, southern Rocky Mountains, Alberta, *Palaeontogr. Can.,* 1986, no. 3, pp. 1–75.

Westrop, S.R. and Adrain, J.M., Biogeographic shifts in a transgressive succession: The Cambrian (Furongian, Jiangshanian; Latest Steptoean–Earliest Sunwaptan) agnostoid arthropods *Kormagnostella* Romanenko and *Biciragnostus* Ergaliev in North America, *J. Paleontol.,* 2013, vol. 87, no. 5, pp. 804–817.

Westrop, S.R., Adrain, J.M., and Landing, E., The Cambrian (Sunwaptan, Furongian) agnostoid arthropod *Lotagnostus* Whitehouse, 1936, *Bull. Geosci.*, 2011, vol 86, no. 3, pp. 569–594.

Westrop, S.R. and Eoff, J.D., Late Cambrian (Furongian; Paibian, Steptoean) agnostoid arthropods from the Cow

Head Group, Western Newfoundland, *J. Paleontol.,* 2012, vol. 86, no. 2, pp. 201–237.

Westrop, S.R., Ludvigsen, R., and Kindle, C.H., Marjuman (Cambrian) trilobites of the Cow Head Group, Western Newfoundland, *J. Paleontol.,* 1996, vol. 70, no. 5, pp. 804–829.

Whitehouse, F.W., The Cambrian faunas of North–Eastern Australia, *Mem. Queensland Mus.,* 1936, vol. 11, parts 1 and 2, pp. 1–114.

Whitehouse, F.W., The Cambrian faunas of northeastern Australia: Part 3. The Polymerid trilobites, *Mem. Queensland Mus.*, 1939, vol. 11, pp. 179–282.

Xiang, L. and Zhang, T., Stratigraphy and trilobite faunas of the Cambrian in the western part of northern Tianshan, Xinjiang, *Geol. Mem., Ser. 2,* 1985, vol. 4, pp. 1–243.

Zhang, T., *Trilobita. Paleontological Atlas of Northwest China, Xinjiang Province*, Beijing: Geol. Publ. House, 1981, vol. 1, pp. 134–213.

Zhou, Zh., Notes on Chinese Ordovician agnostids, *Acta Palaeontol. Sin.,* 1987, vol. 26, pp. 639–661.

Zhou, Z. and Zhen, Y., *Trilobite record of China*, Beijing: Sci. Press, 2008.

Zhu, Z., Lin, H. Zhang, Z., Trilobites, in *Atlas of the Palaeontology of Northwestern China, Qinghai,* Beijing: Geol. Publ. House, 1979, vol. 2, pp. 81–116.

Żylińska, A., Late Cambrian trilobites from the Holy Cross Mountains, central Poland, *Acta Geol. Polon.*, 2001, vol. 51, no. 4, pp. 333–383.

Translated by S. Nikolaeva