Lower to Middle Ordovician trilobite faunas along the Ural border of Baltica

HELJE PÄRNASTE & JAN BERGSTRÖM†

Recent revision of the Ölandian trilobite faunas in Baltoscandia and the Ural Mountains throws new light on the development of the trilobite faunas in Baltica and possible migration links to surrounding terranes. The trilobite assemblages of 104 genera on the Uralian side of Baltica show different development patterns for the south and north through the Tremadocian to the Darriwilian. The oldest Uralian trilobites – disputably of latest Cambrian or earliest Ordovician age – arrived probably from the Siberian and Kazakh terranes being represented by mostly endemic genera such as *Kujandaspis* and *Jdyia*, but also with pandemic *Akoldinioidia* and *Micragnostus*. The following Kidryasian, Kolnabukian and Kuagachian faunas change gradually to show increasing difference between the sections in the South Urals and those in the northern Polar Urals or Pay-Khoy. In Kidryasian the olenids dominate in the South Urals as they do in many other regions during the early Tremadocian. The Kolnabukian trilobites represent the most diverse trilobite association in the region, and are comparable to the *Ceratopyge* fauna. The Kuagachian fauna contains a few additional elements, increasing the difference between south and north but with reduced generic diversity. The routes of faunal exchange are modified too. Thus during the Early Ordovician migration between the Uralian side of Baltica and the Baltoscandia, Kazakh and Altai-Sayan terranes becomes more important than that between the Uralian side of Baltica and the Siberia, North and South China plates. The Darriwilian Karakol'-Mikhailovskian faunal association shows a clear separation between north and south Urals with the former region, as in Baltoscandia, dominated by asaphids, while in south a reefal illaenid-cheirurid association of Laurentian genera occurs. This is rather intriguing given the widely accepted palaeogeographical disparate position and latitude of Laurentia at the time. • Key words: Ordovician, trilobites, Urals, Baltica, palaeogeography.

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Most Baltic Early to Middle Ordovician trilobites are endemic with a prevalence of asaphid genera and hence known as the Asaphid Province (Whittington 1963, Fortey & Cocks 2003, Bergström *et al.* 2013, Pärnaste & Bergström 2013). The Uralian border of Baltica is less well known. Even though what faunal lists exist, suggest some similarity between the east and west of Baltica. The aim of this study is (1) to compare the development of trilobite faunas along the Uralian side of Baltica, and (2) to compare the generic composition of the earliest faunas with the Baltoscandian side and with those of neighbouring terranes in order to assess possible migration routes for the earliest Uralian trilobite faunas.

Material and methods

Based on available photographs and descriptions, all early published trilobite data from the Urals have been assembled and revised. These include the work of Lermontova & Razumovskiy (1933), Weber (1948), Balashova (1961), Burskiy (1966, 1970), Antsygin (1973, 1977, 1978, 1991, 1993, 2001), and Antsygin *et al.* (1977). In comparing published faunas known from Baltoscandian side of Baltica with those of the Uralian side, it is obvious that the latter are relatively smaller in number possibly because of fewer studies or because publications are available only in Russian. All together about 220 species belonging to 104 genera from the latest Cambrian to the middle Darriwilian are listed in Bergström *et al.* (2013).

We use the genus level here for our analyses to investigate the development and variability of the trilobite faunas in an extended area such as the Urals together with Pay-Khoy and Vaygach in the north, extending south to the Mugodzhars in Aktyube Region and northwestern Kazakhstan. The faunas of different regions are listed separately. We follow the stratigraphical data of Antsygin (2001) to

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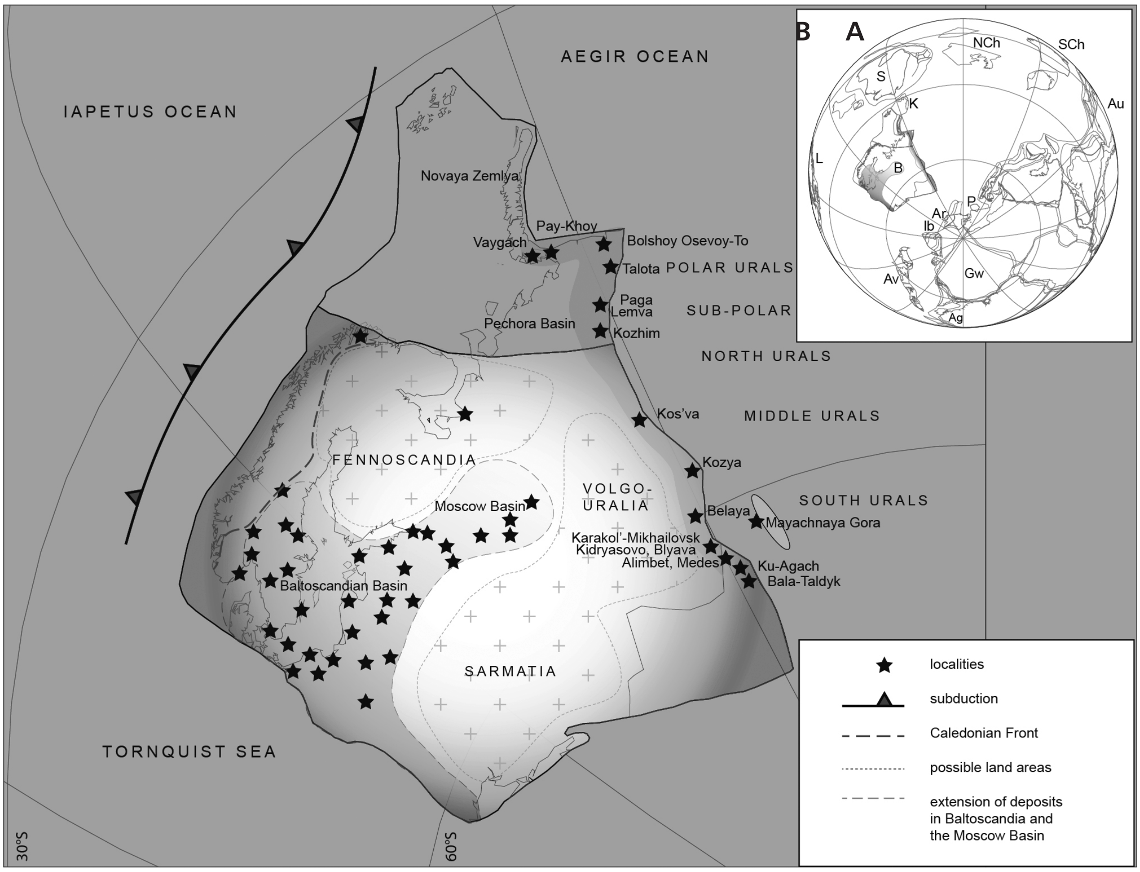

Figure 1. The Baltica Palaeoplate (A – global view; B – zoom in) with its complex borders and development of restricted marine sedimentary rocks in Baltoscandia in the west, the Moscow Basin deep within the plate, and the Cis-Ural belt in the east in its suggested position at about transition from Tremadocian to Floian (map generated using the T.H. Torsvik's GIS-oriented software from 2009, BugPlates: linking biogeography and palaeogeography). Abbreviations: Ag – Argentina; Av – Avalonia; Ar – Armorica; Au – Australia; B – Baltica; Gw – Gondwana; Ib – Iberia; K – Kara; L – Laurentia; NCh – North China; P – Perunica; S – Siberia; SCh – South China.

avoid mixing units introduced by authors dealing with other aspects than trilobites. The comparison presented here embodies our revision of the Baltoscandian taxa in Pärnaste *et al.* (2013).

Geological setting

The Lower Palaeozoic Baltica Palaeoplate (Cocks & Torsvik 2005) comprises the East European Craton as its core with three major crustal segments Fennoscandia, Sarmatia and Volgo-Uralia that collided between *ca* 2.0 and 1.7 Ga (Bogdanova *et al.* 2008), and the Pechora Basin that became accreted to Baltica in the late Vendian as a part of the Timanide Orogeny (Bogolepova & Gee 2004, O'Leary *et al.* 2004, Gee *et al.* 2008). The Kara block has been interpreted as a part of Baltica (Fig. 1A; *e.g.* Lorenz *et al.* 2008) or as an independent terrane (*e.g.* Metelkin *et al.* 2000, 2005; Torsvik & Andersen 2002; Cocks & Torsvik 2005) between Baltica and Siberia in the Ordovician Period. During the Cambrian and Ordovician, Baltica rotated through more than 120 degrees and drifted northwards from high to low palaeolatitudes. Thus the Uralian side that initially faced the Gondwana in high latitude changed its orientation to become more or less north-south oriented by the beginning of the Floian with its northern areas reaching into temperate climate zone (Fig. 1B).

In the Urals, the Ordovician facies are approximately meridional, as this mountain range is oriented today. The alluvial deposits in the westernmost facies belt are replaced to the east by shelf sediments followed by deep oceanic and rift sediments, which are allochthonous (*e.g.* Varganov *et al.* 1973, Savelieva & Nesbitt 1996, Bogolepova & Gee 2004, Ryazantsev *et al.* 2008). The shore-most facies, the Eletsk [Eletskaya] contains a cyclic succession of various sandstones alternating with conglomerates (Manitanyrd Formation) of mainly continental and coastal shallow-water deposits, mostly without trilobites (Bogolepova & Gee 2004). Eastwards, the Sakmara-Lemva [Lemvinskaya] facial zone consists of shelf sediments of the Pogurey [Pogureyskaya] Formation in the north and the Kidryas [Kidryasovskaya] Formation in the south, where trilobites are known from the upper Cambrian onwards. This facial zone is a relatively narrow region with complicated relief, often showing active hydrodynamic conditions (*i.e.* highly variable thickness of deposits). The upper Cambrian and Lower–Middle Ordovician succession comprises the following regional stages (horizons): Khmelev [Khmelevskiy], Kidryas [Kidryasovskiy], Kolnabuk [Kolnabukskiy], Kuagach [Kuagachskiy], Karakol'-Mikhailovsk (Fig. 2; Varganov *et al.* 1973, Antsygin 2001). The Pogurey [Pogureyskaya Svita] Formation is replaced by the Kibatin [Kibatinskaya] and Grubein [Grubeinskaya] formations. The latter is characterized by a thick complex of deep-water shales alternating with volcanic rocks representing a continental slope facies. During the Middle and Late Ordovician the deeper water conditions reach to the Sakmara-Lemva Zone. Most of the known trilobites come from this Sakmara-Lemva facial Zone.

The Tremadocian trilobites also occur on Pay-Khoy hills, on the Yugorsky Peninsula near the northern end of the Urals at the Kara Sea. Four trilobite beds were recognized in the Sokoli Regional Stage [Sokoliyskiy Horizon]: (1) *Synthrophopsis magna* and *Dikelokephalina* beds, (2) *Nyaya* and *Tersella* beds, (3) *Apatokephalus serratus* beds, and (4) *Megalaspides* beds (Fig. 2; Bondarev *et al.* 1970, Burskiy 1970). The following *Tetragraptus approximatus*, and the *Phyllograptus* aff. *densus* and *Eorobergia nericensis* beds of the Nelidov Regional Stage [Nelidovskiy Horizon] represent broadly the Floian Stage, and *Megistaspis limbata* and *Trigonograptus ensiformis* beds the Dapingian Stage, possibly reaching to the lower Darriwilian Stage. These beds belong to the Amdermin facial zone. The younger sediments with upper Darriwilian and younger Ordovician faunas occur on the southern side of the Yugorsky Peninsula on the coast of the Pechora Sea and on the islands of Vaygach and Novaya Zemlya and are thus named the Vaygach and Novaya Zemlya facial zones (Bondarev *et al.* 1970).

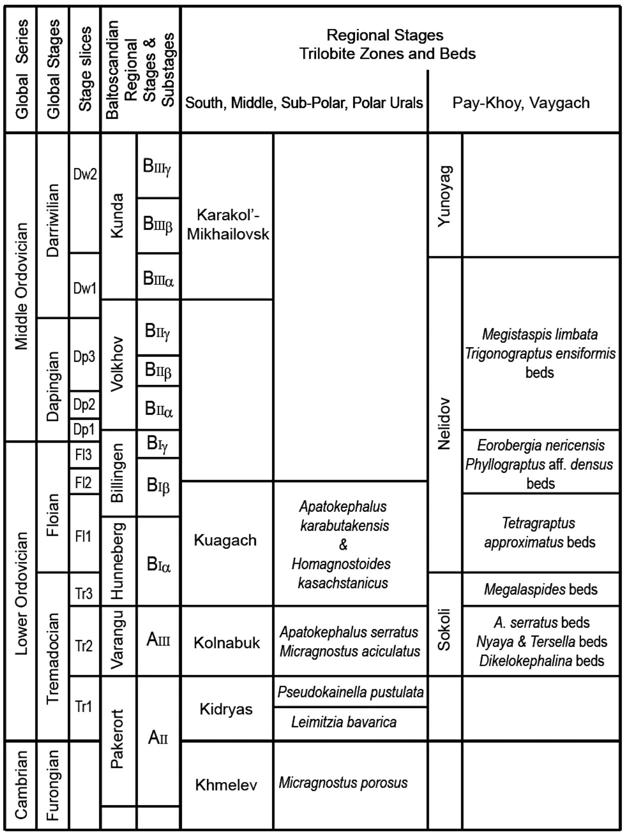

Figure 2. Correlation chart for the lower part of the Ordovician in Baltica. The correlation follows our earlier papers (Pärnaste & Viira 2012, Bergström *et al.* 2013, Pärnaste *et al.* 2013), where the Baltoscandian trilobite zones are compared with the recent data on graptolite (Maletz & Ahlberg 2011) and conodont zonation (Bergström & Löfgren 2009), and the global chronostratigraphy (Bergström *et al.* 2009). The stratigraphical framework of Urals is following that in Antsygin (1977, 2001; see also Bergström *et al.* 2013).

Khmelev Regional Stage

The Khmelevian trilobites (Table 1A) *Akoldinioidia* (det. as *Eoshumardia* Hupé, 1953 in Antsygin 2001), *Jdyia* and *Kujandaspis* together with *Micragnostus* have been regarded as being of Cambrian age (Antsygin 2001, Bogolepova & Gee 2004). The hystricurid *Jdyia* is endemic to the Urals, while *Micragnostus* is widely distributed around Gondwana and the Kazakh terranes since the upper Cambrian (Table 1B). The latter is recorded from Sub-Polar Urals (Bogolepova & Gee 2004) and South Urals (Antsygin 2001). The shumardiid *Akoldinioidia* occurs in the upper Cambrian of North China, South China, and Australia terranes and reaches to the Bolivia and Oaxaca (Mexico) regions in Tremadocian (Fig. 3; see revised list in Peng 1992, Zhu & Peng 2006). The eulomid *Kujandaspis* (including species of *Ketyna*; see for discussion on taxonomy in Rushton *et al*. 2002) is known from the upper Cambrian of the Kazakh terranes (Ivshin 1956, Apollonov & Chugaeva 1983), from Severnaya Zemlya (Rushton *et al*. 2002) and the Kulyumbe and Chopko rivers in the Siberia Plate (Fig. 3; Rozova 1968, Varlamov *et al.* 2006, Lazarenko *et al.* 2011) that possibly faced to the north of the Baltica Plate at that time (Fig. 1A; Cocks & Torsvik 2002). This is one of several pieces of evidence suggesting a possible Cambrian age of the Khmelev beds in the Urals and linking biogeographical connections between the listed terranes. The Khmelevian fauna may have arrived south through the Pechora Basin (Fortey & Cocks 2003, fig. 14; Cocks & Torsvik 2005, figs 5–6). Alternatively these allochthonous belts belonging to the Sakmara Zone (Guberlya microcontinent in Ryazantsev *et al*. 2008, fig. 11) possibly drifted differently from the main body of Baltica and were closer to Siberia in the lower latitudes during the Khmelevian or

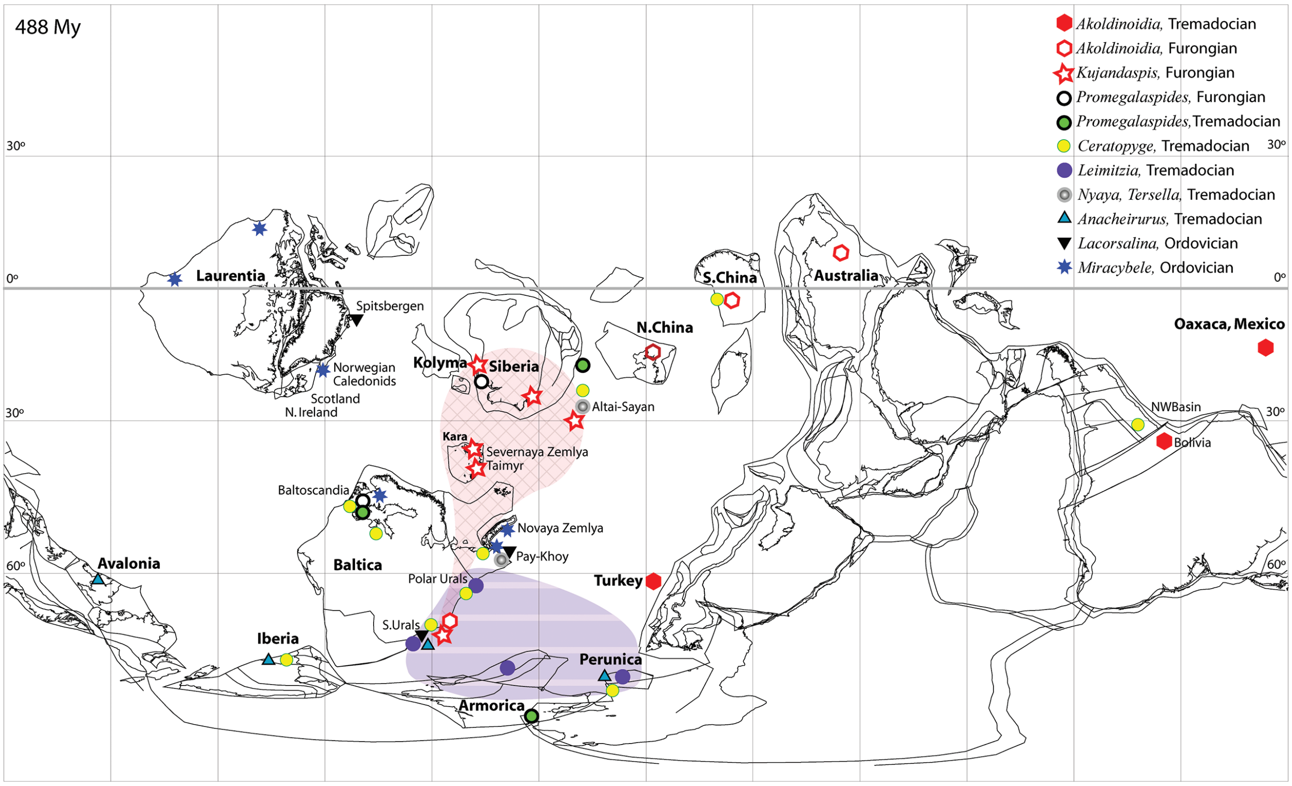

Figure 3. Global reconstruction in early Ordovician (488 Ma) time (map generated using the T.H. Torsvik's GIS-oriented software from 2009, BugPlates: linking biogeography and palaeogeography) to show distribution of selected genera regionally restricted to certain areas. The chequered shading marks the occurrences of *Kujandaspis*, while lined shading that of *Leimitzia*.

the fauna migrated via the Kazakh terranes (*cf.* palaeogeographic situation in Fortey & Cocks 2003, fig. 14). The overlying beds with a hungaiid *Leimitzia* are most probably of Ordovician age, as *Leimitzia* is common in the Lower Tremadocian of Bavaria (Fig. 3; Sdzuy *et al.* 2001) and the Tremadocian of Perunica (Mergl 2006).

Kidryas Regional Stage

In the Tremadocian the most common trilobites in the Urals were olenids (*Peltocare*, *Saltaspis*, *Triarthrus*?), hungaiids (*Leimitzia*, *Dikelokephalina*), cyclopygids (*Pricyclopyge*, *Tyrmancyclopyge*), remopleuridids (*Apatokephalus*), trinucleoids (*Orometopus*), asaphids (*Niobe*), ceratopygids (*Ceratopyge*), shumardids (*Akoldinioidia*), and a possible hystricurid *Jdyia* (Antsygin 2001, pp. 111–113, table 1).

The Kidryasian trilobites represent at least most of the Lower Tremadocian fauna in the South and Polar Urals (Table 1A). All three genera known from the Sub-Polar and Polar Urals (*Leimitzia*, *Jdyia*, *Dolgedola)* also occur in the South (Fig. 4). Five olenid genera and one eulomid, one pterocephalid and one acrocephalitid are ptychopariids. Nearly thirty per cent of the genera belong to the Asaphida, with three remopleuridids, two asaphids, two hungaiids and one ceratopygid.

Of nineteen genera recorded from the Kidryasian of the South Urals, four are endemic (*Alimbetaspis*, *Dolgedola*, *Jdyia*, *Medeselaspis*) and nearly half of them are shared with Baltoscandia (Table 1B). A similar number of genera, but with slight variation in content, is recorded from the Tremadocian of Laurentia, Argentina, South China and Armorica plus Perunica. Of Furongian genera, only three of them show a wide distribution in the Urals during the Tremadocian (*Micragnostus*, *Macropyge* and *Parabolinella*). *Parabolinella* is known from Argentina, Avalonia, Baltoscandia, China, Tasmania and NE Laurentia where it occurs from Furongian to Tremadocian (Bao & Jago 2000, Monti & Confalonieri 2013, fig. 4). A remopleuridid *Apatokephalus*, which appears in Siberia by the end of Cambrian (Mansi Stage, Ogienko 1984; *cf.* correlation in Varlamov *et al.* 2006, fig. 19) is globally widely distributed on the Tremadocian terranes (for taxonomy see Ebbestad 1999). Its sister taxon *Kainella* extends from Argentina to Laurentia and Urals. The earliest asaphids, *Promegalaspides* and *Niobe*, which originate in Cambrian of Siberia or Baltoscandia (Fig. 3; Lazarenko *et al.* 2011, Pärnaste & Bergström 2013) also arrive in the Uralian side of Baltica during the early Ordovician. The poorly known

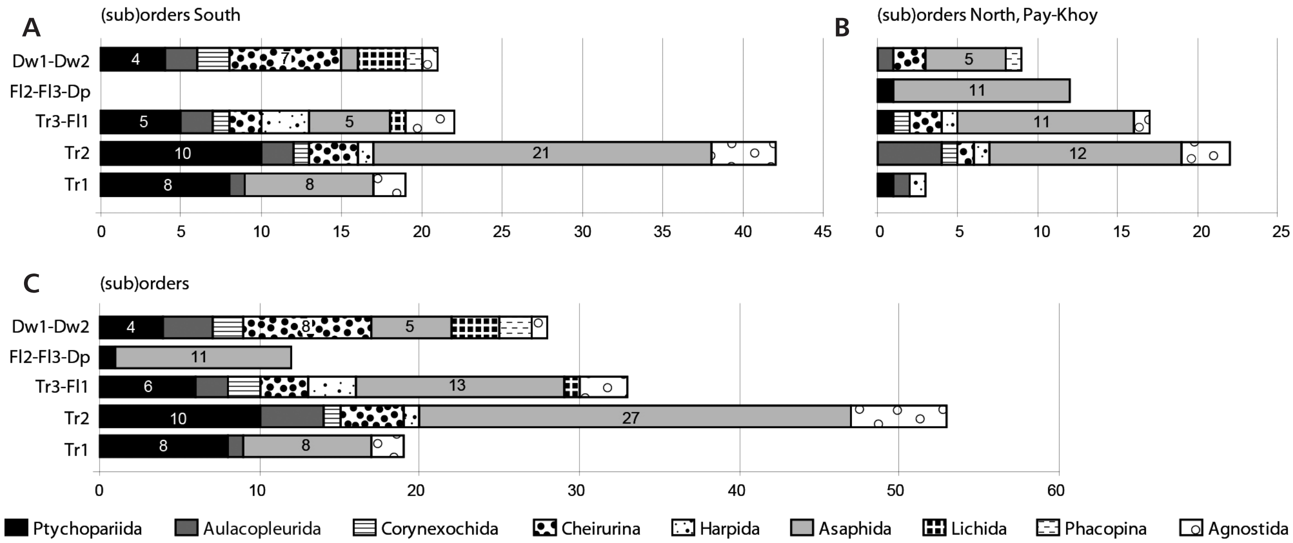

Figure 4. The generic composition of the Uralian trilobites presented in order or suborder level from Tremadocian to the Darriwilian to show differences in faunal development with possible palaeogeographical influence. • A – trilobites of South Urals, including those from Mugodzhars in Aktyube Region, northwestern Kazakhstan. • B – trilobites of Sub-Polar and Polar Urals, and areas collided in Cambrian – Pay-Khoy Peninsula and Vaygach Island. • C – trilobites of both areas combined together.

Hystricurus is shared between Siberia and the Urals (Balashova 1961). Consequently, of fifteen non-endemic genera of the Kidryasian fauna over half of taxa (one agnostid, two ptychopariids and five asaphids) are of Cambrian origin.

Kolnabuk and Sokoli Regional Stages

The Middle Tremadocian Kolnabukian trilobite fauna is more diverse than the older fauna with fifty-three genera: forty-two of them are known from the Urals and twenty-two occur in Pay-Khoy, some of them being present in both last named areas (Fig. 4). Of Kidryasian genera nearly half extend into this stage, including the olenids (Table 1A). Newly appear the orders Phacopida (Cheirurina), Aulacopleurida, Cornexochida and Harpetida. While the number of ptychopariids remains nearly the same, the reverse is the case of the asaphids. The latter diversify remarkably amounting to fifty per cent of all genera. The new Asaphida families to appear are the Alsataspididae, Nileidae and Cyclopygidae. The ptychopariids also become more diverse with ten genera. *Ceratopyge*, *Dikelokephalina*, *Nileus*, *Pricyclopyge* and *Micragnostus* prevail. The morphology of trilobites all together shows a great variation in life style, indicating that they occupied various ecological niches from deeper water continental slope environments to the shelf areas similar to those in outer shelf in Baltoscandia (Bergström *et al.* 2013).

The trilobites of *Synthrophopsis magna* and *Dikelokephalina* beds from the Sokoli Stage are the oldest in Pay-Khoy hills on the Yugorsky Peninsula, possibly corresponding to the Kolnabuk Stage of the southern Urals (Fig. 2, Table 1A; Antsygin 2001). The succeeding two beds with *Nyaya* and *Tersella* and with *Apatokephalus serratus* are also correlated with that stage, while the topmost *Megalaspides* Bed of the Sokoli Stage equates with the lowest Kuagachian of the South Urals. The first three beds seem to correspond to the *Ceratopyge* beds (Varangu Regional Stage; ~ Tr2) in Baltoscandia and the fourth to the lower Hunnebergian Stage (~ Tr3). A comparison of the north (Pay-Khoy) and the south reveals that the number of genera is smaller, possibly because of limited collections, but the names are the same. Only one obscure taxon makes the difference – *Asaphopsoides*(?) for the *S. magna* and *Dikelokephalina* Bed. However, the beds with *Nyaya* and *Tersella* include seven of the fifteen genera not recorded from the south. Noteworthy is the absence of the ptychopariids (including olenids), which are well diversified in south. This can be explained by a limited range of sediments representing only the near-shore conditions in Pay-Khoy while the missing olenids come from the deeper water outer shelf. The Sokolian genera can be compared with Baltoscandia and Laurentia rather than with other regions (Table 1B). *Nyaya* and *Tersella* are related to the Siberia and Altai-Sayan Region.

Outside of Baltoscandia, *Nyaya* appears in the Nyaian Regional Stage in the lowest Ordovician of Siberia (Rozova 1968, 1977; Ogienko 1974, 1984; Gorovtsova & Semenova 1977; for the latest correlation of the Cambrian-Ordovician boundary see Lazarenko *et al*. 2011). Together with *Tersella* it is known also from the lowest Ordovician in the Kuznetsk Alatau (Petrunina 1973, 1990), and from the Tremadocian Sokoli Stage of Pay-Khoy (Fig. 3; Burskiy 1970). Some questionable representatives from

Table 1A. Genera / regions in Urals, and occurrences on other regions and terranes (Table 1B). Abbreviations: SU – South Urals; SPU – Sub-Polar Urals; PU – Polar Urals; PK – Pay-Khoy; MG – Mayachnaya Gora, SE Urals; St. – Stage; Fm. – Formation. Font styles are set as the italic to mark rare occurrence, the regular to mark common species, and the bold to mark abundant occurrences (Antsygin 2001). 1 – Khmelev St., SU, PU; 2 – Kidryas St., SU; 3 – Pogurey Fm., Kidryas St., PU; 4 – Kolnabuk St., SU; 5 – Kibatin Fm., Kolnabuk St., PU; 6 – Bredin beds (partly), MG; 7 – *Synthrophopsis magna* & *Dikelokephalina* beds, Sokoli St, PK; 8 – *Nyaya* & *Tersella* beds, Sokoli St., PK; 9 – *Apatokephalus serratus* beds, Sokoli St., PK; 10 – *Megalaspides* beds, Sokoli St., PK; 11 – Kuagach St., SU; 12 – Grubein Fm., Kolnabuk–Kuagach Sts., PU; 13 – *Tetragraptus approximatus* beds, Nelidov St., PK; 14 – *Phyllograptus* aff. *densus* & *Eorobergia nericensis* beds, Nelidov St., PK; 15 – *Megistaspis limbata* & *Trigonograptus ensiformis* beds, Nelidov St., PK; 16 – Bredin beds (partly), MG; 17 – Karakol'-Mikhailov St., SU; 18 – Karakol'-Mikhailov St., SPU & PU.

Trilobite families & Agnostida		C-O	Tr1		Tr2							Tr3-Fl1			Fl2-3	Dp	Dw		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Agnostida	***Micragnostus* Howell, 1935**	**1**	**1**		**1**														
Eulomidae	*Kujandaspis* Ivshin, 1953	*1*																	
Shumardiidae	***Akoldinioidia* Zhou & Zhang, 1984**	**1**																	
Hungaiidae	***Jdyia* Antsygin, 2001**	*1*	**1**	**1**															
Hystricuridae	***Leimitzia* Sdzuy, 1955**		**1**	**1**															
Agnostida	***Geragnostus* Howell, 1935**		*1*		**1**			*1*	**1**		*1*	**1**	**1**	**1**				*1*	
Acrocephalitidae	***Dolgedola* Antsygin, 2001**		**1**	**1**															
Eulomidae	*Lateuloma* Dean, 1973		*1*																
Olenidae	*Acerocarina* Poulsen, 1952		1		*1*														
Olenidae	*Alimbetaspis* Balashova, 1961		*1*		1														
Olenidae	*Jujuyaspis* Kobayashi, 1936		*1*																
Olenidae	*Parabolinella* Brøgger, 1882		*1*		*1*														
Olenidae	***Peltocare* Henningsmoen, 1957**		**1**																
Pterocephaliidae	***Medeselaspis* Antsygin, 2001**		**1**																
Asaphidae	*Promegalaspides* Westergård, 1939		*1*		1														
Asaphidae	***Niobe* Angelin, 1851**		*1*		**1**							**1**				*1*			
Ceratopygidea	*Macropyge* Stubblefield & Bulman, 1927		*1*		*1*														
Remopleurididae	***Apatokephalus* Brøgger, 1896**		**1**		**1**	**1**		*1*	**1**	*1*	*1*			*1*					
Remopleurididae	*Kainella* Walcott, 1925		*1*																
Remopleurididae	*Pseudokainella* Harrington, 1938		1																
Hystricuridae	*Hystricurus*? Raymond, 1913		*1*					*1*											
Agnostida	*Leiagnostus* Jaekel, 1909				*1*														
Agnostida	*Litagnostus* Rasetti, 1944				1														
Eulomidae	*Euloma* Angelin, 1854				1							*1*			*1*				
Olenidae	***Saltaspis* Harrington & Leanza, 1957**				**1**														
Olenidae	***Triarthrus*? Green, 1832**				**1**														
Raymondinidae	*Pseudoglaphurina* Antsygin, 2001				*1*							1							
Shumardiidae	*Conophrys* Callaway, 1877				1								*1*	*1*					
Shumardiidae	*Hospes* Stubblefield & Bulman, 1927				*1*														
Triplacephalidae	*Amzasskiella* Poletaeva, 1960				*1*														
Alsataspidae	*Hapalopleura* Harrington & Leanza, 1957				*1*														
Alsataspidae	*Haplopleuroides* Petrunina, 1966 *nom. nudum*				*1*														
Alsataspidae	***Orometopus* Brøgger, 1896**				**1**														
Alsataspidae	*Pagometopus* Harrington & Leanza, 1957				*1*														
Asaphidae	*Asaphellus* Callaway, 1877				1		*1*		1	*1*	*1*								
Asaphidae	*Birmanites* Sheng, 1934				*1*														
Asaphidae	*Megistaspis* Jaanusson, 1956				*1*										*1*	*1*			
Asaphidae	*Niobella* Reed, 1931				*1*					*1*	*1*		*1*	*1*	*1*				
Ceratopygidae	***Ceratopyge* Hawle & Corda, 1847**				**1**	**1**						*1*	*1*						*1*
Cyclopygidae	***Pricyclopyge* Richter & Richter, 1954**				**1**				**1**			*1*	*1*						
Cyclopygidae	***Tyrmancyclopyge* Antsygin, 2001**				**1**														
Hungaiidae	***Dikelokephalina* Brøgger, 1896**				**1**			*1*											
Nileidae	***Nileus* Dalman, 1827**				**1**						*1*	*1*		*1*	*1*				
Nileidae	*Platypeltoides* Přibyl, 1949				1														
Nileidae	*Varvia* Tjernvik, 1956				*1*							1							
Remopleurididae	*Lacorsalina* Burskiy, 1970				*1*									*1*					
Remopleurididae	*Richardsonella* Raymond, 1924				*1*														
Hystricuridae	*Nyaya* Rozova, 1963				*1*			*1*	*1*			*1*							
Hystricuridae	*Tersella* Petrunina, 1973				*1*		*1*	*1*	*1*										
Leiostegiidae	*Agerina* Tjernvik, 1956				*1*				*1*										

Trilobite families & Agnostida		C-O	Tr1				Tr2					Tr3-Fl1			Fl2-3	Dp		Dw	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Harpididae	***Harpides* Beyrich, 1846**				1	1				*1*		**1**							
Pilekiidae	*Anacheirurus* Reed, 1896				1														
Pilekiidae	*Parapilekia* Kobayashi, 1934				*1*														
Pliomeridae	*Protopliomerops*? Kobayashi, 1934				*1*														
Asaphidae	*Araiocaris*? Přibyl & Vaněk 1980					*1*								*1*	*1*	*1*			
Pliomeridae	*Pliomeroides* Harrington & Leanza, 1957					*1*		*1*	*1*	*1*	*1*	1	1						
Asaphidae	*Megalaspides* Brøgger, 1886						*1*				*1*			*1*	*1*				
Hungaiidae	*Asaphopsoides*? Hupé, 1953							*1*	*1*										
Agnostida	*Galbagnostus* Whittington, 1965								*1*										
Agnostida	*Geragnostella* Kobayashi, 1939								*1*										
Alsataspidae	*Falanaspis* Tjernvik, 1956								*1*					*1*					
Nileidae	*Symphysurus* Goldfuss, 1843								*1*										
Remopleurididae	*Remopleuridiella*? Ross, 1951								*1*										
Telephinidae	*Carolinites* Kobayashi, 1940								*1*										*1*
Encrinuridae	*Cybelurus* Levitskiy, 1962										*1*							*1*	
Agnostida	*Homagnostoides* Kobayashi, 1939											1							
Agnostida	*Machairagnostus* Harrington & Leanza, 1957											*1*							
Eulomidae	*Bljauloma* Antsygin, 2001											*1*							
Raymondinidae	*Glaphurus* Raymond, 1905											1							
Shumardiidae	*Acanthopleurella* Groom, 1902											1							
Hystricuridae	*Batyraspis* Apollonov & Chugaeva, 1983											*1*							
Illaenidae	***Ottenbyaspis* Bruton, 1968**											**1**							
Harpididae	*Loganopeltis*? Rassetti, 1943											*1*		*1*					
Harpididae	*Scotoharpes* Lamont, 1948											1							
Lichidae	*Lichakephalina* Antsygin, 1973											1							
Cheiruridae	*Bornholmaspis*? Přibyl & Vaněk *in* Přibyl *et al.*, 1985											1							
Raphiophoridae	*Lonchodomas* Angelin, 1854													*1*	*1*				*1*
Styginidae	*Raymondaspis* Přibyl, 1949													*1*					
Raphiophoridae	*Amyxella*? Dean, 1960														*1*				
Remopleurididae	*Eorobergia* Cooper, 1953														*1*				
Asaphidae	*Asaphus*? Brongniart, 1822															*1*			*1*
Asaphidae	*Megistaspis* (*Megistaspidella*) Jaanusson, 1956															*1*			
Cheiruridae	*Cyrtometopus* Angelin, 1854																*1*	*1*	
Encrinuridae	*Cybele* Loven, 1845																*1*		
Pterygometopidae	*Pterygometopus* Schmidt, 1881																*1*		
Isocolidae	*Cyphoniscus* Salter, 1853																	*1*	
Isocolidae	*Holdenia* Cooper, 1953																	*1*	
Isocolidae	*Pseudopetigurus* Prantl & Přibyl, 1949																	*1*	
Raymondinidae	*Glaphurina* Ulrich, 1930																	*1*	
Remopleurididae	*Remopleurides* Portlock, 1843																	*1*	*1*
Holotrachelidae	*Kinderlania* Antsygin, 1977																	*1*	
Telephinidae	*Phorocephala*? Lu *in* Lu *et al.*, 1965																	*1*	
Illaenidae	*Illaenus* Dalman, 1827																	*1*	
Illaenidae	*Platillaenus* Jaanusson, 1954																	*1*	
Lichidae	*Metopolichas* Gürich, 1901																	*1*	
Lichidae	*Platylichas* Gürich, 1901																	*1*	
Odontopleuridae	*Ceratocephala* Warder, 1838																	*1*	
Cheiruridae	*Heliomera* Raymond, 1905																	*1*	
Cheiruridae	*Kawina* Barton, 1916																	*1*	
Cheiruridae	*Pateraspis* Přibyl & Vaněk *in* Přibyl *et al.*, 1985																	*1*	
Pliomeridae	*Pliomera* Angelin, 1854																	*1*	*1*
Asaphidae	*Plectasaphus* Jaanusson, 1953																		*1*
Cheiruridae	*Ceraurinella* Cooper, 1953																		*1*
Pterygometopidae	*Calyptaulax* Cooper, 1930																		*1*
	Number of taxa	4	19	3	42	5	3	8	15	5	8	22	6	12	9	5	3	19	9

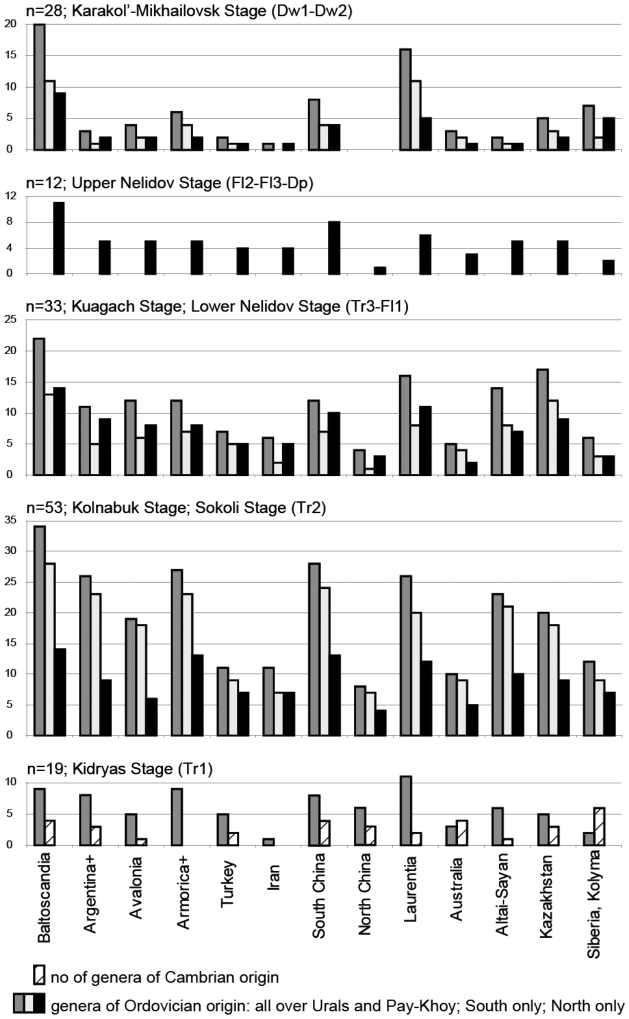

Figure 5. Palaeogeographic distribution of the Tremadocian–Darriwilian genera found in the Uralian side of Baltica (for the intervals and data see Fig. 2, Table 1B).

the South Urals (Antsygin 1977, Korinevskiy 1989) were attributed to the genus *Jdyia* (Antsygin 2001) but without any comment. It is not clear whether this genus alone occurs in the South Urals to the exclusion of *Nyaya* and *Tersella*. A problematic taxon *Hystricurus conicus* (Billings, 1859) figured by Balashova (1961, pl. 1, figs 12–14) may also belong to *Jdyia*. Burskiy's (1970) taxa from Pay-Khoy (*Nyaya novozemelica* Burskiy, 1970; *N. paichoica* Burskiy, 1970; *N. sokoliensis* Burskiy, 1970; *Tersella*? *magnaoculus* Burskiy, 1970) are figured without description and we agree with Adrain & Westrop (2006) that they are *nomina nuda*. The latter authors discussed the systematic position of *Nyaya* and *Tersella* and considered them more similar to the hystricurids (as suggested already by Rozova 1968, and Antsygin 2001) than to the aphelaspidines (see Shergold 1982, Jago 1987, Shergold *et al.* 2000). In general, the hystricurids tend to have a fairly small and crescentic palpebral lobe and highly vaulted glabella, while *Tersella*, *Nyaya* and *Jdyia* have a flat glabella, and a larger, sausage-shaped palpebral lobe that is closer to the glabella and separated by a deep furrow from the fixigena. These characters are fairly stable within families, and they are therefore clearly different from any hystricurid. The major difference between the hystricurids and *Jdyia-Tersella-Nyaya* group is that the former has a median preglabellar depression causing the glabella to appear more pointed medially. In the *Jdyia-Tersella-Nyaya* group the preglabellar area is inflated and the glabella is trapezoidal anteriorly. Still, the *Jdyia-Tersella-Nyaya* group is very similar to some of the latest Cambrian aphelaspidine genera from the outer shelf of the Siberia such as *Nganasanella* Rozova, 1963, *Olentella* Ivshin, 1956, *Amorphella* Rozova, 1963, and *Monosulcatina* Rozova, 1963 (Rozova 1968, pls 7–9; Pegel 2000, fig. 9). They also resemble the Cambrian parabolinoidid *Taenicephalops* Ergaliev, 1980, which possibly includes *Aphelaspis*? *kazachstanica* Lisogor, 1977, both known from Maly Karatau, Kazakhstan (Ergaliev 1980). The Lower Tremadocian *Lusampa* Petrunina, 1990 from the northeastern Salair, Altai-Sayan region is rather variable. Of the three species listed, *Lusampa tenuis* Petrunina, 1990 is very similar to *N. paichoica* Burskiy, 1970 *nom. nudum*, while *Lusampa interposita* Petrunina, 1990 resembles *Jdyia*, and leaves the type species *Lusampa cupoides* Petrunina, 1990 sufficiently different. Unfortunately, it is difficult to judge the similarity by the photographs. However, all these Cambrian genera possess smaller palpebral lobe than the Uralian group. In that character the latter resembles a hystricurid *Millardicurus* Adrain & Westrop, 2006, and we include these genera tentatively within the hystricurids in our data set (Fig. 4).

Several widely distributed Tremadocian genera, such as *Dikelokephalina, Ceratopyge* and *Amzasskiella* first appear within the Kolnabuk Stage in the Urals. Ebbestad (1999) recently revised the type material of *Ceratopyge* and lists its occurrence as being Baltica, China, Argentina and Kazakhstan. The latter, a record from Balashova (1961) actually represents the Aktyube region of South Urals. In addition, *Ceratopyge* has been known from Armorica (Hammann *et al.* 2008), and Perunica (Mergl 2006), and from Altai-Sayan (Fig. 3; Petrunina 1960, 1990). In the Urals *Ceratopyge* occurs from the Kolnabuk to Kuagach stages in South and Polar Urals. More problematic is the record from Pay-Khoy. Some of the specimens ascribed to *Ceratopyge*, *e.g.* two cranidia figured by Burskiy (1970, pl. 6, figs 10, 15) are better to assign to *Agerina*. These resemble most *Agerina ferrigena* (Růžička, 1926) from the upper Tremadocian Třenice Formation in Bohemia (Mergl 2006, text-fig. 14), and *Agerina praematura* (Tjernvik, 1956) from the Bjørkåsholmen Formation in Baltoscandia. Otherwise *Agerina* is recorded from the southern Urals (Popov & Holmer 1994).

This genus may have been derived from the Lower Tremadocian *Brackenbuschia* Harrington & Leanza, 1957 of Argentina (for discussion see Adrain & Fortey 1997, Sdzuy *et al.* 2001, Mergl 2006). Thus during the Tremadocian times *Agerina* and associates mainly lived in the West Gondwana but extended to both sides of Baltica.

Dikelokephalina was common in the Tremadocian of the Urals and contemporaneously worldwide (for discussion on systematics and distribution see Fortey 2010). Specimens reached a large size in the Morocco region (Fortey 2009, 2010) at high latitudes of West Gondwana. Gigantism is more pronounced for Darriwilian trilobites in the Valongo region of the Armorica terrane also located at high latitudes (Gutiérrez-Marco *et al.* 2009). In Baltoscandia the largest trilobites are the Kundan (Darriwilian) asaphids (Pärnaste *et al.* 2013), a group of similar morphology and possibly of similar life style (Pärnaste & Bergström 2013). To date no large dikelokephalids or asaphids have been recorded from the Uralian side of Baltica even though the palaeolatitude is similar.

Amzasskiella, a peculiar trilobite genus with a bulb in front of the glabella possibly developed as a brood pouch (Fortey & Hughes 1998), has been recorded in many regions, mainly from assumed warm climate areas of East Gondwana, Siberia, Altai-Sayan, and Kazakhstan. However, the early Tremadocian representatives appear in Cordillera Oriental and Western Puna (Vaccari & Waisfeld 2008) in temperate climates at similar latitudes to Baltica (*e.g.* Monti & Confalonieri 2013). The Uralian species of Kolnabuk age may have arrived from both areas.

Saltaspis is restricted to the South America and Baltica. The earliest occurrences are from the Lower Tremadocian Olenid fauna of the Cordillera Oriental and southern Bolivia (Přibyl & Vaněk 1980, Waisfeld & Vaccari 2003), and from the Digermul Peninsula of Finnmark, northern Norway (Nikolaisen & Henningsmoen 1985). The distribution of *Saltaspis* extends towards higher latitudes by the Middle Tremadocian involving southern part of the Baltoscandian Palaeobasin and South Urals.

Thirty-four Kolnabukian genera are shared with Baltoscandia and only two (*Tyrmancyclopyge* and *Alimbetaspis*) are endemic. Of the new arrivals two thirds are of Cambrian origin. The largest number of these genera is shared with South China (7), Kazakhstan (6) and Argentina (5). When comparing the faunas of the Ordovician origin, the greatest similarity is with faunas of Baltoscandia, reaching 65%, and nearly half of the Uralian genera are shared with South China, Armorica, Argentina and Laurentia terranes. Slightly less than 40% of the Kolnabukian genera occur in the Altai-Sayan, Kazakhstan and Avalonia, while only a fifth occur in other terranes (Fig. 5, Table 1B). All together, the Kolnabukian fauna shows high rate of globalization.

Kuagach and Nelidov Regional Stages

The Kuagachian fauna is of latest Tremadocian and earliest Floian age (Figs 2, 4). The number of genera is reduced to thirty-three. Otherwise there is little change compared to the preceding fauna, except the new addition of the Lichida. The family Olenidae within Ptychopariida disappears. Thus the ptychopariids decrease by half, leaving more space for corynexochids and harpetids. This replacement possibly reflects shallower shelf conditions and also the *Ceratopyge* Regressive Event well recorded on the Baltoscandian side of the Baltica (Ebbestad 1999). In numbers, the most abundant species of the Kuagachian fauna belong to the genera *Ottenbyaspis*, *Pricyclopyge*, *Nileus* and *Ceratopyge*. By this time, as in the previous interval, a differentiation between the development of faunas in north and south can be detected. In Pay-Khoy two thirds of the recorded genera belong to the Asaphida, while in the Sakmara Zone the figure is only about one quarter. In addition to the Asaphida seven other trilobite orders are represented. The ptychopariids disappear, except for *Shumardia* (Fig. 4, Table 1A).

In comparison with other areas where Uralian genera occur, there is a change towards sharing proportionately more genera with Baltoscandia, and fewer with the North China Plate and Laurentia. Also fewer genera connect the Urals with the Kazakh, Altai-Sayan and Iran terranes at the time (Fig. 5, Table 1B).

The Late Floian–Dapingian deposits are less known on the Uralian side of Baltica and the trilobite fauna is recorded only from the upper part of the Nelidov Regional Stage in Pay-Khoy hills on Yugorsky Peninsula at the northern tip of the Urals. The two beds included here are the *Phyllograptus* aff. *densus* & *Eorobergia nericensis* bed, and the *Megistaspis limbata* & *Trigonograptus ensiformis* Bed, containing mainly asaphids (*Niobe*, *Niobella*, *Megistaspis*, *Megalaspides*), plus remopleuridids (*Apatokephalus*, *Lacorsalina*, *Eorobergia*), *Euloma* and *Raymondaspis* (Fig. 4). A fauna from Pay-Khoy shares all genera with Baltoscandia except for the remopleuridid, *Lacorsalina*, which is shared with Spitsbergen, where it occurs in the younger beds (Fortey 1980). The asaphids are clearly dominant in number of species, followed by remopleuridids.

Karakolʹ-Mikhailovsk Regional Stage

The Darriwilian Karakolʹ-Mikhailovsk Stage contains a diverse trilobite fauna (Fig. 4, Table 1A) but the difference in faunal content between the north and south Urals becomes greater. Families making their first appearance in the region are Pterygometopidae and Odontopleuridae. All nine genera from the Sub-Polar and Polar Urals in the north (*i.e.* *Asaphus*, *Lonchodomas*, *Remopleurides*, *Pliomera*,

Table 1B. List of the trilobite genera of the Uralian border of Baltica (Weber 1948; Bondarev *et al.* 1965; Burskiy 1966, 1970; Varganov *et al*. 1973; Antsygin 1977, 1978, 1991, 1993, 2001; Antsygin *et al.* 1977; Klyuzhina 1985; Puchkov 1991; Bergström *et al.* 2013) shown with distribution on the other terranes. Main references to the faunas reviewed from different areas are as follows: Baltoscandia (Tjernvik 1956; Henningsmoen 1957; Ebbestad 1999; Żylińska 2002; Terfelt *et al*. 2011; Pärnaste *et al.* 2009, 2013), Argentina plus Bolivia (Robison & Pantoja-Alor 1968; Přibyl & Vaněk 1980; Waisfeld & Vaccari 2003; Tortello & Esteban 2007; Balseiro & Marengo 2008; Vaccari & Waisfeld 2008), Avalonia (Owens *et al*. 1982; Fortey & Owens 1991), Armorica: Iberia (Álvaro *et al.* 2007, Hammann *et al*. 2008), Montagne Noir (Vizcaïno *et al*. 2001, Vizcaïno & Álvaro 2003, Shergold *et al.* 2007), Bavaria (Sdzuy *et al.* 2001), Perunica (Mergl 2006), Turkey (Shergold & Sdzuy 1984, Dean 2006), Alborz, Iran (Ghobadi Pour 2006, Ghobadi Pour *et al.* 2007, Bruton *et al.* 2004), South China (Lu 1975; Peng 1990a, 1990b, 1992; Zhou & Zhen 2008; Zhou *et al*. 2011), North China (Kuo *et al.* 1982, Sohn & Choi 2002), Australia (Jell 1985, Jell & Stait 1985, Shergold *et al*. 2007), Laurentia including Western Ireland, Scotland (Ludvigsen 1982, Pratt 1988, Adrain & Fortey 1997, Fortey & Droser 1999), Siberia (Rozova 1968, 1977, 1984; Ogienko 1974, 1984; Timokhin 1989; Pegel 2000; Lazarenko & Pegel 2001; Lazarenko *et al*. 2011), Kolyma (Chugaeva 1973), and Kazakhstan: Kokchetav – Middle Tianshan Microcontinent (Ulutau-Karatau-Naryn) (Lisogor 1977a, 1977b; Ergaliev 1980, 1983; Apollonov & Chugaeva 1983), Stepnayk – Northern Tianshan Microcontinent (Kendyktas Range) (Lisogor 1961, Popov & Holmer 1994), Zheľtau and Atasu-Junggar volcanic arcs (Chu-Ili) (Chugaeva 1958), Baydaulet-Akbastau arc (Olenty River and Dzhungaria) (Ivshin 1956, 1962; Popov & Holmer 1994), Altai-Sayan (Kuznetsk-Alatau, Gornaya Shoria, Salair, Gorny Altai) (Sivov 1955; Petrunina 1960, 1990; Poletaeva 1960, 1977; Rozova 1960; Rozova *et al*. 1985).

Uralian genera / Other regions / terranes	Cambrian											Ordovician												
	Baltoscandia	Argentina+	Avalonia	Turkey	South China	North China	Laurentia	Australia	Altai-Sayan	Kazakhstan	Siberia, Kolyma	Baltoscandia	Argentina+	Avalonia	Armorica+Perunica	Turkey	Iran	South China	North China	Laurentia	Australia	Altai-Sayan	Kazakhstan	Siberia, Kolyma
Acanthopleurella Groom, 1902									1					1								1		
Acerocarina Poulsen, 1952	1											1	1											
Agerina Tjernvik, 1956												1	1		1	1		1		1				
Akoldinioidia Zhou & Zhang, 1984					1	1		1					1			1								
Alimbetaspis Balashova, 1961																								
Amzasskiella Poletaeva, 1960		1											1					1	1		1	1	1	1
Amyxella? Dean, 1960												1		1				1						
Anacheirurus Reed, 1896														1	1							1		
Apatokephalus Brøgger, 1896									1		1	1	1	1	1	1	1	1	1	1		1	1	1
Araiocaris? Přibyl & Vaněk, 1980													1											
Asaphellus Callaway, 1877		1			1			1					1	1	1		1	1	1	1		1	1	
Asaphopsoides? Hupé, 1953															1		1							
Asaphus? Brongniart, 1822												1												
Batyraspis Apollonov & Chugaeva, 1983																							1	
Birmanites Sheng, 1934													1		1			1		1				
Bljauloma Antsygin, 2001																								
Bornholmaspis? Přibyl & Vaněk *in* Přibyl *et al*., 1985												1		1										
Calyptaulax Cooper, 1930												1		1				1		1				
Carolinites Kobayashi, 1940												1				1	1			1				1
Ceratocephala Warder, 1838												1								1				
Ceratopyge Hawle & Corda, 1847												1	1		1			1				1		
Ceraurinella Cooper, 1953												1								1				1
Conophrys Callaway, 1877		1			1	1				1		1	1	1	1		1	1	1	1		1	1	1
Cybele Loven, 1845												1												
Cybelurus Levitskiy, 1962												1		1						1		1		
Cyphoniscus Salter, 1853														1						1				
Cyrtometopus Angelin, 1854												1												
Dikelokephalina Brøgger, 1896												1		1	1		1	1	1		1	1	1	1
Dolgedola Antsygin, 2001																								
Eorobergia Cooper, 1953												1								1		1		
Euloma Angelin, 1854					1							1		1	1	1	1	1		1		1	1	1
Falanaspis Tjernvik, 1956												1								1				
Galbagnostus Whittington, 1965														1						1				
Geragnostella Kobayashi, 1939															1			1						
Geragnostus Howell, 1935												1			1	1		1		1			1	
Glaphurina Ulrich, 1930												1								1			1	
Glaphurus Raymond, 1905																				1		1		1
Hapalopleura Harrington & Leanza, 1957		1											1											
Haplopleuroides Petrunina, 1966 *nom. nudum*																								
Harpides Beyrich, 1846				1						1		1	1		1			1		1	1	1	1	
Heliomera Raymond, 1905																				1				
Holdenia Cooper, 1953															1									
Homagnostoides Kobayashi, 1939															1								1	
Hospes Stubblefield & Bulman, 1927		1			1					1		1	1	1				1					1	

Uralian genera	Cambrian											Ordovician												
Other regions / terranes	Baltoscandia	Argentina+	Avalonia	Turkey	South China	North China	Laurentia	Australia	Altai-Sayan	Kazakhstan	Siberia, Kolyma	Baltoscandia	Argentina+	Avalonia	Armorica+Perunica	Turkey	Iran	South China	North China	Laurentia	Australia	Altai-Sayan	Kazakhstan	Siberia, Kolyma
Hystricurus? Raymond, 1913															1			1	1	1	1			1
Illaenus Dalman, 1827												1												
Jdyia Antsygin, 2001															1									
Jujuyaspis Kobayashi, 1936												1	1		1				1	1	1			
Kainella Walcott, 1925		1											1							1				
Kawina Barton, 1916																				1				
Kinderlania Antsygin, 1977																								
Kujandaspis Ivshin, 1953										1	1													
Lacorsalina Burskiy, 1970												1								1		1		
Lateuloma Dean, 1973																1								
Leiagnostus Jaekel, 1909					1			1		1		1	1	1	1			1		1			1	
Leimitzia Sdzuy, 1955																								
Lichakephalina Antsygin, 1973																								
Litagnostus Rasetti, 1944							1			1				1										
Loganopeltis? Rassetti, 1943							1																	
Lonchodomas Angelin, 1854												1	1	1	1			1		1			1	1
Machairagnostus Harrington & Leanza, 1957		1											1										1	
Macropyge Stubblefield & Bulman, 1927	1			1	1			1		1	1			1	1			1		1		1	1	
Medeselaspis Antsygin, 2001																								
Megalaspides Brøgger, 1886												1					1	1						
Megistaspis (*Megistaspidella*) Jaanusson, 1956												1												
Megistaspis Jaanusson, 1956												1	1		1		1	1		1	1	1		
Metopolichas Gürich, 1901												1												
Micragnostus Howell, 1935		1		1	1	1	1	1		1		1	1		1	1		1		1				
Nileus Dalman, 1827												1	1	1		1	1	1		1	1		1	
Niobe Angelin, 1851											1	1			1	1		1	1	1		1	1	
Niobella Reed, 1931	1		1	1	1		1	1			1	1	1	1	1	1		1			1	1	1	
Nyaya Rozova, 1963																						1		1
Orometopus Brøgger, 1896												1	1	1	1							1	1	
Ottenbyaspis Bruton, 1968										1		1											1	
Pagometopus Harrington & Leanza, 1957												1	1											
Parabolinella Brøgger, 1882	1	1	1		1	1	1	1			1	1	1	1				1	1	1		1	1	
Parapilekia Kobayashi, 1934		1										1	1	1	1			1		1	1			
Pateraspis Přibyl & Vaněk *in* Přibyl *et al.*, 1985															1									
Peltocare Henningsmoen, 1957												1	1	1						1				
Phorocephala? Lu *in* Lu *et al.*, 1965												1						1		1				
Platillaenus Jaanusson, 1954												1	1							1	1			
Platylichas Gürich, 1901												1												
Platypeltoides Přibyl, 1949					1					1	1	1		1	1			1				1	1	1
Plectasaphus Jaanusson, 1953												1												
Pliomera Angelin, 1854												1												1
Pliomeroides Harrington & Leanza, 1957												1	1							1			1	
Pricyclopyge Richter & Richter, 1954												1	1	1	1	1		1					1	
Promegalaspides Westergård, 1939	1										1	1			1							1		
Protopliomerops? Kobayashi, 1934																								1
Pseudoglaphurina Antsygin, 2001												1												
Pseudokainella Harrington, 1938													1	1				1	1	1	1	1		
Pseudopetigurus Prantl & Přibyl, 1949															1			1						
Pterygometopus Schmidt, 1881												1			1					1				
Raymondaspis Přibyl, 1949												1								1				
Remopleurides Portlock, 1843												1						1		1	1		1	1
Remopleuridiella? Ross, 1951												1								1		1		1
Richardsonella Raymond, 1924							1						1											
Saltaspis Harrington & Leanza, 1957												1	1											
Scotoharpes Lamont, 1948										1		1		1							1		1	
Symphysurus Goldfuss, 1843												1	1		1	1	1	1				1	1	
Tersella Petrunina, 1973																				1		1		1
Triarthrus? Green, 1832												1	1	1	1			1		1	1			
Tyrmancyclopyge Antsygin, 2001																								
Varvia Tjernvik, 1956												1								1		1		
Number of taxa	5	10	2	4	11	4	6	7	2	11	8	61	35	29	35	13	11	35	10	46	14	28	28	17

Cyrtometopus, *Illaenus*, *Platillaenus*, *Metopolichas*, and *Platylichas*) occur also in Baltoscandia, but of twenty-one genera in the south, ten are absent in Baltoscandia (Table 1B). This is the case with the holotrachelid *Kinderlania*, which is endemic to the Urals, the three isocolids: *Holdenia*, *Pseudopetigurus*, and *Cyphoniscus* with an origin in Armorica, Perunica and Avalonia respectively, and a cheirurid *Pateraspis* that is common in Armorica and Perunica. The two other cheirurids *Kawina* and *Heliomera* are found on the Iapetus-side of Laurentia, including western Newfoundland and Spitsbergen. There is thus a clear faunal separation between south and north in the Early Darriwilian, with no connection at the species level (Bergström *et al.* 2013). The only exception is *Pliomera fisheri* (Eichwald, 1825) a broadly defined species in need of revision. This taxon contains a group in which the anterior-most glabellar furrows terminate in the anterior border furrow instead of the axial furrow and the anterior border is denticulated to receive the pygidial spines during enrolment (see Öpik 1937, pl. 19, fig. 4; Schmidt 1881, pl. 13, figs 1–4). *Pliomera fisheri asiatica* (Chugaeva, 1973) from Kolyma has reduced lateral lobes similar to those on specimens from the Urals (Antsygin 1977, pl. 5, figs 7–8; 1991, pl. 25, figs 1–3) and to those from the allochthonous Otta serpentine conglomerate of Norway, which possibly represents an intra-Iapetus island located somewhere between Baltica and Laurentia in Darriwilian times (Bruton & Harper 1981, Harper *et al.* 2009). *Pliomera* first appears in the Dapingian and early Darriwilian of Baltoscandia (Pärnaste *et al.* 2013), where it is often associated with the mud mounds that might signal the occurrences of similar environments for the accumulation of such formations in the Urals, as well as in Kolyma. *Pliomera* is also reported from the lower Darriwilian Kunda Stage of the Moscow Basin (Dmitrovskaya 1989, Bergström *et al.* 2013), which may indicate a direct pathway of these faunas via that basin.

The separation of the Karakol'-Mikhailovskian faunas is also characterised by a major difference in diversity and in dominant groups (Fig. 4). The trilobite assemblage from the Polar and Sub-Polar Urals is strongly dominated by asaphids that agree well with Baltoscandian Asaphid fauna, while in the south Urals there occurs a reef-related cheirurid facies fauna comparable to that known from Laurentia (see *e.g*. Whittington 1963, 1965; Ross 1972; Fortey 1980). Besides, of these cheirurid and raymondinid genera, connecting the Uralian fauna with the Laurentian, only a very few are common to the other regions (Fig. 5, Table 1B). This condition does not fit with the pattern of the palaeogeographical maps for the Mid-Darriwilian (Dw2). However, conodont distributions show a similar influx of the North American faunas at this level (*e.g*. Nasedkina 1981, Dubinina & Ryazantsev 2008). The most probable interpretation is that we are dealing with deep-water conditions, known to conodont specialists as the Tropical Domain of the Open-Sea Realm (Zhen & Percival 2003, Dubinina & Ryazantsev 2008). The South Urals is thus distinguished from the rest of Baltica by having a Laurentian fauna equivalent to that conodont fauna. An explanation for this is difficult in terms of available palaeogeographical reconstructions (*e.g*., Cocks & Fortey 1998, Torsvik & Andersen 2002, Cocks & Torsvik 2005, Harper *et al.* 2009). Perhaps a similar marginal fauna existed northwest of present-day Norway, but the proof is missing, because much of the Baltic crust was subducted (Cocks & Fortey 1998). Or perhaps the allochtonous belts of the Oslo region formed links between Baltica and Spitsbergen or other regions related to Laurentia earlier than in Late Ordovician as referred by Bergström *et al.* (2010).

Summary

All together 96 genera of trilobites and 8 genera of agnostid arthropods are recorded from the Uralian side of Baltica from the Tremadocian to the middle Darriwilian (= Ölandian of Baltoscandia). This number is about one fifth fewer than recorded from the Baltoscandian side (Pärnaste *et al.* 2013) though figures from the east are based on a fewer studies and localities.

Summarizing the evolution of faunas, it can be noted that the lower Tremadocian in the south contains a fairly rich fauna with some 16 genera, plus 3 agnostoids. Half of this fauna belongs to genera of Cambrian origin, including the olenids and the earliest asaphids and ceratopygids. The later Tremadocian, both in the north and the south, includes the *Ceratopyge* Biofacies, with much variation in composition and richer than earlier. The post-Tremadocian development involved a wider divergence between north and south. In the north there was a strong diversification of asaphids. Although the Asaphid Biofacies is recognisable, it is notably different and much poorer than that of Baltoscandia. Thus the upper Floian and Dapingian levels contain some ten asaphids in north. The lower Darriwilian is dominated by cheiruroids in south and only a few asaphids, indicating connections with Baltoscandia. In the North Urals, however, the taxonomic composition resembles that in Baltoscandia.

The richness of faunas in different terranes depends on the timing, extension and variability of the sedimentary environment, preservation of the rock and range of the areas (compare South China with Alborz), which in turn influences the number of shared taxa. Thus terranes with the highest number of shared taxa may reflect the existence of linking pathways for so called pandemic taxa rather than a close proximity of these terranes. In the late Cambrian and early Tremadocian, terranes lined up as a border of Gondwana with Baltica, made possible the connection farther north towards Siberia and other low latitude terranes and may have favoured the global distribution of numerous trilobite genera.

Of all genera known from the Early to early Middle Ordovician of the Urals three-fifths are present also in Baltoscandia, and only eight genera are endemic to the Urals. About half of the genera recorded there occur also in Laurentia, and about one-third are known in South China, Argentina, Avalonia, Armorica (together with Iberia and Perunica), Altai-Sayan and Kazakh terranes. Fewer genera are shared with Siberia, North China, Australia, and with the smaller terranes of Turkey and Iran. Thus, approximately one-third of the Uralian trilobite fauna consists of cosmopolitan elements. A different aspect is revealed when comparing fauna of the Cambrian origin – the closest match is with Siberia and Kazakhstan. Obviously, there is a big change in the palaeogeographical situation between the Furongian and the early Ordovician when the Siberian Palaeoplate drifted away from Baltica and restricted the exchange of faunas.

In the case of shared exotic taxa this may be explained by the existence of continuous migration routes related to relatively close proximity of terranes or by special oceanic currents. Thus on the Uralian side of Baltica the occurrence of *Kujandaspis* in Khmelevian beds shows evidence of migration of the Cambrian fauna with Siberia and Kazakhstan and *Promegalaspides* with the Baltoscandian side. In both cases the Pechora Basin as a pathway is one possible option. Elsewhere the hungaiid, *Leimitzia*, indicates a migration between the Urals and Bavaria with the Perunica terrane positioned at high latitudes during Kidryasian times and way south of Baltica. Other examples include the co-occurrence of the Uralian isocolids *Holdenia*, *Pseudopetigurus*, and *Cyphoniscus* in Armorica, Perunica and Avalonia respectively, and the cheirurid *Pateraspis* in Armorica and Perunica. Extraordinarily, the two other cheirurids *Kawina* and *Heliomera*, occur from the Urals as far as to the Iapetus-side of Laurentia in the Darriwilian reefs of Nevada, western Newfoundland and Spitsbergen, marking a pathway of migration.

In summary, the gradual decrease of the number of genera shared between the Urals and other parts of the world shows decrease of pandemism during the Early Ordovician. The loss of the Olenid fauna first, and then the *Ceratopyge* fauna to be replaced by the Asaphid fauna, which later becomes almost endemic to Baltica and is joined by a few exotic immigrants from East Gondwana and Laurentia in the early Middle Ordovician. This gradual endemism coincides with an eventual separation of the Uralian side of Baltica from neighbouring terranes.

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