

Trilobites and biofacies in the Early–Middle Ordovician of Baltica and a brief comparison with the Yangtze Plate

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Abstract. Baltica except for Baltoscandia was subject to an early Tremadocian immigration of trilobites similar to that on other plates. In Baltoscandia the Olenid biofacies lingered on until it was replaced by the late Tremadocian *Ceratopyge* biofacies. For the rest of the time (Floian to mid-Darriwilian), Baltoscandia had fairly monotonous lithologies and faunas, constituting a single Asaphid biofacies with lateral variations expressed as differences largely in the relative abundance of species. In the South Urals immigration started in the earliest Tremadocian with fairly rich deep-water faunas. A poorer fauna is known from the Polar Urals. A slightly younger, sparse fauna is known from Paj-Khoj. Over most of the Ural border north of the South Urals there was a further development of first a *Ceratopyge* biofacies, then an eastern Asaphid biofacies, together with more siliciclastic input to the lithofacies and with fewer asaphids than in Baltoscandia. In the South Urals there was a development in the Darriwilian of a Cheirurid biofacies following the *Ceratopyge* biofacies. By contrast, the shelf part of the South China Plate shows a development of fifteen biofacies distinguished on the genus level, and the number of species for each biofacies is notably small. The major difference in the pattern of distribution of the biofacies probably reflects the faunal development in rather different climatic conditions, suggesting that the Yangtze block is supposedly positioned rather distant from Baltica, but still close enough to share genera inhabiting the outer shelf.

Key words: Ordovician, Baltica, Urals, China, asaphid, *Ceratopyge*, olenid, trilobite biofacies.

INTRODUCTION

Striking similarities in lithologies and conodont faunas between the Ordovician Pagoda Limestone of the Yangtze Block in China and the Orthoceratite Limestone in Baltica (Lindström et al. 1991; Zhang 1998a, 1998b) have prompted a comparison between trilobite faunas in the same areas (Zhou et al. 2011 and this contribution). As a general rule, the Cambrian–Ordovician transition resulted in taxonomically reduced faunas that differed strongly between regions. It is therefore important to learn, if possible, how initial similarities and dissimilarities would have influenced the further faunal development in Baltica and the Yangtze Block, and what influence the similar lithological development and different palaeogeographic positions would have had.

The study necessitated an updating of the knowledge on some trilobite faunas in Scandinavia, of the century-old determinations of a large proportion of the East Baltic faunas (for the revision of taxa and their distribution, and notes in stratigraphy see Pärnaste & Viira 2012; Pärnaste & Bergström 2013; Pärnaste et al. 2013), and of the faunas of the Urals (for the revised list see Appendix here and the palaeogeographical analysis

Pärnaste & Bergström in press). The trilobite biofacies of the Yangtze terrane were studied in relation to onshore–offshore bathymetric and lithofacies gradients in a similar interval and the regional palaeogeographical changes described by Zhou et al. (2011). The aim of this study is (1) to establish the configuration and arrangement of the trilobite biofacies along the confacies belts in Baltoscandia from the Tremadocian to the Darriwilian interval; (2) to establish the faunal development on the Uralian side of the Baltica Plate, yielding the faunal associations indicating possible biofacies conditions and the palaeogeographical connections via the Moscow Basin or elsewhere; (3) to compare the faunal development in the Baltica and South China plates, where the carbonate facies share similar features (Lindström et al. 1991).

GEOLOGICAL SETTINGS AND STRATIGRAPHY Baltica Plate – extension and movement

Baltica formed a discrete continental block before the Caledonian collisions (Fig. 1; see also, e.g., Torsvik 1998; Cocks & Torsvik 2002, 2005). On present-day maps its southwestern boundary follows the west coast

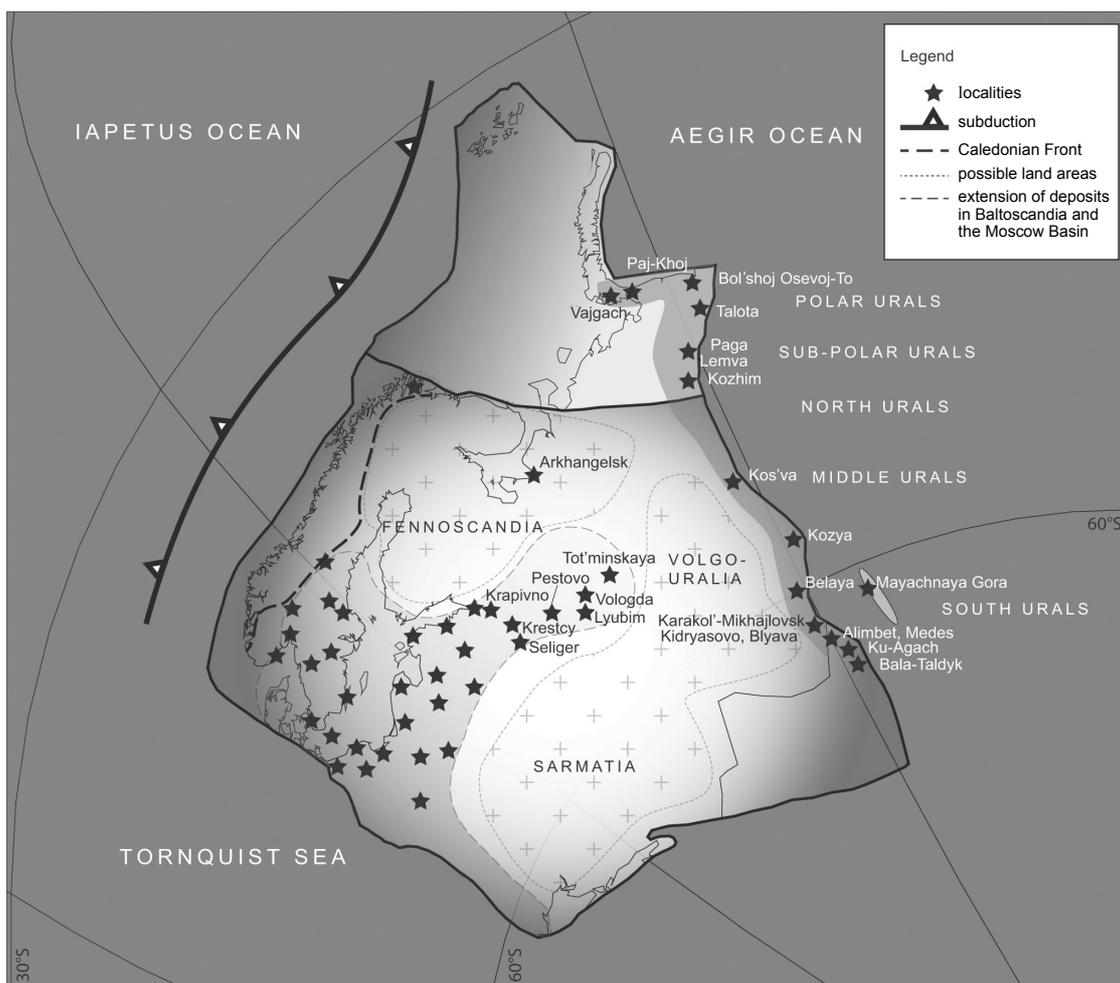


Fig. 1. The Baltica continent in the early Ordovician with its complex borders and development of restricted marine sedimentary rocks in Baltoscandia in the west, the Moscow Basin deep within the plate and the Uralian belts in the east.

of Norway (although nappes originating from Greenland today extend over parts of Norway) to the east of Spitsbergen, then includes the Tajmyr Peninsula (where middle Cambrian trilobite faunas are close to those of Baltoscandia), before extending west and south along Novaya Zemlya and the Urals to the Caspian Sea, and finally west to the Black Sea and northwest along the Tornquist zone to the North Sea southwest of Norway (Cocks & Fortey 1998; Cocks & Torsvik 2005). A series of Caledonian nappes with often metamorphosed rocks have been transported from offshore onto western Scandinavia (Bruton & Harper 1988; Ebbestad 1999, fig. 2; Harper et al. 2009; Lamminen et al. 2011, fig. 11) and the evidence for litho- and biofacies in these areas is largely destroyed. Magmatic rocks included in some nappes bear evidence of the emergence of island arcs off the coast in the late Arenig (Bruton & Bockelie 1982; Harper et al. 2008). At the Ural border part of the

original continental plate is thought to have been lost through subduction under the Magnitogorsk volcanic island arc and the Siberian plate, thus indicating an example of continental subduction (Matte 1998; Brown 2009; Puchkov 2009). In the southwest marginal parts of the Baltica Plate appear to have been lost through major strike-slip fault movements along the Tornquist–Teisseyre zone, which separates areas with contrasting thicknesses of the crust and different Ordovician faunas. In the Ordovician, long before this happened, the Uralian border was being subjected to extensional strain associated with volcanism.

Baltica had a long journey before it arrived at its present position, with its centre around 55°N. At the beginning of the Tremadocian (earliest Ordovician) the centre was around 55°S (Fig. 2A). At the end of the Darriwilian (part of the Middle Ordovician), about the time our overview ends, the position was around 40°S

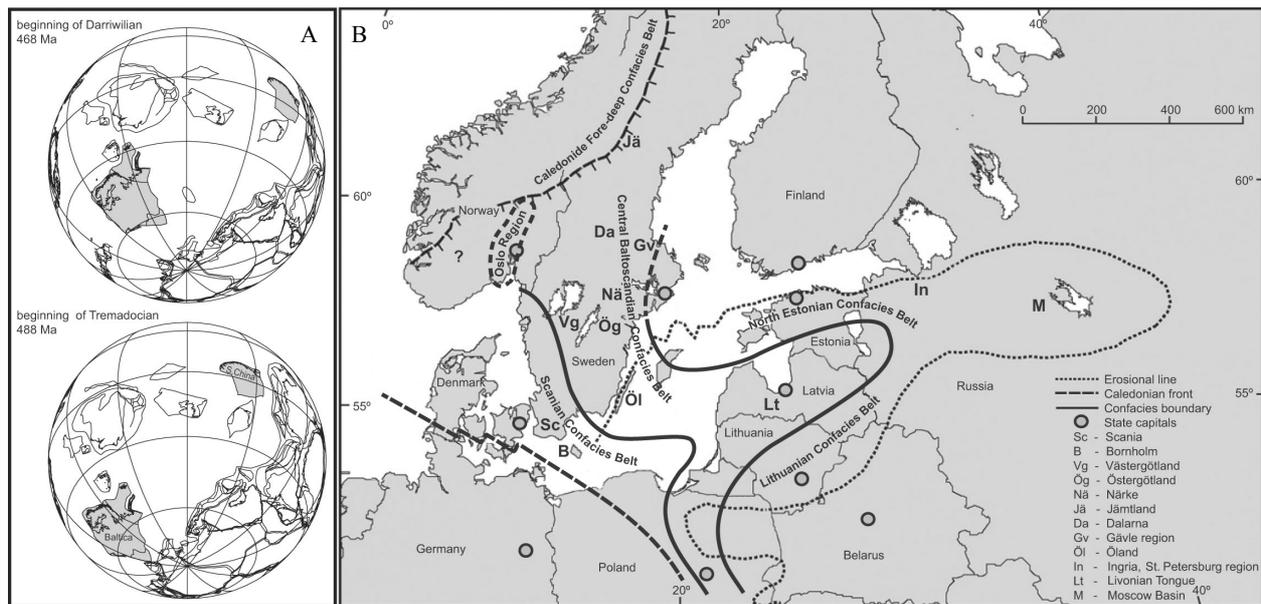


Fig. 2. (A) Palaeogeographical position of Baltica during the Ölandian. (Map generated using T. H. Torsvik's GIS-oriented software from 2009, BugPlates: linking biogeography and palaeogeography). (B) The confacies (bio-lithofacies) belts of Baltoscandia modified from Jaanusson (1982a). The conventional Oslo Confacies Belt is here considered to be a delimited region of unusual relief rather than an extended belt with intermediate low relief. The Scanian Confacies Belt is thought to bend to the southwest south of the fault-bounded Oslo Region. The basin with shale extending from the Oslo Region north over Jämtland according to Hansen (2009, figs 3, 4) and Hansen et al. (2011, fig. 2) is not supported in this reconstruction. The Jämtland autochthon has Central Baltoscandian-type limestone from the upper Tremadocian to the middle Darrivilian and clastic sediments occur only in allochthonous rocks transported from the Caledonian area in the west (Jaanusson & Karis 1982, p. 44).

(e.g. Cocks & Torsvik 2002, 2005, fig. 6). During the same time the Yangtze block had moved from 45° to 30°S according to Cocks & Torsvik (2002), but alternative views place it close to the equator (Scotese & Denham 1988; Zhang & Erdtmann 2004). Based on the type of biofacies, Shergold (1988) believed that it was much closer to the equator than Baltica.

Baltoscandia

The palaeogeographic maps of the western part of the Baltica Plate reveal a series of facies belts (Fig. 2B; Jaanusson 1976, 1982a; Pärnaste et al. 2013). The most offshore, and most deep-water, belt is known as the Scanian Confacies Belt. It widens in the west, extending as an embayment towards the Oslo Region (Bruton et al. 2010), which has been regarded to represent the next shoreward belt. However, there is much variation in depth, lithologies and faunas within the Oslo Region, which may indicate that it is a tectonically confined area rather than a regular confacies belt. The next inward belt is the Central Baltoscandian Confacies Belt. In Ölandian times an orogenic foredeep started to develop between this belt and the Caledonian Orogenic Belt. The Central

Baltoscandian Confacies Belt extends into the East Baltic area as the Livonian Tongue. The most shoreward zone consists of the North Estonian Belt and its counterpart to the south, the Lithuanian Confacies Belt. A somewhat deeper channel in between these two appears to extend to the centre of Baltica as the Moscow Basin. Part of the sequence in this basin is rich in graptolites (Dmitrovskaya 1989). Some levels contain also an impoverished Central Baltoscandian-type trilobite fauna.

A general characteristic of the Ordovician deposits is that sedimentation was extremely slow – in the Central Baltoscandian Confacies Belt the thickness of the entire Ordovician is only 75–150 m in general, whereas it reaches some 200 m in the Scanian Confacies Belt (Jaanusson 1982a). In reality the sedimentation rate could be even more remarkable. The Kundan Orthoceratite limestone has about 5 cm thick beds separated by leaf-thin clayey lamina. The beds contain shells in all possible orientations, indicating very rapid sedimentation (Bohlin 1949, fig. 7). The most impressive examples of trilobites embedded at an angle to bedding are from the North Estonian Confacies Belt (Dronov 2005; Pärnaste 2006a, fig. 4). Sedimentation of one bed may thus have happened in a day, with next sedimentation following only some

50 000 years afterwards (Bohlin 1949; Dronov 2005). Some minor erosion is probably part of the picture. The Oslo Region forms an exception. Notable variations in facies and thickness, the latter reaching about 1000 m (Bjørlykke 1974; Bruton & Owen 1982; Owen et al. 1990; Bruton et al. 2010), indicate exceptional relief conditions and perhaps synsedimentary tectonic movements. Thus the development suggests that the Oslo Region should be interpreted as a local mixed zone rather than a regular band in the system of Baltoscandian confacies belts (Braithwaite et al. 1995). General shallowing westwards within the Oslo Region (Størmer 1967; Bockelie 1978; Bruton et al. 2010) points in the same direction.

A stratigraphic gap, locally covering much of the lower and middle Tremadocian sequence in parts of Baltoscandia (Figs 3, 4), has been interpreted as an indication of a regression in the earliest Ordovician, with limited extension of the sea (e.g. Erdtmann 1982). However, there is much local variation in the development of the Alum Shale Formation, indicating local erosion or lack of deposition rather than terrestrial conditions. An exception may be the transition from the lower Tremadocian Alum Shale to the middle Tremadocian *Ceratopyge* Shale (lower part of the Bjørkåsholmen Formation), which seems to be complete only in the Oslo Region (Jaanusson 1982a). Terrigenous clastic sediments are found in this level in Dalarna (Jaanusson 1982b). The Alum Shale is black, bituminous and fissile with occasional bituminous limestone concretions. The middle Cambrian to lowest Ordovician Alum Shale has a mineral composition of 50–65% quartz, 5–15% feldspar and 10–15% muscovite (Pedersen 1989, p. 156). The quartz is very fine-grained. The muscovite may have a mixed detrital and diagenetic origin. The shale owes its black colour to organic material. In Scania (southernmost Sweden) it has been strongly heated and occurs as kerogen with the content of total organic carbon averaging 9% (Pedersen 1989, fig. 11). It contains remains of unicellular and larger algae. In the Central Baltoscandian Confacies Belt the organic content can be in part extracted as oil. Sedimentation was slow. The composition and the preservation of algal remains indicate a dysoxic–anoxic depositional environment. The evidence for burrowing activity is poor. There is some indication that trilobites occur suddenly after intervals without fossils and then again become increasingly rare and disappear when conditions for life deteriorate (summarized by Pedersen 1989; see also Clarkson et al. 1998; Eriksson & Terfelt 2007).

The Alum Shale is succeeded by a thin succession of black to grey shale and limestone. This unit used to be named the *Ceratopyge* Shale and Limestone but is now referred to as the Bjørkåsholmen Formation (Owen et al. 1990; Ebbestad 1999) except in Öland (Fig. 4; Frisk & Ebbestad 2008). The limestone is locally rich in

glauconite. In the North Estonian Confacies Belt the lower Tremadocian (A_{II}) consists of sandstone and Alum Shale of the Kallavere and Türisalu formations, whereas the middle Tremadocian (A_{III}) consists of shale and glauconitic silt- and sandstone of the Varangu Formation.

The sedimentary rocks overlying the Alum Shale and the sediments with the *Ceratopyge* fauna present the general division into confacies belts (Jaanusson 1976, 1982a). Most offshore is the Scanian Confacies Belt with a dominance of graptolitic shales: the Tøyen and Almelund shales. The middle belt is the Central Baltoscandian Confacies Belt. The dominant facies is a bedded limestone, the upper part of which (occasionally all of which) is known as the Orthoceratite Limestone, lithologically corresponding to limestones in the South China Plate (Lindström et al. 1991; Zhou et al. 2011, p. 36). The lower part, up to the base of the *Asaphus expansus* Zone, is typically calcilititic, without observable grains, whereas the upper, Kundan, part is fine-grained calcarenitic, indicative of a higher-energy depositional environment (Jaanusson 1982b, p. 19; Nielsen 1995). The shift is abrupt. Authigenic silicate minerals, where present in lower strata, are invariably represented by glauconite with shifts to chamosite only in intervals where the rock is lutitic. This is the pattern all over Baltoscandia (Jaanusson 1982b, p. 19). In the Central Baltoscandian Belt the Kundan limestone turns red towards the top but is grey as it extends into southern Norway as the Huk Formation and further as a tongue, the Komstad Limestone, into the Scanian Confacies Belt. In southern Norway the Kundan portion has limestone with shale interbeds.

The development in the wide western belt was influenced by Caledonian tectonics and is not known in detail because of metamorphism. Turbidites in allochthonous lower nappes in Jämtland (the Caledonian Fore-deep Confacies Belt; Fig. 2B) become thicker westwards in the Volkhovian(?) and Kundan (Jaanusson & Karis 1982), indicating rising land further west. In Hardangervidda in southwest Norway, the source of quartzitic sediments is thought to be in a ‘Telemark Land’ to the south, whereas the sea became deeper in a northwestern direction (Rasmussen et al. 2011). A limestone (Bjørnaskalle Formation) in the lower Darriwilian contains deformed trilobites, brachiopods and conodonts that confirm the Baltoscandian affinity (Bruton et al. 1989). In the Iapetus Ocean further west there were island arcs, the remains of which are now preserved in strongly metamorphosed upper nappes thrust onto Scandinavia (Harper et al. 2008; Rasmussen et al. 2011, figs 1, 4).

Hansen (2009, figs 3, 4) and Hansen et al. (2011, fig. 2) attempted to outline the situation in the western, Caledonian, region. Their block diagram shows elevations where the land surface is elevated today (in Telemark and towards Trondheim) and a deep trough extends

Baltoscandian regional														
Global series	Global stages	Stage slices	British stages	stages	substages	trilobite zones	conodont zones	graptolite zones						
Middle Ordovician	Darrillian	Dw2	Llanvirn	Kunda	γ B _{III}	Aluoja	9	Asaphus sulzevi / Megistaspis gigas ----- Megistaspis obtusicauda ----- Asaphus vicarius ----- Asaphus raniceps ----- Asaphus expansus	Eoplacognathus pseudoplanus	Nicholsonograptus fasciculatus Holmograptus spinosus Holmograptus lentus ?Corymbograptus retroflexus Undulograptus sinicus Arenigraptus zhejiangensis				
		Dw1									Välaste	8	Yangtzeplacognathus crassus Lenodus variabilis	
		Dp3												Hunderum
	Dp2	Väana	6	Asaphus lepidurus / Megistaspis limbata ----- Asaphus broeggeri / Megistaspis simon ----- Megistaspis polyphernus	Baltoniodus navis Baltoniodus triangularis									
	Dp1					Saka	5	Oepikodus evae						
	F3	Billingen	γ β B _I	6 5	Megistaspis estonica Megalaspides daiecarilicus Megistaspis aff. estonica				Phoniodus elegans					
	F2					Hunneberg	α	4		Megalaspides daiecarilicus Megistaspis aff. estonica	Paroistodus proteus			
	F1	Tremadoc	Tr3	Hunneberg	α				3			Megistaspis planilimbata ----- Megistaspis armata	Hunnegraptus copiosus Aranecograptus murrayi ----- Kiaerograptus supremus	
	Lower Ordovician					Tremadocian	Tr2	Tremadoc		Varangu	A _{III}			2
		Tr1	Pakerort	A _{II}	1		Boeckaspis spp.		Adelograptus fenellus Rhebdinopora spp.					

Fig. 3. Correlation chart for the lower half of the Ordovician in Baltoscandia. The upper boundary corresponds to a major faunal turnover. The correlation follows recent data on graptolite zones (Maletz & Ahlberg 2011), conodont and trilobite zonation (Bergström & Lofgren 2009, Pärnaste & Viira 2012; Pärnaste et al. 2013) and global chronostratigraphy (Bergström et al. 2009).

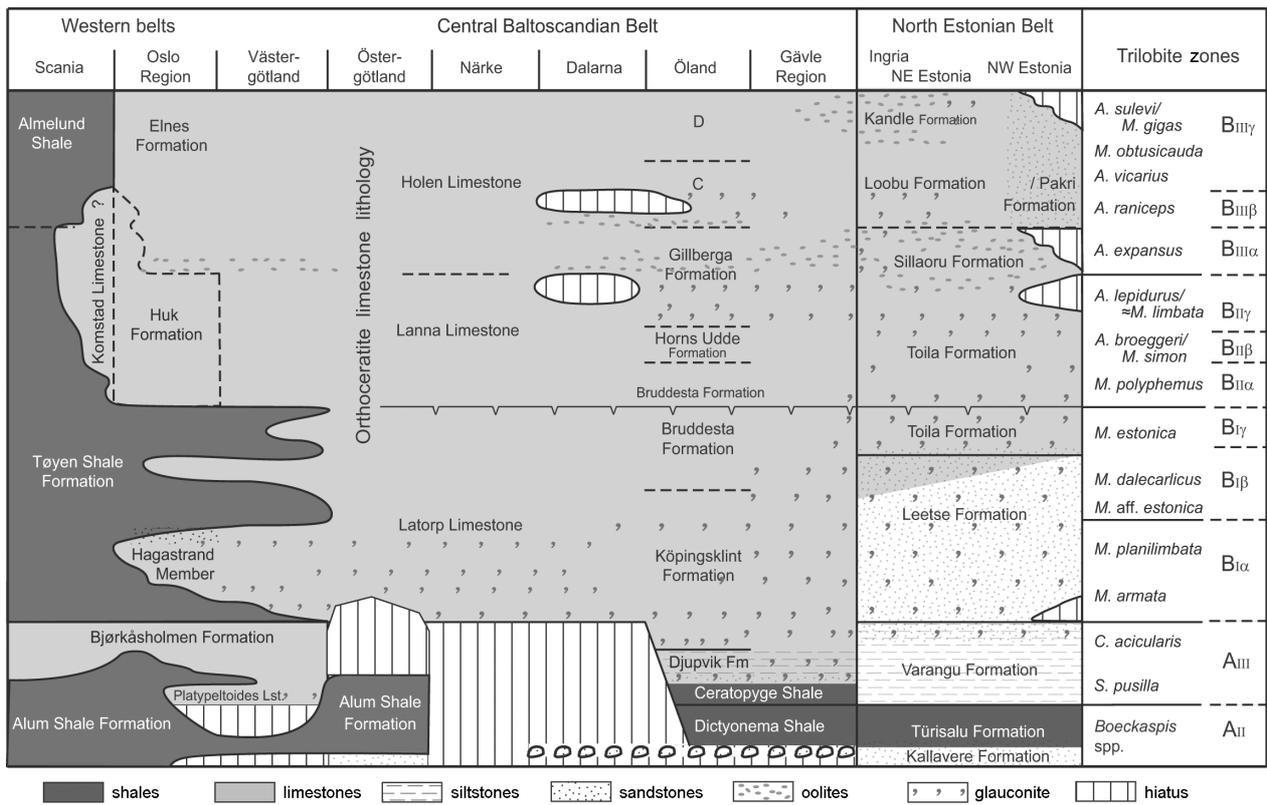


Fig. 4. Distribution of main lithologies in Baltoscandia, with generally deeper facies to the left, shallower to the right.

from the Oslo Region to Jämtland. This is an unlikely topography. If we take the situation before the onset of the Caledonian Orogeny, most likely a sub-Cambrian peneplain extended all over Norway (cf. Lidmar-Bergström 1995), except perhaps for the Oslo Region. One piece of evidence is the presence of lower Cambrian rocks overlying a low-relief basement surface what is today the elevated Hardanger area. The present uplift of the Scandinavian mountain range, the Scandes, is not inherited from any possible uplift resulting from the Caledonide Orogeny but is the result of mainly Neogene uplift (Lidmar-Bergström et al. 2000; Lidmar-Bergström & Näslund 2002; Bonow et al. 2003). In Jämtland the autochthonous lower Ordovician has the typical lithological and biological characters of the Central Baltoscandian Confacies Belt. Allochthonous beds from the lower Caledonian nappes, which were transported a fairly short distance from the west, have the same character (Karis 1982). There is thus no evidence for an Oslo-Jämtland trough in the basement.

In consequence, the Caledonian collision zone was most probably bordered in the east by a wide zone of low relief. Nappes, pushed high as a result of the collision, could slide far to the east on this essentially planar surface. When piled up on each other, they formed a massive

rocky front from which detritus was washed down and deposited in the east as clay, sand and coarser sediments. This zone successively moved eastwards. At the same time the original basement surface was pressed down by the load of the overthrust nappes (cf. Lidmar-Bergström 1995, fig. 8, summit surface line; Lidmar-Bergström & Näslund 2002, fig. 7, blue line). There is evidence that the sub-Cambrian peneplain, covered by Cambrian strata, extended far to the west below the present Caledonian Nappes. For instance, Cambrian strata cover the peneplain in parts of Hardangervidda (the Hardanger plain) some 250 km west of the Oslo Region. As a result, a foreland basin may have been formed just east of the nappe cover (Greiling et al. 1998, fig. 9). Even if this development was largely post-early Ordovician, deposition of siliciclastic sediments in this zone had started in the early Ordovician (Klemm 1982, fig. 3).

Moscow Basin

The sedimentation history of the Moscow Basin was summarized by Kheraskova et al. (2005). In the upper Cambrian and possibly the lower Tremadocian the sediments are terrigenous. Following a gap, the upper Tremadocian (roughly the lower Hunneberg) sediments

are silty-clayey beds in the centre, sandy-silty in the basin slopes and sandy in the shallow-water coastal zone. The lower Arenig (roughly the Billingen and Volkhov levels) sediments are sandy in the far northwest. In the remaining parts of the basin a clay and carbonate-clay facies dominates. The clay has a variable content of carbonate and has thin intercalations of clayey calcilitites. In places organic-rich sediments indicate stagnant conditions. Elevated areas without influx of terrigenous material have organogenic-detrital limestones and bioherms with varied faunas. Transgression through the Arenig widened the sedimentation area and caused a decrease in terrigenous influx. In the upper Arenig and lower Llanvirn (roughly corresponding to the Kundan) the facies are therefore dominantly of two types, one with clayey limestones and marls, the other with limestones.

Uralian border of Baltica

A hiatus seems to exist underneath the Ölandian sequence everywhere along the Uralian border of Baltica. The age of the oldest strata is hotly debated and is discussed below in the section on the trilobite faunas. As preserved, sediments cover different parts of the sequence in different parts of the Urals (Fig. 1). In the South, Sub-polar and Polar Urals the sequence has its base in the alleged upper Furongian. The sequence with trilobites generally extends through the Tremadocian. In the Paj-Khoj (also spelt Pay-Khoy or Pai-Khoi) Peninsula and Vajgach (also spelt Vaygach or Vaigach) Island it ranges through the Volkhovian and in the South Urals it also extends into the Kundan (Fig. 5; Pärnaste & Bergström in press).

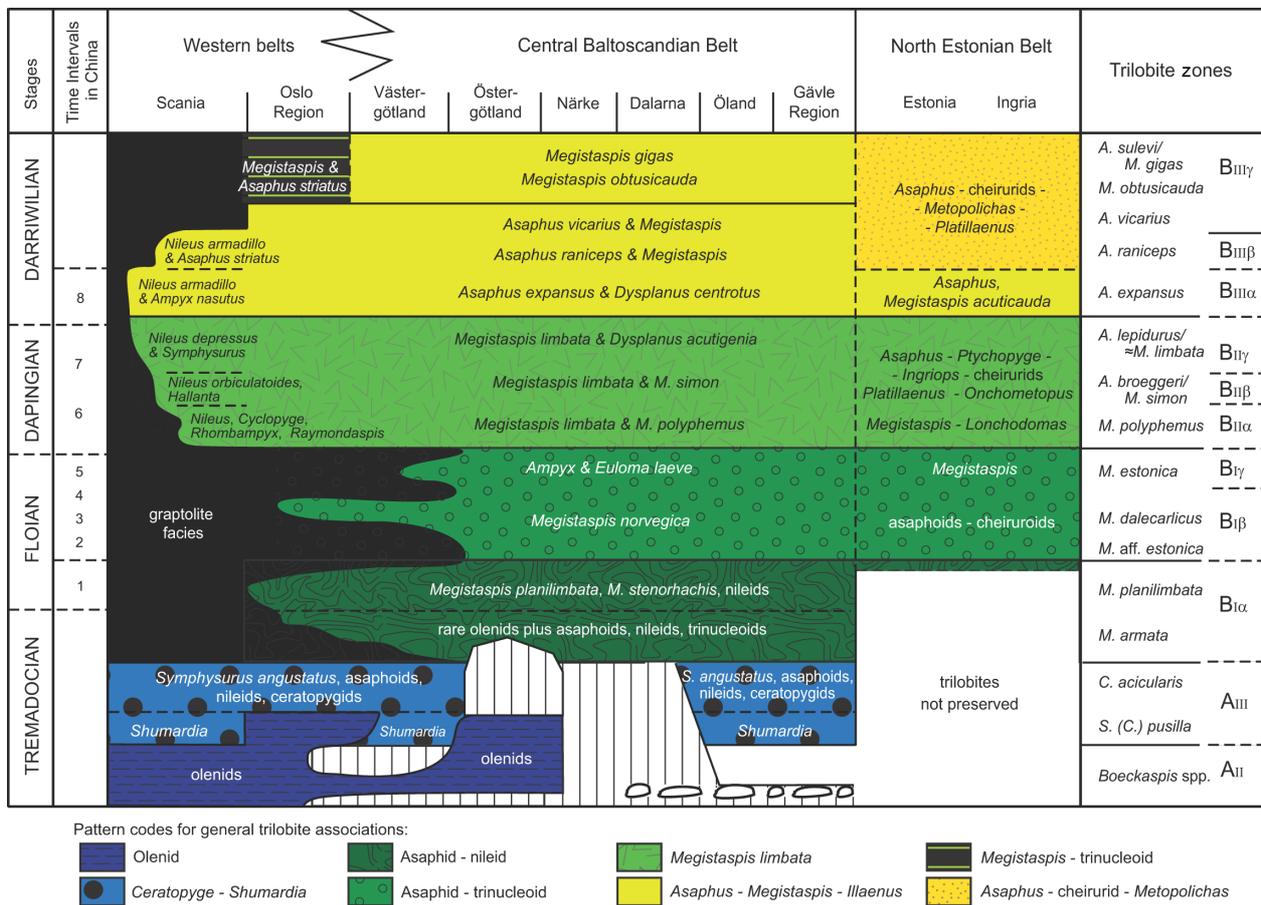


Fig. 5. Biofacies associations in Baltoscandia with regional dominance variations. There are only three major biofacies: the Olenid (shown with horizontal stripes), *Ceratopyge* (shown with black circles) and (western) Asaphid biofacies (all other patterns except the previous two marking different variations in association), with evolutionary and local/regional differences mostly on the species level. A strong regional differentiation occurs only in the Darriwilian, where the Oslo Region and the North Estonian Belt have rich trilobite faunas that share only a few species, and the Central Baltoscandian Belt has an impoverished fauna, consisting of a single species in many localities. The trilobite sub-biofacies are marked with different patterns (see the legend at the bottom of the figure) and the most characteristic taxa are pointed out below the regions.

In Baltoscandia sedimentation occurred in a wide and shallow starved basin. This means that sediments are strikingly uniform over large areas. In sharp contrast, the Uralian border was open to the ocean, and tectonic and volcanic events contributed to a rich variation in the lithologies. Compared to the tens of metres of Ölandian rocks in Baltoscandia, the thickness reaches hundreds of metres and more. Trilobite morphologies indicate that the sequence in the South Urals may have been deposited on the continental slope (see below).

Bogolepova & Gee (2004) presented a summary of lithologies and faunas along the Urals. The Ordovician facies extend approximately meridionally as this mountain range is oriented today. Shelf sediments are succeeded eastwards by deep oceanic and rifting sediments, which are allochthonous (Klyuzhina 1985). Alluvial deposits, known as the Manitanyrd Series of Eletsck facies, contain a cyclic succession of various sandstones alternating with conglomerates of mainly continental and coastal shallow-water origin devoid of trilobite fossils. Eastwards, the Sakmara–Lemva facial zone consists of shelf sediments of the Pogurej Formation in the north and the Kidryas Formation in the south, where trilobites are known from the lower Tremadocian onwards. This facial zone is a relatively narrow region with complicated relief, often showing active hydrodynamic conditions (evidenced, e.g., by highly variable thicknesses; see, e.g., Varganov et al. 1973, app. 2; Klyuzhina 1985, fig. 2). Due to transgression the shelf deposits reached further west during the Arenig. A thick complex of deep-water shales alternating with volcanic rocks representing the continental slope facies characterizes the easternmost series – Grubejn (Grubejnskayan). During the Middle and Late Ordovician the deeper-water conditions extended to the Sakmara–Lemva zone. Most of the known trilobites come from this Sakmara–Lemva facial zone.

TRILOBITE FAUNAS

Baltoscandia

The Ölandian trilobite faunas were listed and commented on by Pärnaste et al. (2013). The Alum Shale in the lowest part of the Tremadocian has a trilobite fauna consisting virtually only of olenids and is called Olenid biofacies (Fig. 6; Pärnaste et al. 2013, table 1). These were largely descended from the rich olenid faunas in the Baltoscandian upper Cambrian (Henningsmoen 1957; see Terfelt et al. 2011 for a list of trilobites). The most characteristic olenid genus is *Boeckaspis*, which may serve as a provisional zonal index taxon for the lower part of the Tremadocian (Fig. 3; Hoel 1999, fig. 2). Exceptional non-olenid forms are a species of the ceratopygid genus *Hysterolenus* and the nileid genus

Global series	Global stages	Stage slices	Baltoscandian regional stages & substages	Regional stages Trilobite zones and beds			
				South, Middle, Sub-polar, Polar Urals	Paj-Khoj, Vajgach		
Middle Ordovician	Darniwillian	Dw2	Kunda	B _{IIIγ}	Karakol'-Mikhailovsk	Yunoyag	
				B _{IIIβ}			
		Dw1		B _{IIIα}			
	Dapingian	Dp3	Volkhov	B _{IIγ}	Kuagach	Apatokephalus karabutakensis & Homagnostoides kasachstanicus	Neilidov
				B _{IIβ}			
				Dp2			
		Dp1	Billingen	B _{Iγ}			Neilidov
		F13		B _{Iβ}			
		F12		B _{Iβ}			
	Floian	F11	Hunneberg	B _{Iα}	Kuagach	Apatokephalus karabutakensis & Homagnostoides kasachstanicus	Neilidov
Tremadocian		T3	Hunneberg	B _{Iα}			
		T2	Varangu				
Tremadocian	T1	Pakerort	A _{II}	Kidryas	Pseudokainella pustulata Leimitzia bavarica	Sokoli	
					Khmelev		Micragnostus porosus
Cambrian	Furongian						

Fig. 6. Correlation of regional stages and trilobite zones of the Urals with Baltoscandian and global chronostratigraphy. The faunal zonation of the Urals follows that in Antsygin (1977, 2001) and Puchkov (1991), and of Paj-Khoj and Vajgach that in Burskij (1970). For legend see Fig. 5.

Platypeltoides found from the topmost part of the Alum Shale (Fig. 4). Both genera are interpreted as immigrants to Baltica as they also occur in the Tremadocian of the Bol'shoj Karatau and Ulutau, Kazakhstan (Ergaliev 1983), where there is a non-Baltica-type trilobite fauna. The preservation potential is poor in the Alum Shale. Most specimens come therefore from limestone concretions or beds, meaning that the fauna is fragmentarily known.

The strong dominance of olenids in sea-floor environments that were poor in oxygen but rich in sulphur suggested to Fortey (2000) that they may have been chemoautotrophic symbionts. However, Farrell et al. (2011) present arguments against such an interpretation. Based on a broad analysis, Balseiro et al. (2011) suggest that olenids are tied to siliciclastic sedimentation more than to anything else, but that some species may have tolerated low oxygen levels.

Associated with the introduction of more oxygenated, lighter shales and limestones higher in the Tremadoc there is a successively growing number of new groups (Pärnaste et al. 2013, table 2). These form the so-called

Ceratopyge biofacies (Fig. 6), comprising representatives of the Olenidae (with other species than in contemporary Alum Shale strata), Dikelokephalinidae (possibly of local origin), Ceratopygidae, Trinucleoidea, Asaphidae, Cheirurina, Shumardiidae, Eulomidae, Nileidae, Remopleuridoidea, Harpididae, Leiostegioidea and Illaenoidea. We judge that the trilobite fauna is largely the result of an absolute minimum of 23 immigration events (Table 1). In addition, there were at least two immigrations of agnostid arthropods. The Ceratopygidae is represented already in the upper Cambrian (Furongian; Terfelt & Ahlgren 2007; Terfelt et al. 2011) of Baltoscandia by a genus *Macropyge* reported from the lower Tremadocian of the Uralian border (Antsygin 2001).

In Baltoscandia the olenid and *Ceratopyge* faunas were abruptly terminated by massive extinction. An overview by Ebbestad (1999, fig. 15) shows that only four out of 37 listed species (including three agnostids) of these faunas survived the event. However, 16 trilobite and two agnostid genera persisted to higher stratigraphical levels (Ebbestad 1999, p. 18). These numbers contain a distinct contradiction. Is it possible that many more species survived and produced new species in areas from which we have no information, or could Baltica have received renewed immigration from the same sources as before (largely South America)? Whatever happened, the biofacies changed drastically. For the rest of our interval, the Hunneberg, Billingen, Volkhov and Kunda stages, there is one evolving ‘super-biofacies’ called the Asaphid biofacies. This consists of a core of asaphids, illaenoids and cheiruroids, with nileids and lichids also being

important (Fig. 6). The composition is thus strikingly different from that of the *Ceratopyge* biofacies.

Re-colonization in the Hunnebergian appears to have been fairly rapid. In the Oslo Region the Hagastrand Member of the Tøyen Formation covers the Hunneberg Stage. Already the lowest part has 12 trilobite species, and as a whole there are 19 plus 3 agnostids (Hoel 1999, fig. 4). Of the former, 11 are asaphids (mostly introduced close to the base), 3 nileids, 2 trinucleids, and 1 each of shumardiids, remopleuridids and cheiruroids. Tjernvik (1956) listed 48 trilobites and 7 agnostids for the Hunneberg Stage of Sweden. Asaphids dominate also here with 26 species (Pärnaste et al. 2013, table 3; Pärnaste & Bergström 2013).

The subsequent development of the asaphid-dominated biofacies included both internal evolution and immigrations. The changes seem to be less abrupt than at the appearance and end of the *Ceratopyge* fauna. A minimum of 13 new immigrants had occurred in the Hunneberg Stage (Table 1). The figure for the Billingen Stage is 15 newcomers (Tjernvik 1956; Pärnaste 2003, 2006a, 2006b). These numbers are merely based on the number of new genera or subgenera that are unlikely to have originated in Baltica. Only six of these 28 newcomers represent new major groups: the cyclopygids, odontopleurids, lichids, celmids, calymenoids and telephinids (Pärnaste et al. 2009). All these remained fairly unsuccessful in diversity and abundance throughout our time frame. The first asaphids are niobinids and species of *Promegalaspides*. The unrelated asaphid genus *Megistaspis*, a very commonly represented genus (with subgenera) in higher strata, is

Table 1. Presence (+) and supposed minimum immigrations of new stocks (1, 2, 3, 4, for a minimum number of separate immigrations) of trilobites. Glaphuridae is used instead of the common Raymondinidae because of the inadequate preservation of *Raymondina*

Zones	Agnostid arthropods	Olenidae	Dikelokephalinidae	Ceratopygidae	Trinucleoidea	Asaphidae	Cheiruroidea	Shumardiidae	Eulomidae	Nileidae	Remopleuridoidea	Harpidoidea	Leiostegiidae	Illaenoidea	Cyclopygidae	Odontopleuridae	Lichidae	Glaphuridae	Telephinidae	Calymenoidea	Phacopidea	Aulacopleuridae	New stocks	
<i>vicarius–gigas</i>	+				+	1	+			+	1	+	+	+		+	+	+	1	1	+		4	
<i>expansus–raniceps</i>	+				+	1	+			+	+	+	+	1	+	+	+	+				1		3
<i>polyphemus–limbata</i>	+				1	1	2			+	+	1	+	+	+	1	1	1	1		1			10
<i>estonica</i>	+				1	+	1	+	+	1	1	+	+	+										4
<i>aff. est.–dalecarlicus</i>	+				1	1	4	+	+	+	+	1	1	+	1				1	1				11
<i>planilimbata</i>	+	+			1	1	2	+	+	+	1	+	+	1	+			1						7
<i>armata</i>	+	+			+	3	+		+	+	+	+	+	1		1	1							6
<i>Ceratopyge</i>	2	3	1	1	3	1	2	2	1	3	1	2	1	1	1									23/2
<i>Boeckaspis</i>		+		1						1														2

represented first in the lower part of the Hunneberg Stage (Pärnaste et al. 2013, tables 3, 4).

The Volkhov Stage shows roughly the same pattern, with a dominance of asaphids, nileids, illaenoids and cheiruroids (Pärnaste et al. 2013, table 5). The minimum number of immigrants is ten, of which two represent new groups: raymondinids and phacopoids. In his study of Volkhovian trilobites from Norway (Huk Formation) and south Scandinavia (Komstad Limestone), Nielsen (1995) suggested the presence of a suite of biofacies. From shallower to deeper-water environment, these are the *Megistaspis*, *Symphysurus*, *Geragnostus*, *Nileus* (with possibly three sub-biofacies) and *Cyclopyge* biofacies. Shared species are *Megistaspis limbata*, *M. polyphemus*, *M. triangularis*, *Nileus orbiculatoides* and *N. depressus*. Additional shared genera are *Lonchodomas*, *Niobe*, *Ptychopyge*, *Cyrtometopus*, *Scotoharpes*, *Harpides*, *Metopolichas* and the agnostid genus *Geragnostus*. Admittedly this is a fairly small number of shared species. On the other hand, if we compare the facies belts on the group level, the North Estonian, Central Baltoscandian (Öland) and Scanian (represented by Scania) belts have fairly similar compositions if we consider the number of species of dominant families: Asaphidae: 53%, 70% and 42%, Nileidae 6%, 1% and 6%, Illaenoidea 3%, 4% and 19% and Cheirurina 19%, 9% and 4%. The intermediate Central Baltoscandian Confacies Belt has much stronger connections to its immediate neighbours. The geographic shift in composition is gradual, but there may be considerable differences between localities within a belt, such as between Bornholm and Scania. Another aspect is what happens at a single location. Nielsen (1995, fig. 47) noted that there can be a flickering to and fro of composition even between the extremes of his biofacies within a single profile and a single trilobite zone. His interpretation of the alleged general shallowing at the base of the *A. expansus* Zone as a shift to a deeper-water biofacies (Nielsen 1995, fig. 47) adds to the doubts about the recognition of such subtle biofacies. His biofacies may still provide a useful tool in interpreting ecological aspects including relative water depths, but they seemingly cannot be fixed on a map to show ecological zones or confacies belts.

In the Volkov Stage there is, in general, poor differentiation between the belts (Pärnaste et al. 2013, table 5). Twelve species are shared between the Scanian Belt–Oslo Region and the North Estonian Belt. However, there are also a number of species with restricted distribution, particularly in some groups. Thus the genus *Megistaspis* has five indigenous species in the Scanian Belt (and one shared with only the Oslo Region) and nine species unique to the North Estonian Belt (and three shared with only the eastern border of the Central Baltoscandian Confacies Belt). The *Ptychopyge* group

has nine species mostly restricted to the North Estonian Belt. Cheiruroids, rare in the deeper areas, have no less than 13 species and five genera restricted to the North Estonian Belt. One of them – *Diaphanometopus* – is known only from a (mud)mound and it is possible that others were also restricted to mounds rather than being part of the level-bottom asaphid fauna. The illaenoid genus *Raymondaspis* has six species restricted to the Scanian Belt, one species shared between this belt and the Oslo Region and one species restricted to the Central Baltoscandian Confacies Belt. None is reported from the North Estonian Belt. We therefore have a differentiation, particularly in the upper part of the stage, into the Scanian Belt with extra development of *Megistaspis* and *Raymondaspis*, a North Estonian Belt with diversification of *Megistaspis*, a *Ptychopyge* group (and cheiruroids), and a Central Baltoscandian Confacies Belt sharing a number of other species with the two other belts. It seems to be a matter of taste whether to recognize three biofacies or just variations within one Asaphid biofacies.

Nielsen's data from the Scanian Confacies Belt (Scania and Bornholm; Nielsen 1995, fig. 47) suggest that the beginning of the Kundan Age (corresponding to the base of the *Asaphus expansus* Zone) coincided with a lowstand, and his sea-level curve shows a shallowing event (Nielsen 1995, p. 59, fig. 50). A minor fluctuation to a slight deepening is indicated by varying proportions of *Nileus* versus *Geragnostus*, i.e. a change of biofacies in the lower part of the *A. expansus* Zone, while the major deepening event is presented at the lower part of this zone later on (e.g. Rasmussen et al. 2009, fig. 9). A distinct shallowing of the sea level at the beginning of the Kundan is also seen in the curve presented by Dronov et al. (2011, fig. 2). In the Central Baltoscandian Confacies Belt this event coincides with coarsening of the calcareous sediment from lutite to fine-grained shelly sand (Jaanusson 1982b, pp. 18–19) deposited in higher-energy water. This is accompanied by a shift in the fauna. Fossils become more common and include large brachiopods, gastropods and hyoliths. All this is good indication of a shallowing event and the significance of the proportion between geragnostids and species of *Nileus* in the Scanian Confacies Belt is probably misinterpreted. Species of *Asaphus* and large *Megistaspis* species become common constituents of the faunas. The North Estonian Belt has a similar composition but with more species of presumably shallow-water forms: cheiruroids, lichids and phacopids (Pärnaste 2004; Pärnaste et al. 2013, table 6).

The upper part of the Kunda Stage deviates from what is described above in having a strong differentiation between the confacies belts (Pärnaste et al. 2013, table 7). The Scanian belt has graptolite shale devoid of preserved trilobites. The Oslo Region has an extreme development within the genus *Megistaspis*, with species confined to

this area that is also characterized by having a number of trinucleoids (Hansen 2009; Hansen et al. 2011). The Central Baltoscandian Confacies Belt has a sparse fauna including, among others, a single *Asaphus* species and some large species of *Megistaspis* (Bohlin 1960). The North Estonian Belt has a fairly rich fauna with asaphids being most common, being succeeded in number by cheiruroids and illaenoids. The faunas of the different confacies belts and the Oslo Region are sufficiently different that detailed correlation with trilobites is complicated.

Southern Baltica margins

In Poland, southwest of Sarmatia (Fig. 1), strongly condensed Ordovician deposits have intercalations of thin layers of pyroclastic deposits in the form of bentonites and occasionally tuffites. The pyroclastics occur first in the Floian, then become more common from the Sandbian onwards. In the west the Floian beds are more shaly and contain graptolites. In the east they have yielded the trilobites *Megistaspis planilimbata*, *M. estonica*, *Niobe* aff. *incerta*, *Niobe* cf. *laeviceps*, *Nileus* cf. *exarmatus*, *Raymondaspis brevicauda*, *Globampyx obtusus* and *Rhombampyx* cf. *pater*. In the Volkhovian, *Symphysurus dorsatus*, *S. palpebrosus*, *Megistaspis limbata*, *Raymondaspis limbata*, *Ptychopyge* spp. and *Niobe* spp. are known both from the west and the east, whereas *Asaphus lepidurus*, *Megistaspis hyorrhina*, *M.* cf. *gibba* and *Nileus exarmatus* are recorded only from the east. The Kundan fauna is reported to include *Pseudoasaphus* sp., *Panderia ramosa*, *Illiaenus sarsi*, *Cyrtometopus* cf. *clavifrons*, *Remopleuridiella* sp., *Cybele bellatula*, *Trinodus* sp. and *Nileus armadillo* in the west, and the latter together with *Asaphus raniceps*, *Ampyx nasutus* and *Illiaenus incisus* in the east (Modliński 1973; Modliński & Szymański 1997, 2001). This association corresponds to the Asaphid biofacies in the Baltoscandian region. The shallowest conditions (with Tremadocian conglomerates and sandstones and post-Tremadocian glauconite limestones) were common in the Lublin area in northeastern Poland, to the west of Sarmatia.

Moscow Basin

The faunas discussed here without revision are those documented by Dmitrovskaya (1989) from a deep borehole. The diameter of the drill core is very small and therefore the trilobite data are sparse. The Tremadoc holds a *Dictyograptus* graptolite fauna, with a few brachiopods but without any known trilobite of the Ukhra Formation (Kheraskova et al. 2005). It is succeeded by strata with species of *Tetragraptus* and *Didymograptus*. The Volkhovian contains *Ampyx nasutus*, *Ptychopyge*

plautini, *Asaphus lepidurus*, *Megistaspis 'limbata'* and *M. ex. gr. hyorrhina* together with graptolites of the genera *Didymograptus* and *Phyllograptus*. From the Kundan *Asaphus expansus*, *A. raniceps*, *A. major* and *Pliomera fischeri* have been reported along with a few graptolites including specimens identified as *Didymograptus bifidus* (Dmitrovskaya 1989). The diversity of trilobite faunas is thus small. Despite this fact, and the presence of graptolites indicating fairly deep waters, the trilobite species indicate middle-shelf depths. The trilobites clearly point to direct connections with the Central Baltoscandian Belt via its Livonian Tongue rather than with the Ural belt, where asaphids are notably poorly represented, particularly in the Kundan.

Uralian border of Baltica

A series of areas with trilobites are known along the Urals (Fig. 1). From south to north, these are the South Urals, Middle Urals, North Urals, Sub-polar Urals, Polar Urals and the Paj-Khoj area with inclusion of Vajgach Island (e.g. Bogolepova & Gee 2004). Considering the development of the faunas, we can distinguish between continental slope conditions in the South Urals and shelf conditions in the other areas.

We largely follow Bogolepova & Gee (2004) in their summary of lithology and fossils of the older reports. In practice the oldest faunas are arranged based on their occurrence in successive regional stages or formations. According to Bogolepova & Gee (2004), the Khmelev Regional Stage in the South Urals includes the upper Furongian *Cordylodus proavus* Zone, whereas the Kidryas Regional Stage corresponds to the lower Tremadocian (Fig. 5; Note: the term Regional Stage will be avoided below and we instead use the Khmelevian, Kidryasian, etc.).

However, there are problems with the dating. First, the presence of Furongian and lower Tremadocian strata has been questioned for instance by Popov & Holmer (1994, p. 10), who stated that the oldest strata in the South Urals are late Tremadoc in age and that reports of an older age are 'based on a few poorly preserved endemic species of trilobites, as well as the problematic brachiopod *Billingsella* [= *Porambonites*] *akbulakensis* Andreeva'. However, the reason that other brachiopods are not known from below the upper Tremadoc may be that the right lithologies are missing in the Urals. Likewise, Dubinina & Ryazantsev (2008) and Ryazantsev et al. (2008) concluded on the basis of conodont faunas that the Ordovician sequence in the South Urals extends from the upper Tremadoc to the upper Caradoc.

The taxa mentioned as coming from the alleged upper Furongian Khmelevian at the Ak-Bulak-Sai River, South Urals (Antsygin 2001) include *Micragnostus porosus*, *Akoldinioidia pustulata*, *Jdyia* sp. indet. and *Kujandaspis*

aff. *kujandensis*. *Kujandaspis* is known from the Cambrian of Siberia, the Kazakh terranes and the North China plate. *Akoldinioidea* and *Micragnostus* are also found in the Cambrian (see for discussion Pärnaste & Bergström in press).

Polar Urals strata of the *Cordylodus proavus* Zone contain species of the trilobite taxa *Dolgedola*, *Leimitzia*, *Jdyia*? (mentioned as *Neoaldanaspis nomen nudum*) and Hystricuridae (Bogolepova & Gee 2004, p. 149). It is probably significant that *Leimitzia* is otherwise known only from the Tremadocian. Also, there is no characteristic Cambrian genus. The conodont *Cordylodus* ranges from the upper Furongian into the lower part of the lower Tremadocian. The dendroid graptolite *Rhabdinopora flabelliforme* has been found together with *Leimitzia bavarica*, and *Rhabdinopora? inexpectata* has also been reported from the upper part of the Pogurej Formation of the Kidryas Regional Stage in the Polar Urals (Antsygin 2001, p. 120, table 2) as well as from the Kidryasian of the South Urals (Antsygin in Varganov et al. 1973, appendix 2). In summary, there is overwhelming evidence that the Kidryasian, or at least part of it, as well as the fauna from the sandy-silty middle part of the Pogurej Formation in the Polar Urals belong to the lower part of the lower Tremadocian (Klyuzhina 1985; Bogolepova & Gee 2004). Limestones of the Kibatin Formation, overlying the sandy-silty Pogurej sediments in the Polar Urals, contain conodonts indicative of the lower Tremadocian *Cordylodus angulatus* Zone, and species of the trilobite genera *Apatokephalus*, *Jdyia* and *Niobe* together with the agnostid *Geragnostus adductus* (see Table 2 in Appendix; Klyuzhina 1985; Dembovskij et al. 1990, Antsygin 2001).

The southeastern corner of the Baltica plate lies in the Orenburg Oblast of Russia and the Aktobe Province (earlier Aktyubinskaya Oblast) of northwestern Kazakhstan around the southern tip of the Urals (Fig. 1). Cocks & Fortey (1998, fig. 1, p. 175) showed the trilobite localities on a map and provided a list of trilobite taxa shared with Baltoscandia. The fauna was partly described by Balashova (1961) and determinations were reconsidered by Fortey (in Cocks & Fortey 1998). Antsygin (see Varganov et al. 1973; Antsygin 2001) gave a more detailed overview with description of the new taxa, listing their stratigraphical and geographical distribution (shown also in Table 2). Of the trilobite taxa, *Platypeltoides* cf. *incipiens* and *Ceratopyge forficula*, if correctly determined (which in the case of the latter was questioned by Ebbestad 1999, p. 76), show the presence of the *Shumardia pusilla* Zone. However, the *Ceratopyge* species found in the *Apatokephalus serratus* Zone, previously identified as *C. forficula*, is now known as *C. acicularis* in Baltoscandia (see Ebbestad 1999; Pärnaste et al. 2013). Also *Ceratopyge* specimens, first described as *C. forficula*

from the South Urals, belong to three different species according to Antsygin (2001). It is therefore uncertain whether the *S. pusilla* Zone in the Urals corresponds to the same zone in Baltoscandia. The presence of the *A. serratus* Zone would be verified by the zonal species itself, but Ebbestad (1999, p. 54) regards the determination as incorrect. The genera *Euloma*, *Niobe* and *Niobella* range from the supposed *A. serratus* Zone up into the Arenigian. *Saltaspis viator* is a lower Hunnebergian species in Baltoscandia and confirms that the sequence includes a basal Asaphid fauna. However, *Ceratopyge* and *Saltaspis* appear in the Kolnabukian, while there are lower strata (Kidryasian) with genera remaining from the older Olenid fauna including *Jujujaspis*, *Peltocare*, *Kainella* and the agnostid genus *Micragnostus*. The Kidryasian can be correlated with the upper Pakerortian in the west (Tr1; Fig. 5, Table 2).

With this correlation problem resolved, we can concentrate on the successive development in the two major depth ranges, the shelf from the Middle Urals to Paj-Khoj in the north and the continental slope and possibly the deeper shelf in the South Urals. The taxa from the partly glauconitic sandstones and calcareous or silty sandstones and siltstones of the Pogurej Formation from the localities Paga and Pokoinitsa Shor in the Polar Urals (Table 2), which are considered to represent the Eletsck facial zone (shelf), are also distributed in the Kidryasian of the South Urals. This may indicate that the shelf is preserved in the south as well (with sandy-silty sediments sharing *Jdyia* in the lowest part, and *Dolgedola* and *Leimitzia* above).

Middle Urals to Paj-Khoj

The lower Tremadocian shallower shelf fauna is known only from the Pogurej Formation in the Polar Urals, where it is restricted to a single species of each of *Dolgedola* and *Jdyia*, and two species of *Leimitzia* (Table 2). The fauna includes also a species of the agnostid genus *Micragnostus*. In the same area, the Kibatin and Grubejn formations of the Kolnabukian and Kuagachian contain an middle–upper Tremadocian shelf fauna of the *Ceratopyge* type. A distinct difference occurs between a lower level with representatives of *Pliomeroides*, *Harpides*, *Apatokephalus*, *Araiocaris*? and *Ceratopyge*, and an upper level with *Ceratopyge*, *Niobella*, *Pliomeroides*, *Pricyclopyge*, *Shumardia* (*Conophrys*) and the agnostid genus *Geragnostus* (Antsygin 2001).

Upper Tremadocian (Tr2–Tr3, including the lower Hunnebergian) faunas were also reported by Burskij (1970) from the Sokolian of the Paj-Khoj Uralides. Four successive levels with radically different associations are recognized: the *Syntrophopsis magna* and *Dikelokephalina*, *Nyaya* and *Tersella*, *Apatokephalus serratus* and the

Megalaspides beds. The first three seem to correspond to the *Ceratopyge* beds in Baltoscandia, the fourth to the lower Hunnebergian (Fig. 5). Altogether these faunas comprise some 35 species, nine of which are from the Hunnebergian (Table 2).

Burskij (1970) further reported upper Hunnebergian (Fl2–Fl3) to Volkhovian (Dp) faunas from the Nelidov Regional Stage in Paj-Khoj. The Hunnebergian fauna appears to be derived from the *Ceratopyge* faunas. In the Billingenian and Volkhovian this changes so that the majority of the species belong to ‘Baltoscandian’ asaphid genera such as *Niobella* and *Megistaspis*. In the Billingenian eight species out of 14 are asaphids, in the Volkhovian all seven species are asaphids. Seven Billingenian and Volkhovian species are shared with Baltoscandia, or are close to Baltoscandian species.

A fauna from Paj-Khoj at the northern land end of the Urals is notably larger and shares a number of species with Baltoscandia and one with Spitsbergen, the remopleuridid *Lacorsalina limbata* (Burskij 1970). The asaphids are clearly dominant in the number of species, followed by remopleuridoids.

By contrast, the Kundan and higher (Darriwilian) Karakol'-Mikhajlovskian of the Sub-polar and Polar Urals and Paj-Khoj, Vajgach has a fauna of thirteen species of eight different families (Burskij 1966; Antsygin in Varganov et al. 1973; Varganov et al. 1973; Antsygin in Puchkov 1991). The abundant *Plectasaphus plicicostis* is the only asaphid and together with *Pliomera fisheri* the only species indicating Baltoscandian affinities. Genera such as the trinucleid *Hapalopleura*, the Nileid *Nileus*, the asaphid *Ogygiocaris* and the telephinid *Carolinites* refer to comparatively deep waters on the shelf.

South Urals

As shown by the discussion above, the Khmelevian trilobite fauna gives evidence of immigration in the latest Cambrian and the earliest Tremadocian. The fauna consists of eight species of six families, including one agnostid. In the middle of the lower Tremadocian, the Kidryasian, some groups were added: remopleuridids (*Apatokephalus*, *Kainella*, *Pseudokainella*), asaphids (*Niobe*, *Promegalaspis*), olenids and a member of the ceratopygid genus *Macropyge*. The fauna now comprises 28 species plus two agnostids.

The middle Tremadocian fauna from the Kolnabukian of the South Urals (Balashova 1961; Antsygin 1977, 1978, 2001; Korinevskij 1989) has great similarities to the contemporaneous *Ceratopyge* fauna in Baltoscandia, with shared species among the olenids, dikelokephalinids, ceratopygids, trinucleoids, asaphids, shumardiids, cheiruroids, eulomids, Nileids, remopleuroids, harpidoids, illaenoids, leiostegiids and agnostid arthropods. There are also

some members of these groups that appear to be unique to the Urals. In addition, a number of species of *Nyaya*, *Tersella* and *Hystericurus* are referred to the Hystericuridae. The presence of *Scotoharpes excavatus*, *Ottenbyaspis* aff. *oriens*, *Niobe emarginula*, *Harpides nodorugosus* and *Pricyclopyge gallica* may indicate either an Hunnebergian or Billingenian age, or perhaps both for the Kuagachian (Fig. 5).

A microcontinent appears to be represented by the fauna in the Mayachnaya Gora north of the South Urals (Weber 1948; Antsygin 1978; Klyuzhina 1985). *Asaphellus*, *Tersella* and *Megalaspides* indicate the middle or late Tremadocian. *Cybele*, *Cyrtometopus* and *Pterygometopus* show the presence of the Dapingian to Darriwilian (upper Volkhov–Kunda).

Kundan trilobites are known from the Karakol'-Mikhajlovskian in the South Urals (Antsygin in Varganov et al. 1973; Antsygin 1977). Twenty-one trilobite species and one agnostid have been reported. Only *Pliomera fisheri* and *Geragnostus crassus* are shared with Baltoscandia. There is not a single asaphid in the fauna, which is dominated by cheiruroids with six species. Next come isocolids with three species and illaenids, lichids and raymondinids each with two species. The fauna indicated a cheirurid biofacies from fairly deep waters.

Evolution of faunas in the Urals

We can note that the lower Tremadocian in the south has a fairly rich fauna with some 30 species belonging to 19 genera, plus three agnostids in two genera. Six of the genera are reported from the latest Cambrian and the lowermost Tremadocian (Khmelevian): *Leimitzia*, *Akoldinioidia*, *Kujandaspis*, *Dolgedola*, *Lateuloma*, *Jdyia* and the agnostid genus *Micragnostus*. In the north (Pogurej Formation) there is an impoverished version of the Khmelevian fauna. The only genera present are *Leimitzia*, *Dolgedola* and *Jdyia* among trilobites and *Geragnostus* among agnostids. The trilobite species are shared with the south Urals.

The middle and upper Tremadocian has a *Ceratopyge* biofacies both in the south and the north, with much variation in composition. South Urals species identical or close to those in Baltoscandia are *Ceratopyge forficula*, *Orometopus elatifrons*, *Nileus limbatus*, *Apatokephalus serratus*, *Harpides rugosus*, *Pricyclopyge latifrons*, *P. gallica*, *Geragnostus sidenbladhi*, *G. aff. crassus* and *Leiagnostus* aff. *peltatus*. North Urals similarities include *Ceratopyge forficula*, *Falanaspis* cf. *aliena*, *Megalaspides* aff. *nericiensis*, *Niobella* aff. *laeviceps*, *Shumardia* (*C.*) *pusilla*, *Symphysurus angustatus*, *Pricyclopyge* aff. *latifrons* and *Apatokephalus serratus*.

The post-Tremadocian development involved a wider divergence between north and south. In the north in the

Paj-Khoj region a strong diversification of asaphids took place, particularly within the genera *Niobella* and *Megistaspis*. Notably, the genus *Asaphus*, so important in Baltoscandia, is virtually absent, and only a single nileid is reported. Although we can recognize an Asaphid biofacies, it is notably different from that biofacies of Baltoscandia. Some eight species, half of which belong to *Niobe* or *Niobella*, are identical or close to species in Baltoscandia. In the South Urals the successive faunas in general have few species and are not easily classified as belonging to the Asaphid biofacies.

The Volkhovian has two asaphid genera (*Asaphellus* and *Megalaspides*), neither of which is found from this interval in Baltoscandia, two cheirurids, one phacopid and one hystricurid. The Kundan is dominated by cheiruroids. *Asaphus expansus?*, *Plectasaphus plicicostis* and an ogygicarinid are the only asaphids. They indicate connections with Baltoscandia.

Nasedkina (1981) and Dubinina & Ryazantsev (2008) stated that starting from the upper Arenig, the Urals are divided into two palaeobiogeographical regions with different conodont faunas, with no taxa shared. The Elets facial zone of the Urals have the genera *Acodus*, *Scandodus*, *Phragmodus* and *Zygognathus*, characteristic of North America and Siberia (Nasedkina 1981). These genera are indicative of the North American Mid-Continent Conodont Province of Sweet & Bergström (1974). The rest of the Urals instead has the conodont genera *Drepanodus*, *Oistodus*, *Periodon*, *Amorphognathus* and *Keislognathus*, i.e., a European-type fauna, or North Atlantic Province. According to the new concept on Ordovician conodont biogeography eliminating these terms (Zhen & Percival 2003), Dubinina & Ryazantsev (2008) described a number of (relatively) deep-water conodont biofacies of the biogeographic Open-Ocean Realm of the tropical Domain in the South Urals. Similar to the situation with the conodonts, the trilobite faunas differ in the Darriwilian, and the Laurentian taxa, such as the cheirurids *Kawina*, *Heliomera*, etc., known from the reefal associations in western Newfoundland (Whittington 1963), western Ireland (Lane 1971), Nevada (Ross 1972) and eastern Spitsbergen (Fortey 1980), appear in the South Urals. In the north, however, the taxonomic composition resembles that in Baltoscandia. Dubinina & Ryazantsev (2008, p. 5) stated that, unlike palaeoenvironments in Baltoscandia, those of Central Kazakhstan and the South Urals belong to deep-water environments of the North Atlantic Conodont Realm. A look at the Tremadocian trilobites described by Antsygin (2001) reveals that some 15% of the species (72 species counted) have eyes of roughly normal size (judging from the length of the palpebral lobe), whereas about half of the rest have notably large eyes and the other half have notably small eyes or are blind. This strongly indicates life in a

depth with low light intensity, possibly on the continental slope. However, the geological situation is complicated, and there are limestones which may refer to shallower depth.

Origin of faunas

The Cambrian–Ordovician transition was a time of massive extinction of trilobite lineages all over the world. Detailed studies have been particularly yielding in North American profiles where there seems to be a continuous trilobite record (Westrop et al. 1995; Westrop & Adrain 1998; Westrop & Cuggy 1999). The extinction seems to be at least two or three events separated by enough time for them to be recognized. Loch et al. (1993) suggested that they were caused by an invasion of the shelf by cold, anoxic water.

Shergold (1988) reviewed the facies and trilobite faunas at the Cambrian–Ordovician transition. He recognized four or five biogeographic provinces. These were the Baltic, North China, Southeast China, North American, and possibly a Siberian province that could also be part of the North American province. He concluded that the biofacies characters were probably controlled by temperature, a conclusion drawn from the position on the globe. It should be noted that the late Cambrian Baltic province was held to include the whole of Baltica, the Avalon Platform, the maritime eastern North America, central Mexico, Argentina and Bolivia. These were areas with typically dark, poorly oxygenated sediments and restricted olenid faunas. South America had lighter-coloured sandstones, and conditions improved also in the late Tremadocian of Europe. An area in Wales is noteworthy since it has yielded a lower Tremadocian trilobite assemblage with species of *Apatokephalus*, *Proteuloma*, *Niobella* and *Shumardia* (Owens et al. 1982), an assemblage similar to that of Southeast China and extending into the Mediterranean region. The Southeast China province extends from Southeast China (south of the Yangtze block) to the Malyj Karatau, Kazakhstan. The North China province *sensu* Shergold (1988, fig. 1), including the Yangtze block, has an upper Cambrian fauna that comprises *Euloma* and *Niobella*, but an abrupt faunal break occurs at the Cambrian–Ordovician boundary, indicating that the older fauna did not survive the transition (Lu & Zhou 1990). For more detailed discussion on the origin of the latest Cambrian and earliest Ordovician genera of the Baltica Plate see Pärnaste & Bergström (in press).

Ebbestad (1999, p. 18) summarized the understanding of the origin of the Tremadocian faunas in Baltoscandia. The Olenid fauna was a survivor of the late Cambrian fauna in Baltoscandia. Among its genera, *Bienvillia* and *Parabolinella* also had a cosmopolitan distribution.

The *Ceratopyge* fauna lacks an earlier connection in Baltoscandia. Many of its genera are cosmopolitan. *Apatokephalus*, *Agerina*, *Harpides*, *Parapilekia* and *Pliomeroides* have their oldest known occurrences in South America. The oldest known species of *Nileus* is from Baltoscandia. *Varvia* and *Pagometopus* may have been endemic to Baltica, and *Ottenbyaspis* and *Falanaspis* are rare outside the plate.

Comparison with conditions in the Yangtze Plate

The striking similarity between the Baltoscandian Orthoceratite limestone and the Yangtze platform limestone in lithofacies (e.g. Zhou et al. 2011) and conodont faunas (e.g. Bergström & Löfgren 2009) raises the question why the post-Tremadocian trilobite faunas are different in most respects.

In comparison with the post-Tremadocian trilobite faunas in the Yangtze Plate (Zhou et al. 2011), remarkably little lateral variation is observed in Baltoscandia. Above the *Ceratopyge* level there is no separation into biofacies having completely different compositions on the genus level, but more differences occur in the number of shared species. A separation into sub-biofacies, which are more distinctive in their composition at least on the species level, is recorded only in the Kundan. Another difference is that genera in Baltoscandia show much more diversification than in the Yangtze Plate. Tjernvik (1956) listed 39 trilobite genera from the asaphid–nileid and asaphid–trinucleoid associations in the Hunnebergian and Billingenian in Sweden. Zhou et al. (2011) reported a maximum of 12 genera in any Yangtze Plate biofacies and a total of 15 biofacies in a sequence roughly corresponding to the Baltic Hunnebergian to Kundan.

A comparison of the Tremadocian preludes to the later faunal development is illuminating. In Baltoscandia the indigenous Olenid fauna gave way to the meager immigrant *Ceratopyge* fauna, which in turn was replaced by the Asaphid fauna in a new immigration wave beginning in the late Tremadocian. The shallow-water fauna of the Yangtze inner shelf is generally comparable to the *Ceratopyge* and early Asaphid fauna and consists of species of shumardiids, remopleuroids, asaphids and dikelokephalinids, but also lelostegiids (e.g. Peng 1990a). The deeper part, extending to the southeast has an incomparably richer fauna. Peng (1990b) listed 45 species, 30 genera and 23 families or subfamilies (including agnostids) from the Panjiazui (lower Tremadocian) and Madaoyu (Upper Tremadocian) formations. This was an environment that is more comparable to what we see in the Ural border of Baltica, from where we have listed some 130 species. The abrupt shift from the *Ceratopyge* to the Asaphid biofacies in Baltoscandia has a counterpart in the Yangtze Plate. However, in striking contrast to

the situation in Baltoscandia, the shelf now became divided into a number of biofacies that differ on the genus level from the shore to the deepest part (Zhou et al. 2011).

The biofacies concept used by Nielsen (1995) for Baltoscandia is thus very different from that of Zhou et al. (2011). Rather than being based on clearly distinguishable lithofacies and great differences in generic composition, it is based on shifting balances between the same genera in muddy, variable calcareous rocks. Moreover, shifts between Nielsen's biofacies occur frequently in a single profile so that it is rather impossible to illustrate the distribution on a map. Shifting frequencies between species is not the only problem. The island of Öland may exemplify what can happen within a distance of less than 100 km. The Volkhov and Kunda faunas are very rich in the north of the island but almost non-existent in the south. No new species occur in the south, it is just a rarefaction.

In the Ural border, post-Tremadocian trilobite faunas are known from the continental slope of the South Urals and from the Polar Ural and Paj-Khoj shelf regions. The faunas include a number of *Niobe*, *Niobella*, *Megalaspides* and *Megistaspis* species in the north, which is a clear similarity to conditions in Baltoscandia. Virtually no species are shared, however, which is evidence of the isolation of the latter region. A hundred and three trilobite genera together with agnostids have been listed from the Tremadocian–lower Darriwilian interval of the Urals (Table 2). Of those, 65 are shared with Baltoscandia and 37 with South China, but all these are more or less globally distributed and not restricted to these regions only (Pärnaste & Bergström in press).

All together we listed 172 genera from the Öland Series in the Baltica Plate, 120 of which are known in the Baltoscandian side of Baltica and 103 in the Uralian side (Pärnaste & Bergström in press). Fifty-one genera are common for both sides. Of genera known from Baltica, 22 occur also in the slope and buildups on the outer shelf of the Yangtze block, which comprises nearly a third of the Chinese 65 genera, but only one eighth of the Baltic genera. Fourteen genera are common in all three regions. Besides, the Uralian side that supposedly was facing the Yangtze block shared only three species with that region, while Baltoscandia shared five. Consequently, the Early Ordovician faunas of the Yangtze Plate were more influenced by the Baltic fauna than vice versa, suggesting that these plates were rather distant from each other and the immigration was directed towards China.

Zhen & Percival (2003) refined the division of conodont biogeographic realms, suggesting that the old division into only the North American Midcontinent Province and the North Atlantic Province should be abandoned. They suggested the division into Shallow-

Sea and Open-Sea Realms, corresponding to shelf and slope areas, each divisible into Tropical, Temperate and Cold Domains. Baltica would be in the Cold Domain, the Yangtze Plate in the Temperate Domain. Both would range from the Shallow-Sea to the Open-Sea Realm. The only difference would therefore be in the temperature. This, of course, is an insufficient way to classify trilobite faunas, whose systematic composition, especially in post-Tremadocian times, is much more characteristic of the continental block on which they occur.

As indicated above by the separation into cold and temperate zones, temperature may be one factor behind the fundamental difference in post-Tremadocian faunas between the Yangtze Plate and Baltoscandia. There may be a number of other factors, such as (1) precursors of lineages leading to elements of the Asaphid fauna may have survived the Cambrian-Ordovician transition in the Ural border area, (2) Baltica and the Yangtze Plate belonged to different benthic biogeographic provinces (Shergold 1988), (3) the immigration in the Tremadoc of Baltoscandia already included a number of asaphid lineages, (4) subsequently there was some stagnation in the shelves of Baltica, possibly because of uniform sedimentary conditions (particularly in Baltoscandia), whereas the Yangtze shelf faunas diversified on a biofacies level between areas with different sedimentary substrate conditions, (5) Baltica appears to have been much isolated, with only a few immigrations of pelagic or planktic forms (including planktic larvae) and with new immigrations of benthic forms basically restricted to groups that were already present, such as asaphids, illaenoids and cheiruroids. Still, geographical isolation was relative. Tremadocian immigrations were notably similar between Baltica and Montagne Noire in France (Vizcaïno et al. 2008) at the same time as the Yangtze Plate evolved in another direction.

CONCLUSIONS

1. In Baltoscandia only three major biofacies, the Olenid, *Ceratopyge* and Asaphid biofacies, are distinguished with evolutionary and local variations mostly on the species level. A strong regional differentiation occurs only in the late Kundan (mid-Darriwilian), where the Oslo Region and the North Estonian Belt have rich trilobite faunas that share only a few species, and the Central Baltoscandian Belt has an impoverished fauna, consisting of a single species in many localities. That interval is followed by a major change in trilobite fauna marking the boundary between the Öland and Viru series.
2. The trilobite succession in the Urals starts with the Olenid fauna common in the transition of the Cambrian–Ordovician periods. The oldest taxa indicate the latest Cambrian age. The following early Tremadocian faunas are fairly rich along the Uralian side of the Baltica Plate. The association of 20 genera includes several olenids, the oldest hystricurids, and the asaphids originating from the Furongian. Four of them are shared with the Baltoscandian flank. The richness of the fauna probably results from its palaeogeographical position close to the terranes bordering the Gondwana. Thus the new stocks arrived along its margin from Argentina, Avalonia, Armorica and Perunica, but also from the terranes surrounding Baltica in the north and northeast like the Siberia, Altaj-Sayan and Kazakh terranes.
3. The middle Tremadocian *Ceratopyge* fauna is much richer in the Uralian side with its nearly 100 species belonging to 50 genera, while about 50 species and 33 genera are known from Baltoscandia. Twenty-four genera are shared. However, the richness in the east is actually relatively lower, considering that the fauna is split between the north and the south. About 60 species are known from the South Urals, 30 from Paj-Khoj and 10 species, linking the two regions, occur in the Sub-polar and Polar Urals. Only a small part of the fauna of both tips is related to the *Ceratopyge* fauna of Baltoscandia.
4. The latest Tremadocian and Floian faunas in the north and south are reduced to the half with no species shared. Although largely differing from that in Baltoscandia, the assemblage in Paj-Khoj is recognizable as the Asaphid biofacies. However, the fauna in the south is difficult to assign to that classification. *Niobe* is the only asaphid, while the other taxa belong to illaenids, harpidids, eulomids, remopleuroids, cheirurids and lichids. Half of them originate from the earlier interval, some are unique and some are invaders from the neighbouring terranes.
5. The Dapingian of Paj-Khoj clearly represents the Asaphid biofacies with its *Megistaspis* fauna widely distributed also in Baltoscandia, and with *Ogygiocaris* marking the outer shelf similar to that in the western side. The middle Darriwilian is mainly represented by the shales devoid of trilobites. In the South Urals the Cheirurid biofacies developed in the Darriwilian, following the *Ceratopyge* and Asaphid biofacies.

4. Despite similarities in the lithologies of the Baltoscandian and Yangtze Basins the trilobite biofacies developed in very different patterns. The fauna of the former basin is rather monotonous both in spatial and temporal aspects. The biofacies of the latter basin, however, changed quickly in regionally rather restricted areas, depending strongly on lithofacies. Most of the 22 genera shared between the two terranes occur on the slope or buildups of the outer shelf in the Yangtze Basin. The genera known from carbonatic buildups in China are elements of the *Cyclopyge stigmata* association of the outer shelf carbonates on Bornholm in the lowest Dapingian. Although the shared taxa indicate the possible closeness of these terranes, a *Neseuretus* fauna, which is characteristic of terranes

along Gondwana, is missing there. The Yangtze block was thus supposedly positioned rather distant from Baltica.

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APPENDIX

Table 2. List of trilobite species of the Uralian border of Baltica

	C/O	Tr1	Tr1	Tr2	Tr2	Tr2	Tr2	Tr2	Tr2	Tr2	Tr3	Tr3–F11	F11	F12–F13	Dp	?Tr–Dp–Dw	Dw	Dw
Revised taxa with latest references.																		
Occurrence data: small letters in italic – rare occurrence; small regular letters – common species; capital letters in italic – abundant occurrence; question mark shows uncertainty of a level.																		
Regions: s – South Urals; sM – Mayachnaya Gora, SE of Urals; c – Middle Urals; n – (Sub-)Polar Urals; n2V – Sub-polar Urals, Vajgach, the upper part of the stage; p – Paj-Khoj; p1 – Paj-Khoj, the lower part of the bed.																		
References following stratigraphical units are: (1) Weber 1948; (2) Bondarev et al. 1965; (3) Burskij 1970; (4) Antsygin in Varganov et al. 1973; (5–7) Antsygin 1977, 1978, 2001; (8) Klyuzhina 1985; (9) Antsygin in Puchkov 1991.																		
	Khmelev RS (7)	Kidryas RS (7)	Pogurej Fm (7)	Kolnabuk RS (7)	Kibatim Fm, Kolnabuk RS (7)	Grubejn Fm, Kolnabuk-Kuagach Sts (7)	<i>Synthrophopsis magna</i> & <i>Dikelekephalina</i> beds, Sokoli RS (2, 3)	<i>Nyaya</i> & <i>Tersella</i> beds, Sokoli RS (2, 3)	<i>A. serratus</i> beds, Sokoli RS (2, 3)	<i>Megalaspides</i> beds, Sokoli RS (2, 3)	Kuagach RS (7)	<i>T. approximatus</i> beds, Nelidov RS (2, 3)	<i>P. aff. densus</i> & <i>Eorobergia nericensis</i> beds, Nelidov RS (2, 3)	<i>Megist. limbata</i> and <i>Trigonograptus ensiformis</i> beds, Nelidov RS (2, 3)	Bredin beds (1, 6, 8)	Karakol'-Mikhajlovsk RS (4, 5)	Karakol'-Mikhajlovsk RS (4, 9)	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
<i>Micragnostus porosus</i> (Antsygin 2001)	S																	
<i>Akoldinoidia pustulata</i> (Antsygin 2001)	S																	
<i>Kujandaspis</i> aff. <i>kujandensis</i> (Antsygin 2001)	s																	
<i>Jdyia</i> sp. indet. (Antsygin 2001)	s																	
<i>Leimitzia pagica</i> (Antsygin 2001; Bogolepova & Gee 2004)	?s	S	n															

Continued overleaf

APPENDIX. *Continued*

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Leimitzia bavarica</i> (Antsygin 2001; Bogolepova & Gee 2004)	?s	S	n														
<i>Dolgedola multicava</i> (Antsygin 2001)	?s	s	n														
<i>Micragnostus</i> sp. (Bogolepova & Gee 2004)	p																
<i>Jdyia tuberosa</i> (Antsygin 2001))		S, c	n														
<i>Jdyia excussa</i> (Antsygin 2001)		S															
<i>Jdyia kosagachica</i> (Antsygin 1977) [HP: incl. <i>Hystericurus conicus</i> in Balashova 1961]		S															
<i>Hystericurus?</i> sp. (Antsygin in Varganov et al. 1973)		s															
<i>Parabolinella limitis</i> (Antsygin 2001)	?s																
<i>Acerocarina keisaranica</i> (Antsygin 2001) [HP:incl. <i>Cyclognathus micropygus</i> in Balashova 1961]		s															
<i>Jujujaspis keideli</i> (Antsygin 2001)		s															
<i>Peltocare recta</i> (Antsygin 2001)		s															
<i>Peltocare inconspica</i> (Antsygin 2001)		S															
<i>Medeselaspis amplus</i> (Antsygin 1977, 2001)		S															
<i>Leimitzia furculosa</i> (Antsygin 2001)		S															
<i>Leimitzia</i> sp. (Antsygin 2001)		s															
<i>Dolgedola obunca</i> (Antsygin 2001)		S															
<i>Lateuloma</i> sp. (Korinevskij 1989)		s															
<i>Niobe</i> sp. (Antsygin 2001)		s															
<i>Promegalaspides</i> sp. (Antsygin 2001)		s															
<i>Apatokephalus?</i> <i>macilentus</i> (Antsygin 2001)		S															
<i>Apatokephalus arduus</i> (Antsygin 2001)		s															
<i>Kainella alimbetica</i> (Balashova 1961)		s															
<i>Kainella</i> sp. (Antsygin in Varganov et al. 1973)		s															
<i>Pseudokainella pustulata</i> (Antsygin 2001)		s															
<i>Micragnostus kidrasensis</i> (Antsygin 2001)		S															
<i>Alimbetaspis kelleri</i> (Balashova 1961)		s		s													
<i>Macropyge foliacea</i> (Antsygin 2001)		s		s													
<i>Promegalaspides kasachstanensis</i> (Balashova 1961; Antsygin 2001)	?s			s													
<i>Hospes</i> sp. (Korinevskij 1989)				?s													
<i>Geragnostus</i> aff. <i>crassus</i> (Antsygin 2001)				?s													
<i>Leiagnostus</i> aff. <i>peltatus</i> (Korinevskij 1989)				?s													
<i>Parabolinella</i> sp. (Korinevskij 1989)				s													
<i>Acerocarina</i> sp. (Korinevskij 1989)				s													
<i>Saltaspis koftugaensis</i> (Antsygin 2001)				S													
<i>Triarthrus</i> cf. <i>beckii</i> (Antsygin 2001)				S													
<i>Dikelokephalina dicraeura</i> (Antsygin 2001)				S													
<i>Dikelokephalina?</i> <i>amzassensis</i> (Antsygin 2001)				S													
<i>Birmanites</i> sp. 1 (Antsygin 2001)				s													
<i>Ceratopyge rotundata</i> (Antsygin 2001)				S													
<i>Macropyge xiphias</i> (Antsygin 2001)				s													
<i>Orometopus elatifrons</i> (Antsygin 2001)				S													
<i>Orometopus</i> aff. <i>grypos</i> (Antsygin 2001)				s													
<i>Pagometopus tumidus</i> (Antsygin 2001)				s													
<i>Haplopleuroides pismenensis</i> (Antsygin 2001)				s													
<i>Haplopleura optima</i> (Antsygin 2001)				s													
<i>Niobe</i> sp. 1 (Antsygin 2001)				s													
<i>Niobe</i> sp. (Antsygin 2001)				s													
<i>Niobe insignis</i> [Antsygin 2001 incl. <i>Niobe alimbetica</i> in Balashova 1976]				S													
<i>Niobe</i> cf. <i>explanata</i> (Antsygin 2001)				s													
<i>Niobella</i> sp. (Korinevskij 1989)				s													

APPENDIX. *Continued*

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Asaphellus alimbeticus</i> (Balashova 1961)				s													
<i>Megistaspis</i> sp. (Korinevskij 1989)				s													
<i>Anacheirurus bucerus</i> (Antsygin 2001)				s													
<i>Protopliomerops kasachstanicus</i> (Balashova 1961) [HP: too obscure, ? <i>P.</i> aff. <i>speciosa</i>]				s													
<i>Parapilekia</i> aff. <i>speciosa</i> (Antsygin 2001)				s													
<i>Parapilekia?</i> sp. (Korinevskij 1989)				s													
<i>Shumardia</i> (<i>Conophrys</i>) <i>salopiensis</i> [<i>S. (C.) oelandica</i> in Antsygin 2001, partly]				s													
<i>Euloma kasachstanica</i> (Balashova 1961)				s													
<i>Platypeltoides uralicus</i> (Antsygin 2001) [= <i>Platypeltoides incipiens</i> in Balashova 1961]				s													
<i>Apatokephalus mutilus</i> (Antsygin 2001) [<i>A. mutilus</i> nom. nud. Antsygin 1973]				s													
<i>Apatokephalus ornatus</i> (Antsygin 2001)				S													
<i>Apatokephalus</i> cf. <i>exiguus</i> (Antsygin 2001)				S													
<i>Richardsonella</i> sp. (Antsygin 2001)				s													
<i>Lacorsalina kolnabukia</i> (Antsygin 2001)				s													
Remopleuridae gen. indet. (Antsygin 2001)				s													
<i>Harpides rugosus</i> (Antsygin 2001)				s													
<i>Varvia</i> n. sp. [<i>Varvia longicauda</i> in Antsygin 2001]				s													
<i>Tersella?</i> sp. (Korinevskij 1989)				s													
<i>Pseudoglyphurina acanthera</i> (Antsygin 2001)				s													
<i>Tyrmanicyclopyge corrugata</i> (Antsygin 2001)				S													
<i>Pricyclopyge latifrons</i> (Antsygin 2001)				S													
<i>Amzasskiella monandra</i> (Antsygin 2001)				s													
<i>Geragnostus</i> sp. (Antsygin 2001)				s													
<i>Litagnostus alimbeticus</i> (Balashova 1961)				s													
<i>Leiagnostus</i> sp. (Korinevskij 1989)				s													
<i>Micragnostus aciculatus</i> (Antsygin 2001)				S													
<i>Ceratopyge forficula</i> (i.e. Balashova 1961; Antsygin 2001)				s	n	n											
<i>Apatokephalus serratus</i> (i.e. Balashova 1961; Antsygin 2001)				s	n				p								
<i>Shumardia</i> (<i>Conophrys</i>) <i>pusilla</i> [<i>S. (C.) oelandica</i> in Antsygin 2001, partly]				s		n											
<i>Agerina</i> aff. <i>praematura</i> (Korinevskij 1989)				?s													
<i>Agerina</i> aff. <i>praematura</i> [<i>Ceratopyge forficuloides</i> in Burskij 1970]									p								
<i>Geragnostus sidenbladhi</i> (Balashova 1961; Antsygin 2001)		?s		S							S						
<i>Nyaya</i> sp. (Korinevskij 1989)				?s							?s						
<i>Ceratopyge uralica</i> (Antsygin 2001)				S							s						
<i>Nileus limbatus</i> (Antsygin 2001)				S							s						
<i>Varvia</i> sp. (Korinevskij 1989)											?s						
<i>Niobe emarginula</i> Angelin (Antsygin 2001)											S						
<i>Bornholmaspis?</i> <i>taiketskensis</i> (Antsygin 2001)											s						
<i>Acantopleurella plana</i> (Antsygin 2001)											s						
<i>Bljauloma bljavica</i> (Antsygin 2001)											s						
<i>Euloma ornatum</i> var. <i>alimbetica</i> (Balashova 1961)											s						
<i>Apatokephalus karabutakensis</i> (Antsygin 2001)											s						
<i>Harpides</i> sp. 1 (Antsygin 2001)											s						
<i>Harpides nodorugosus</i> (Antsygin 2001)											S						
<i>Loganopeltis?</i> <i>nanus</i> (Balashova 1961)											s						
<i>Scotoharpes excavatus</i> (Antsygin 2001)											s						
<i>Batyraspis</i> aff. <i>inceptoris</i> (Antsygin 2001)											s						
<i>Varvia squarrosa</i> (Antsygin 2001)											s						

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APPENDIX. *Continued*

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Ottenbyaspis</i> aff. <i>oriens</i> (Antsygin 2001)											S						
<i>Lichakephalina schilikta</i> (Antsygin 1973, 2001)											s						
<i>Pseudoglaphurina insolita</i> (Antsygin 2001)											s						
<i>Glaphurus alimbeticus</i> (Balashova 1961)											s						
<i>Pricyclopyge gallica</i> (Antsygin 2001)											s						
<i>Pseudorhaptagnostus</i> (<i>Machairagnostus</i>) sp. (Ahlberg 1992) [<i>Trinodus agnostiformis</i> in Balashova 1961]											s						
<i>Homagnostoides kasachstanicus</i> (Balashova 1961)											s						
<i>Pliomeroides</i> sp. (Antsygin 2001)						n											
<i>Harpides</i> sp. (Antsygin 2001)						n											
<i>Niobe</i> sp. (Antsygin 2001)						n											
<i>Niobella</i> aff. <i>laeviceps</i> (Antsygin in Varganov et al. 1973)							n										
<i>Pliomeroides?</i> <i>subdefensus</i> (Antsygin 2001)							n				s						
<i>Pricyclopyge</i> aff. <i>latifrons</i> (Antsygin 2001)							n										
<i>Geragnostus adductus</i> (Antsygin 2001)							n										
<i>Geragnostus longirhachis</i> (Burskij 1970)										?p							
<i>Dikelocephalopsis timokhini</i> (Rozov in Rozova et al. 1985) [<i>Dikelocephalina</i> aff. <i>dicraeura</i> in Burskij 1970]										p							
<i>Dikelocephalina</i> sp. N 1 (Burskij 1970)										p							
<i>Dikelocephalina</i> sp. N 2 (Burskij 1970)										p							
<i>Apatokephalus</i> sp. N 1 (Burskij 1970)										p							
<i>Nyaya paichoica nomen nudum</i> (Burskij 1970)										p							
<i>Tersella</i> sp. (Burskij 1970)										p							
<i>Hystericurus?</i> sp. (Burskij 1970)										p							
<i>Asaphellus</i> sp. [<i>Asaphellus</i> sp. 1 (cran) & sp. 2 (pyg) in Burskij 1970]										p							
<i>Apatokephalus pecten</i> Wiman (Burskij 1970)										p							
<i>Nyaya sokoliensis nomen nudum</i> (Burskij 1970)										p							
<i>Tersella?</i> <i>magnaoculus nomen nudum</i> (Burskij 1970)										p							
<i>Galbagnostus karskensis</i> (Burskij 1970)										p							
<i>Asaphellus nelkajugaensis</i> (Antsygin 2001)											?p	p					
Pliomerid [<i>Pliomeroides primigenius</i> (Burskij in Bondarev et al. 1965)]											?p						
<i>Niobella parvula</i> (Burskij 1970)										p							
<i>Symphysurus angustatus</i> (Antsygin 2001)										p							
<i>Apatokephalus</i> sp. N 2 (Burskij 1970)										p							
<i>Remopleuridiella?</i> sp. (Burskij 1970)										p							
<i>Galbagnostus breverhachis</i> (Burskij 1970)										p							
<i>Geragnostella limbata</i> (Burskij 1970)										p							
<i>Pliomeroides defensus</i> (Burskij in Bondarev et al. 1965)											?p						
<i>Megalaspides</i> sp. N 1 (Burskij 1970); cranidium											p						
<i>Megalaspides</i> sp. aff. <i>nericiensis</i> [<i>Megistaspis</i> (<i>Megistaspis</i>) sp. N 2 in Burskij 1970; pyg.]											p						
<i>Cybelurus sokoliensis</i> (Burskij 1970)											p						
<i>Carolinites</i> sp. (Burskij 1970)											p						
<i>Geragnostus</i> sp. n. 2 (Burskij 1970)											p						
<i>Falanaspis</i> aff. <i>aliena</i> (Antsygin 1991)											p	p					
<i>Niobella</i> sp. N 3 (Burskij 1970)											p	p					
<i>Apatokephalus heterosulcatus</i> (Burskij 1970)											p	p					
<i>Araiocaris?</i> sp. nov. [<i>Ogygiocaris</i> aff. <i>sarsi</i> in Burskij 1970]												p					
<i>Araiocaris?</i> sp. [<i>Ogygiocaris?</i> sp. N 1 & N 2 in Burskij 1970]												p					
<i>Shumardia</i> (<i>Conophrys</i>) sp. [<i>Shumardia</i> sp. in Burskij 1970]												p					
<i>Lacorsalina limbata</i> (Burskij 1970)												p					
<i>Loganopeltis?</i> sp. (Burskij 1970)												p					

APPENDIX. *Continued*

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Raymondaspis</i> sp. (Burskij in Bondarev et al. 1965)												<i>p</i>					
<i>Geragnostus</i> sp. n. 5 (Burskij 1970)												<i>p</i>					
<i>Geragnostus</i> sp. n. 4 (Burskij 1970)												<i>p</i>					
<i>Geragnostus</i> sp. n. 3 (Burskij 1970)												<i>p</i>					
<i>Geragnostus</i> sp. n. 1 (Burskij 1970)												<i>p</i>					
Gen. et sp. indet. (Burskij 1970)												<i>p</i>					
<i>Ampyxella?</i> <i>nekhoroshevae</i> (Burskij 1970)													<i>p</i>				
<i>Araiocaris?</i> sp. [<i>Niobe?</i> sp. N 1 in Burskij 1970]													<i>p</i>				
<i>Niobella imparilimbata</i> (Burskij 1970)													<i>p</i>				
<i>Niobella</i> aff. <i>lindstroemi</i> [<i>N. laeviceps</i> in Burskij 1970]													<i>p</i>				
<i>Niobella</i> sp. N 1 (Burskij 1970) [HP: ? <i>N.</i> aff. <i>imparilimbata</i>]													<i>p</i>				
<i>Megalaspides</i> sp. N 2 (Burskij 1970)													<i>p</i>				
<i>Megistaspis similis</i> (Burskij 1970)													<i>p</i>				
<i>Megistaspis</i> (<i>Megistaspis</i>) sp. N 1 (Burskij 1970)													<i>p</i>				
<i>Euloma</i> aff. <i>laeve</i> Angelin (Burskij 1970)													<i>p</i>				
<i>Eorobergia burskyi</i> (Rozov in Rozova et al. 1985) [<i>E. nericiensis</i> in Burskij 1970]													<i>p</i>				
<i>Eorobergia</i> sp. (Burskij 1970)													<i>p</i>				
<i>Niobella</i> sp. N 2 (Burskij 1970) [HP: ? <i>N.</i> aff. <i>bohlini</i>]													<i>p1</i>				
<i>Nileus ellipticaudata</i> [<i>Niobella ellipticaudata</i> Burskij 1970]													<i>p1</i>				
<i>Niobe</i> aff. <i>emarginula</i> (Burskij 1970)														<i>p</i>			
<i>Araiocaris?</i> sp. [<i>Ogygiocaris</i> sp. N 3 in Burskij 1970]														<i>p</i>			
<i>Megistaspis</i> aff. <i>elongata</i> [<i>Megistaspis</i> (<i>Megistaspis</i>) sp. N 3 in Burskij 1970]														<i>p</i>			
<i>Megistaspis</i> aff. <i>elongata</i> [<i>M. limbata</i> in Burskij 1970, partly]														<i>p</i>			
<i>Megistaspis limbata</i> (Burskij 1970), partly														<i>p</i>			
<i>Megistaspis</i> (<i>Megistaspidella</i>)? sp. (Burskij 1970)														<i>p</i>			
<i>Asaphus?</i> sp. (Burskij 1970)														<i>p</i>			
<i>Tersella oculus</i> (Antsygin 1978)																	<i>sM</i>
<i>Asaphellus glabratus</i> (Antsygin 1978)																	<i>sM</i>
<i>Megalaspides mamaevi</i> (Antsygin 1978)																	<i>sM</i>
<i>Cybele rotundata</i> (Antsygin 1978)																	<i>sM</i>
<i>Cyrtometopus</i> aff. <i>priscus</i> (Antsygin 1978)																	<i>sM</i>
<i>Pterygomotopus brendensis</i> (Weber 1948)																	<i>sM</i>
<i>Cybele</i> aff. <i>bellatula</i> (Antsygin 1977)																	<i>s</i>
<i>Cyrtometopus anygini</i> (Přibyl et al. 1985; Antsygin 1977)																	<i>s</i>
<i>Pseudosphaerexochus</i> (<i>Pateraspis</i>) <i>tumefactus</i> (Antsygin 1977)																	<i>s</i>
<i>P.</i> (<i>Pateraspis</i>) <i>ornatus</i> (Antsygin 1977)																	<i>s</i>
<i>Kawina spinigena</i> (Antsygin 1977)																	<i>s</i>
<i>Heliomera</i> sp. 1 (Antsygin 1977)																	<i>s</i>
<i>Remopleurides karakolensis</i> (Antsygin 1973)																	<i>s</i>
<i>Platillaenus ladogensis</i> (Antsygin 1977)																	<i>s</i>
<i>Illaeus polymitus</i> (Antsygin 1977)																	<i>s</i>
<i>Phorocephala?</i> <i>venusta</i> (Antsygin 1977; as <i>Goniophrys venustus</i>)																	<i>s</i>
<i>Platylichas micus</i> (Antsygin 1973)																	<i>s</i>
<i>Metopolichas verrucosus</i> (Antsygin 1977)																	<i>s</i>
<i>Glaphurina berkutensis</i> (Antsygin 1977)																	<i>s</i>
<i>Glaphurina baikassia</i> (Antsygin 1977)																	<i>s</i>
<i>Ceratocephala micula</i> (Antsygin 1977)																	<i>s</i>
<i>Holdenia putilla</i> (Antsygin 1977)																	<i>s</i>
<i>Cyphoniscus radiculosus</i> (Antsygin 1977)																	<i>s</i>
<i>Pseudopetigurus enodis</i> (Antsygin 1977)																	<i>s</i>
<i>Kinderlania tschegodaevi</i> (Antsygin 1977)																	<i>s</i>
<i>Geragnostus crassus</i> (Antsygin 1977)																	<i>s</i>

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1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Pliomera fischeri</i> (Antsygin 1977, 1991)																s	n
<i>Asaphus expansus?</i> (Antsygin 1973)																	n
<i>Ceratopyge? expectata</i> (Antsygin 1991)																	n
<i>Hapalopleura xaimensis nomen nudum</i> (Antsygin 1991)																	n
<i>Plectasaphus plicicostis</i> (Antsygin 1991)																	n
<i>Ceraurina aff. frequens</i> (Antsygin 1991)																	n
<i>Remopleurides consuetus</i> (Antsygin 1991)																	n
<i>Carolinites dissectus</i> (Antsygin 1991)																	n
<i>Calyptaulax incepta</i> (Antsygin 1991)																	n
<i>Lonchodomas cf. rostratus</i> (Antsygin in Varganov et al. 1973)																	n
<i>Lonchodomas aff. parvulus</i> (Burskij 1966; Antsygin 1991)																	n2V
<i>Nileus peculiaris</i> (Antsygin 1991)																	n2
<i>Ogygiocaris aff. sarsi</i> (Antsygin 1991)																	n2

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Baltika paleolaama Vara- ja Kesk-Ordoviitsiumi trilobiidid ning biofaatsiesed ja põgus võrdlus Yangtze laamaga

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Vara-Tremadoki immigratsiooni etapp oli globaalne, puudutades ühtlasi elustiku arengut ka Baltika laamat ümbritsevat meredes. On kokku võetud trilobiitide levik kuni liigitasemeni nii Baltoskandia paleobasseinis, ulatudes selle sopistusse Moskva basseinis, kui ka laama vastasküljel Uuralite läänenõlval. Trilobiidifaunade eripära ja muutumist Baltika eri osades läbi Vara- ning Kesk-Ordoviitsiumi on võrreldud Lõuna-Hiina Yangtze ploki fauna omapära ja muutustega. Kuigi kivimiliselt on tegemist suure sarnasusega, mis oligi tõukeks nende alade võrdlemisel, selgub, et trilobiitide jagunemine erinevate keskkondade vahel assotsiatsioonideks, nende mitmekesisus ja muutumine on väga erinevad.

Baltoskandias vahetus Kambriumi ajastust pärinev Olenid-biofaatsies suhteliselt mitmekesise *Ceratopyge*-biofaatsiesega basseini sügavamas osas. See vahetus äkki välja totaalselt uue elustikuga, Asaphid-biofaatsiesega, mis levis peaaegu monotoonselt üle kogu basseini Flost Darriwilini välja. Enamikku liikidest võib samaaegsetes kihtides kohata pea kõikjal üle basseini kuni Kunda ea teise pooleni. Selleks ajaks oli toimunud liikide kitsam geograafiline spetsialiseerumine ja igas regioonis moodustusid erinevad erikooslused ehk nn subbiofaatsiesed.

Uuralite-poolsel Baltika laama nõlval aga arenesid analoogsed biofaatsiesed: Olenid-, *Ceratopyge*- ja Asaphid-biofaatsies. Need olid oma perekondlikust koosseisust mõnevõrra erinevad ja liigiliselt Baltoskandiaga väheühilduvad ning Uuralite lõuna- ja põhjaosa võrreldes erinesid nende assotsiatsioonid. Aja jooksul see erinevus aina suurenes, kusjuures Darriwili ajast on Uuralite põhjaosast teada peamiselt vaid asaphiidsed trilobiidid, samas kui lõunaosas saab üksnes kaudselt Asaphid-biofaatsiese identifitseerida. Lõunas esinev cheiruriide ja illaeniide sisaldav assotsiatsioon sarnaneb enim Laurentia laama riffide trilobiidikooslusega, mis veidi peegeldab konodondifaunade kooslust.

Erinevalt trilobiidi biofaatsiiste suhteliselt monotoonselt levikust Baltikal muutub pilt trilobiidifaatsiistest Yangtze basseini nõlval ruumis ja ajas kiiresti. Kuigi liigiliselt on need suhteliselt vaesed, siis perekondliku koosluse järgi on samast ajavahemikust eristatud viihteist biofaatsiist Baltoskandia kolme vastu. Suhteliselt sarnane kivimiline iseloom ei taga sarnast faunistilist koostist, sest viimase puhul on olulised ka basseini suurus, avatus ookeanile ja paleogeograafiline asend koos migratsioonivõimalustega.