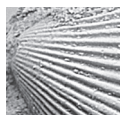


Frasnian–Famennian (Upper Devonian) transition in the northern hemisphere (NE Laurussia and NE Siberia) – an overview

ANDREY V. ZHURAVLEV & ELENA V. SOKIRAN



There is high similarity in sedimentation and taxonomic composition and stratigraphic succession of conodonts and brachiopods across the Frasnian–Famennian (F–F) transition in low- and mid-latitude realms of NE Laurussia and Siberia. This uniformity suggests the presence of low environmental gradients between 10° S and 40° N of the northern hemisphere corresponding to tropical and subtropical climatic zones. The changes in taxonomic diversity in these marine faunas occurred gradually throughout the Frasnian, and were paired with similar, mostly carbonate facies settings, marked by rare development of the Kellwasser-type organic-rich deposits. Moderated ecological effect of the rapid climatic shifts during the F–F crisis is also noteworthy, especially for the shelly benthos, with an exception of the Lilliput effect. • Key words: Frasnian–Famennian boundary, northern hemisphere, conodonts, brachiopods, facies changes, Laurussia, Siberia.

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The Frasnian–Famennian (F–F) boundary interval corresponds to the significant biotic crisis in the middle Palaeozoic (McGhee 2013, Stanley 2016). During the late Frasnian most marine organisms of the tropical realm were affected by the stepwise extinction or diversity reduction due to a decrease in speciation rates (see Stigall 2010 for discussion). Among the terrestrial organisms, the extinction of land plants took place in the Late *Pal. rhenana* conodont Zone, and none of the known fossil tetrapod groups survived the end of the Frasnian (McGhee 2013). Modern overviews of the biotic and abiotic changes at the F–F transition were done by Ma *et al.* (2016), Qie *et al.* (2019) and Carmichael *et al.* (2019).

In contrast to the well-studied F–F transitions in the palaeotropical realm and southern hemisphere (North America, Western Europe, northern Africa, Australia, and China) this interval is less known in the northern hemisphere (Eastern Europe, Urals, northern Siberia). According to palaeoclimatic reconstructions (Boucot *et al.* 2013) the East European Craton (eastern Laurussia) and shelves of the Uralian Strait were located in the equatorial (tropical) realm at the latest Frasnian–earliest Famennian. The Siberia palaeocontinent, excluding its southern part, was in a subtropical climatic zone, even if located at mid-latitudes (Fig. 1B).

The F–F transition beds of north-eastern Laurussia, known from the central and south-eastern parts of the East European Platform (EEP), Pechora Platform (PP), northern Urals, and Pai-Khoi, represent a wide spectrum of facies. Northern Siberia sections (north of Siberian Platform and Kolyma-Omolon Uplift) contain the F–F transition in shallow-water and deep-water facies (Yolkin *et al.* 2006, Gagiev 2009, Yazikov *et al.* 2013). Thus, the most representative of the F–F transition sequences that characterize north-eastern Laurussia (9 sections and boreholes) and northern Siberia (5 sections) were selected for testing palaeolatitudinal and facies gradients in the F–F transition in the northern hemisphere (Fig. 1).

The aims of the article are the following: to analyze distribution of conodonts and brachiopods in the F–F transition in various facies of the tropical and northern subtropical realms of the northern hemisphere; and to evaluate facies and palaeolatitudinal gradients in the F–F fauna turnover in the northern hemisphere in respect of local and regional versus global causes of the biotic crisis. In this context, the regional impact of the highlighted Viluy Large Igneous Province (LIP) of Siberia was first mentioned.

The F–F transition was characterized by the transgressive-regressive sequences reported in different regions. Sandberg *et al.* (1988) considered biotic and lithological

records of the global event in the palaeotropical realm, and according to these authors, the changes of conodont associations were attributed to a eustatic rise followed by an abrupt eustatic fall preceding the F–F mass extinction. Sea level rise at the *Pal. linguiformis* Zone was detected in the Betic Cordillera, Spain (Rodríguez-Cañero & Martín-Algarra 2014), and Appalachian Basin (Lash 2017). The presence of post-Frasnian regression is indicated in the eastern Laurussia basin by a regional unconformity in the shallow-water shelf facies. The unconformity corresponds to stratigraphical gap from (?) *Pal. linguiformis* Zone up to *Pal. delicatula platys* Zone in some regions, exemplified by East European Platform (Aleksiev *et al.* 1996). In contrast, sea level fall at the terminal Frasnian (*Pal. linguiformis* Zone) is reported in Iran (Gholamalian 2007), Moravia (Hladil 2002), and some regions of South China (Ma *et al.* 2016). Thus it is difficult to separate tectonic and eustatic sea level changes around the F–F transition. Hallam & Wignall (1999) suggested that tectonics plays a significant role in regional and local sea level changes in western Laurussia.

The term “Kellwasser (KW) Crisis”, based on classic outcrops of the Rhine Slate Mountains and Harz Mountains, is commonly accepted to describe both the upper Frasnian Kellwasser black shale horizons (lower – LKE, upper – UKE) and the corresponding global anoxic events (see summary in Gereke & Schindler, 2012). In particular, the transgression acme at the latest Frasnian (*Pal. linguiformis* Zone) was accompanied by shelf anoxia (Chen & Tucker 2003; Bond & Wignall 2008; Carmichael *et al.* 2014, 2019; Crasquin & Horne 2018). The signatures of anoxia are well developed mainly in the deep-water shelf environment, however absent or weak in the shallow-water carbonate platform and epicratonic basins, with some local exceptions reported by Bond *et al.* (2013) and Carmichael *et al.* (2014). There are three alternative models for the anoxia event. The first one postulates turnover of oceans bringing deep anoxic water onto the shelves (Joachimski *et al.* 2001, Chen & Tucker 2003). The second model supposes surface and shelf water eutrophication resulting in hypoxia/anoxia accompanied by climate cooling pulses (*e.g.* Carmichael *et al.* 2014, Huang *et al.* 2018). Cooling at the F–F transition was supposed by a number of researchers on the basis of diverse data (*e.g.* Copper 1998, Hallam & Wignall 1999, Lash 2017). According to oxygen isotope ratios in conodont apatites (Huang *et al.* 2018), the extreme greenhouse climate, with surface seawater temperatures above 30 °C, was interrupted by two cooling episodes of ~7 °C during the KW events. The third model proposes development of mid water column oxygen minimum zone between oxygenated surface and deep waters, expanding onto the shelves in response to enhanced primary productivity (Crasquin & Horne 2018).

A recent hypothesis of a primary trigger considers consequence of large-scale volcanism possibly coupled

with the effects of Eovariscan tectonism (Racki 1998a, Pujol *et al.* 2006, Kravchiński 2012, Ricci *et al.* 2013, Winter 2015, Ma *et al.* 2016, Racki *et al.* 2018). The Viluy LIP is considered as possible source of catastrophic volcanic eruptions that triggered the end-Frasnian mass extinction (Kravchiński 2012, Ricci *et al.* 2013, Racki *et al.* 2018). The revised F–F boundary date (371.86 ± 0.08 Ma according to Percival *et al.* 2018) does fall within age uncertainty of a late Frasnian pulse in the Viluy LIP (Percival *et al.* 2018). Thus there is just indirect evidence of coincidence between flood basalt eruption and the F–F biotic crisis, contrary to arc magmatism suggested by Winter (2015).

Material and methods

This study is based on new and published lithological and palaeontological data from the East European Platform, northern Urals, Pai-Khoi, the East Siberian Platform, and north-east Siberia (Pershina & Tsyganko 1980; Alekseeva *et al.* 1996; Yudina *et al.* 2002; Deulin 2006; Yolkin *et al.* 2006; Ovnatanova & Kononova 2008; Zhuravlev 2008, 2016; Gagiev 2009; Tsyganko 2011; Yazikov *et al.* 2013; Zatoń *et al.* 2014; Zhuravlev *et al.* 2015; Ovnatanova *et al.* 2017). The new data comprises lithological and palaeontological (brachiopods and conodonts) information from the sections of the East European Platform (two sections) and Pai-Khoi (two sections).

Illustrated conodonts and brachiopods are deposited in the Geological Museum of the Institute of Geology Komi SC UrB RAS, Syktyvkar, Russia; collection number 713.

Records of $\delta^{13}\text{C}_{\text{org}}$ in conodont elements of three taxa (*Icriodus*, *Jablonnodus*, and *Mitrellataxis*) were studied from the East European Platform sections (Kamenka Quarry and Russkiy Brod Quarry). Separated conodont elements of good preservation were washed with ethanol and distilled water and then used for analysis of carbon isotope values with DELTA V Advantage mass spectrometer equipped with the Thermo Electron Continuous Flow Interface (ConFlo III) and Element Analyzer (Flash EA 1112). The $\delta^{13}\text{C}_{\text{org}}$ values are reported relative to the PDB standard. Isotope analyses were performed at the CKP “Geonauka” of Institute of Geology Komi SC UrB RAS (Syktyvkar, Russia). International standard USGS-40 (L-Glutamic acid) was used. The precision of the $\delta^{13}\text{C}_{\text{org}}$ value is $\pm 0.15\%$. The $\delta^{13}\text{C}_{\text{org}}$ values in conodont elements are considered as a proxy of position in the trophic web and feeding specialization (Zhuravlev & Smoleva 2018).

The maps by Scotese (2016) compose palaeogeographic framework of this study. The plate-tectonic reconstruction model of Scotese (2016) is based on palaeomagnetic reference frames for 410–250 Ma. The model used palaeomagnetic data to constrain the palaeolatitudinal positions and rotation of plates. These

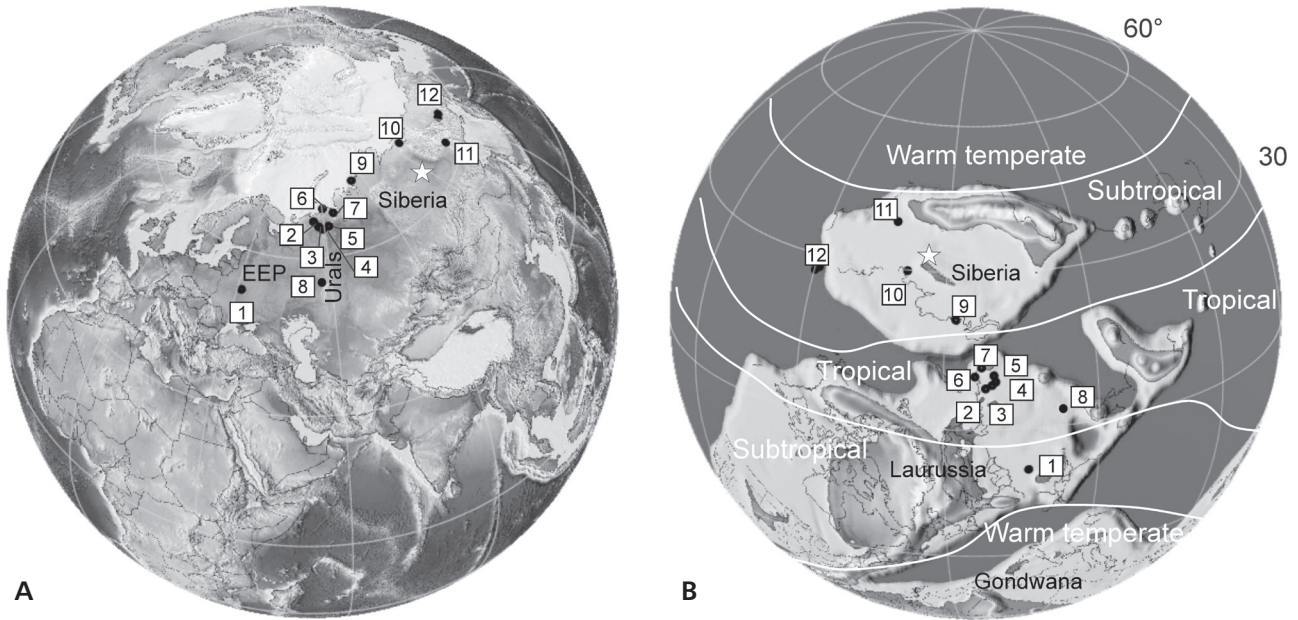


Figure 1. Locations of the Frasnian–Famennian boundary sites (A – recent geography; B – Late Devonian geography based on Scotese 2016, climatic belts after Boucot *et al.* 2013). Viluy LIP is marked by star. Sites: 1 – Voronezh Uplift, East European Platform; 2 – north-western part of the Pechora Platform; 3 – eastern part of the Pechora Platform; 4 – Syv’yu River section, Subpolar Urals; 5 – Lemva River basin, Polar Urals; 6 – northern Pai-Khoi; 7 – Kara River section, Southern Pai-Khoi; 8 – Volga-Ural Uplift; 9 – Domba River section, Taimyr Peninsula, northern Siberia; 10 – Stolb section, Lena River, northern Siberia; 11 – Khandyga River section, Sette-Daban Ridge, north-eastern Siberia; 12 – Kolyma Uplift, north-eastern Siberia.

plate-tectonic reconstructions form the basis of the model of palaeoclimate evolution developed by Boucot *et al.* (2013). The palaeoclimate reconstructions proposed by these authors are based on the distribution of lithologic indicators, such as distribution of bauxites, laterites, kaolinites, evaporites, calcretes, coals, and tillites.

The north-eastern Laurussia craton and shelves of Uralian Strait were located in the equatorial realm, but the north-eastern part of the Siberia palaeocontinent was located in the subtropical realm in the late Frasnian–early Famennian (Boucot *et al.* 2013). The sites under consideration at the F–F transition were distributed within wide palaeolatitudinal interval ranging from 10° S up to 40° N, and were located along the palaeoclimatic gradient from an equatorial climate to a subtropical climate (Fig. 1).

Geochemical data are unavailable for most of the regions under consideration. Some geochemical information was obtained from the East European Platform (Kamenka Quarry) and North Urals (Syv’yu River) sections (Yudina *et al.* 2002, Krawczyński *et al.* 2004).

North-eastern Laurussia

East European Platform

Epicratonic shallow-water environment. – Shallow-water sequences of the F–F transition are represented by successions of the central-western part of the EEP (Voronezh

Uplift, Russkiy Brod Quarry and Kamenka Quarry; Zatoń *et al.* 2014) and Volga-Ural Uplift (Ovnatanova & Kononova 2008) (Fig. 1). The upper Frasnian interval, roughly correlated with Lower *Pal. rhenana*–*Pal. linguiformis* conodont zones, is composed of a lateral transition from a restricted marine carbonate facies through carbonate shoreface to offshore facies in the central-western part of the EEP (Voronezh Uplift sections) (Fig. 2). Latest Frasnian conodont associations are dominated by polygnathids (see Appendix 1). The uppermost part of the *Pal. linguiformis* Zone and lower part of the Famennian (through *Pal. delicatula platys* Zone) were eroded due to the early Famennian regression. Overlying deposits are represented by sandstones of the nearshore facies (Russkiy Brod Quarry section) and by clayey limestone and clay alternation in the shoreface facies (Kamenka Quarry section) (Fig. 2).

The lowermost Famennian conodont associations, comprising polygnathids, spathognathids (*Mehlina*), icriodids, *Jablonnodus*, *Mitrellataxis*, and rare palmatolepids characteristic of the *Pal. minuta minuta*–*Pal. glabra pectinata* conodont zones (see Appendix 1). The abrupt changes in the fauna composition may be consequence of absence of the data corresponding to the gap comprising the interval from the upper *Pal. linguiformis* Zone to *Pal. minuta minuta* conodont Zone.

In the uppermost Frasnian of the Voronezh Uplift (Livny Horizon, Russkiy Brod and Kamenka quarries) the brachiopods are rare (Ljaschenko 1959). The lower

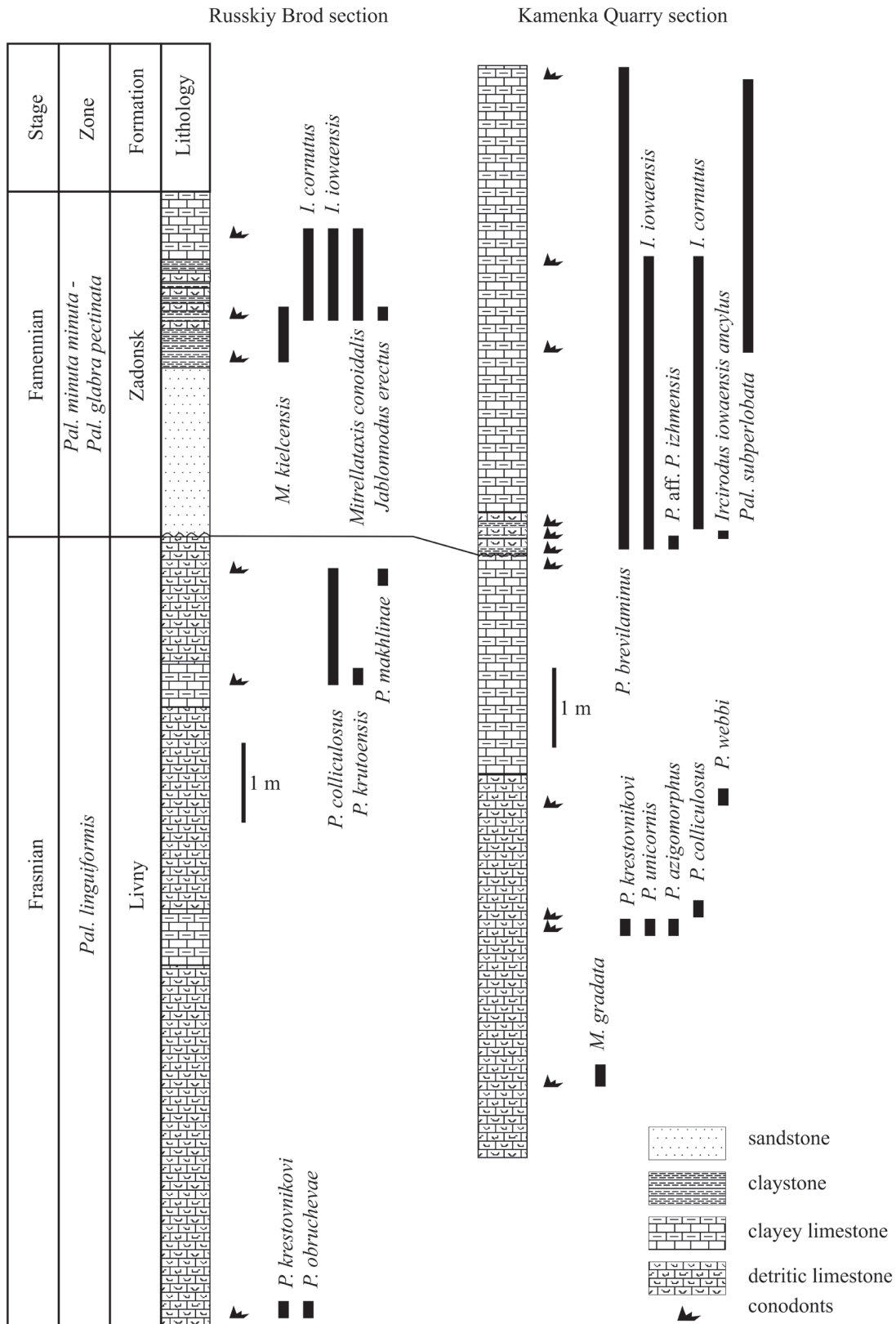


Figure 2. Lithology and conodont distribution in the F–F epicratonic shallow-water sequences of the Voronezh Uplift, East European Platform. Abbreviations: *P.* – *Polygnathus*, *Pal.* – *Palmatolepis*, *M.* – *Mehlina*, *I.* – *Icriodus*.

Stage	Standard Conodont Zone (Ziegler & Sandberg 1990, Spalletta <i>et al.</i> 2017)	EEP Regional Horizon	EEP Conodont Zone (Aristov 1994, Ovnatanova & Kononova 2008)	East European Platform	
				Voronezh Uplift	Volga-Ural Uplift (without Pre-Uralian foredeep)
				Rhynchonellide distribution (Fedorova 1955, Ellern <i>et al.</i> 1955, Novozhilova 1955, Batanova 1955, Mikryukov 1955, Ljaschenko 1959, Sokiran 2002)	
Famennian	<i>Pr. kockeli</i>	Zigansk			
	<i>B. ultimius</i>	Khovanstchina	<i>Pe. peejavi</i>		
	<i>B. costatus</i>	Ozerki			
	<i>B. ac. aculeatus</i>	Plavsk	<i>An. volnovachensis-N. salebrosus</i>		
	<i>Pal. gr. expansa</i>		<i>Apathognathus-Po. irregularis</i>		
	<i>Pa. gr. manca</i>	Optukha	<i>M. buccera</i>		
	<i>Pol. styriacus</i>		<i>Fe. australis</i>		
	<i>Ps. irankousus</i>		<i>Pe. streeli</i>		
	<i>Pa. trachytera</i>	Lebedian	<i>Pe. curtus</i>		
	<i>Pa. gr. gracilis</i>	Eiets	<i>Pa. superlobata-Pa. volskai</i>		
<i>Pa. rhomboidea</i>					
<i>Pa. gl. pectinata</i>	Zadonsk	<i>I. lowaensis</i>			
<i>Pa. m. minuta</i>					
<i>Pa. del. platys</i>	Volgograd				
<i>Pa. subperlobata</i>					
Frasnian	<i>Pa. linguiformis</i>	Livny	Beds with <i>Po. aff. brevilaminus</i>		
	Upper <i>Pa. rhenana</i>	Evlanovo	Beds with <i>Po. brevis-Po. macilentus</i>		
		Voronezh	Beds with <i>Po. churkini-Po. komi</i>		
	Lower <i>Pa. rhenana</i>	Rechitsa	<i>Po. subincompletus</i>		
	<i>Pa. jamiae</i>				
	Upper <i>Pa. hassi</i>	Semiluki	Beds with <i>Po. aspelundi</i>		
	Lower <i>Pa. hassi</i>				
	<i>Pa. punctata</i>		<i>Po. efimovae</i>		
	<i>Pa. transitans</i>	Sargaevo	<i>A. alata-M. bogoslovskiy</i>		
			<i>A. rotundiloba - A. africana</i>		
<i>M. falsiovalis</i>	Timan	<i>Po. pennatus-Po. ljaschenkoi</i>			

Figure 3. Distribution of rhynchonellid brachiopods in the F–F interval of the East European Platform. Grey belt corresponds to the KW Crisis: LKE – Lower Kellwasser Event; UKE – Upper Kellwasser Event.

Stage	Standard Conodont Zone (Ziegler & Sandberg 1990)	EEP Regional Horizon	EEP Conodont Zone (Aristov 1994, Ovnatanova & Kononova 2008)	East European Platform	
				Voronezh Uplift	Volga-Ural Uplift (without Pre-Uralian foredeep)
				Atrypide distribution (Fedorova 1955, Ellern <i>et al.</i> 1955, Novozhilova 1955, Batanova 1955, Mikryukov 1955, Ljaschenko 1959)	
Frasnian	<i>Pa. linguiformis</i>	Livny	Beds with <i>Po. aff. brevilaminus</i>		
	Upper <i>Pa. rhenana</i>	Evlanovo	Beds with <i>Po. brevis-Po. macilentus</i>		
		Voronezh	Beds with <i>Po. churkini-Po. komi</i>		
	Lower <i>Pa. rhenana</i>	Rechitsa	<i>Po. subincompletus</i>		
	<i>Pa. jamiae</i>				
	Upper <i>Pa. hassi</i>	Semiluki	Beds with <i>Po. aspelundi</i>		
	Lower <i>Pa. hassi</i>				
	<i>Pa. punctata</i>		<i>Po. efimovae</i>		
	<i>Pa. transitans</i>	Sargaevo	<i>A. alata-M. bogoslovskiy</i>		
			<i>A. rotundiloba - A. africana</i>		
<i>M. falsiovalis</i>	Timan	<i>Po. pennatus-Po. ljaschenkoi</i>			

Figure 4. Distribution of atrypid brachiopods in the F–F interval of the East European Platform. For explanations see Fig. 3.

Famennian (Zadonsk Horizon, Russkiy Brod and Kamenska quarries) brachiopods are more abundant and diverse (Ljaschenko 1959) (see Appendix 2). The shallow-water sequences of the Volga-Ural Uplift and Voronezh Uplift are similar and characterized by almost the same brachiopods (Figs 3–5).

Epicratonic deep-water environment. – The deep-water facies of the Volga-Ural Uplift (southeastern part of east of

EEP) are distributed within the Kama–Kinel palaeotrough system. The latest Frasnian interval is represented by micritic bituminous limestones with layers of cherty shales and cherts. The deposits contain conodonts of the *Pal. linguiformis* Zone (Ovnatanova & Kononova 2008) (Appendix 1). The lowermost Famennian is similar in lithology (alternation of dark bituminous clayey limestones and siliceous shales) and contains conodont fauna of *Pal. subperlobata*–*Pal. delicatula platys* zones (Ovnatanova &

Stage	Standard Conodont Zone (Ziegler & Sandberg 1990, Spalletta et al. 2017)	EEP Regional Horizon	Conodont Zone (Aristov 1994, Ovnatanova & Kononova 2008)	East European Platform	
				Voronezh Uplift	Volga-Ural Uplift (excluding Cis-Uralian foredeep)
				Spiriferide distribution (Fedorova 1955, Ellern et al. 1955, Novozhilova 1955, Batanova 1955, Mikryukov 1955, Krylova 1955, Ljaschenko 1959, Sokiran 2006)	
Famennian	<i>Pr. kockeli</i>	Zigansk			
	<i>B. ultimus</i>	Khovanstchina	<i>Pe. peejavi</i>		
	<i>B. costatus</i>	Ozerki			
	<i>B. ac. aculeatus</i>	Plavsk	<i>An. volnovachensis</i> <i>N. salebrosus</i>		
	<i>Pal. gr. expansa</i>		<i>Apathognathus-Po. irregularis</i>		
	<i>Pa. gr. manca</i>	Optukha	<i>M. buccera</i> <i>Pe. australis</i> <i>Pe. streeli</i>		
	<i>Pa. granulosus</i> <i>Pa. lechytaria</i> <i>Pa. trichytera</i> <i>Pa. rhomboides</i>	Lebedian	<i>Pe. curtus</i>		
	<i>Pa. gr. gracilis</i>	Eiets	<i>Pa. superlobata-Pa. wolskae</i>		
	<i>Pa. rhomboidea</i> <i>Pa. gl. pectinata</i> <i>Pa. crepida</i>	Zadonsk	<i>I. iowaensis</i>		
	<i>Pa. m. minuta</i> <i>Pa. del. platys</i> <i>Pa. subperlobata</i>	Volgograd			
Frasnian	<i>Pa. linguiformis</i>	Livny	Beds with <i>Po. aff. brevilaminus</i>		
	Upper <i>Pa. rhenana</i>	Evlanovo	Beds with <i>Po. brevis-Po. macilentus</i>		
	Lower <i>Pa. rhenana</i>	Voronezh	Beds with <i>Po. churkini-Po. komi</i>		
		Rechitsa	<i>Po. subincompletus</i>		
	<i>Pa. jamiae</i>				
	Upper <i>Pa. hassi</i>	Semiluki	Beds with <i>Po. aspelundi</i>		
	Lower <i>Pa. hassi</i>				
	<i>Pa. punctata</i>		<i>Po. efimovae</i>		
	<i>Pa. transitans</i>	Sargaevo	<i>A. alata-M. bogoslovskiy</i> <i>A. rotundiloba - A. africana</i>		
	<i>M. falsiovalis</i>	Timan	<i>Po. pennatus-Po. ljaschenkoi</i>		

Figure 5. Distribution of spiriferid brachiopods in the F–F interval of the East European Platform. For explanations see Fig. 3.

Stage	Standard Conodont Zone (Ziegler & Sandberg 1990, Spalletta et al. 2017)	Western Slope of Southern Urals Regional Horizon	Tchernyshev Swell (Bolshaja Synya River, Sher-Nyadeita River)		Subpolar Urals (Kozhym River, Syvyu River)	
			Brachiopod distribution (Persina 1962, Persina & Tsyganko 1980, Yudina 1997)			
			Rhynchonellide		Spiriferide	
Famennian	<i>Pr. kockeli</i>					
	<i>B. ultimus</i>	Lytva				
	<i>B. costatus</i>					
	<i>B. ac. aculeatus</i>					
	<i>Pal. gr. expansa</i>	Kushelga				
	<i>Pa. gr. manca</i>					
	<i>Pol. styriacus</i>					
	<i>Pa. granulosus</i> <i>Pa. lechytaria</i> <i>Pa. trichytera</i> <i>Pa. rhomboides</i>	Murzakaevo				
	<i>Pa. gr. gracilis</i>					
	<i>Pa. rhomboidea</i> <i>Pa. gl. pectinata</i> <i>Pa. crepida</i> <i>Pa. m. minuta</i> <i>Pa. del. platys</i> <i>Pa. subperlobata</i>	Makarovo				
Frasnian	<i>Pa. linguiformis</i>	Barma				
	Upper <i>Pa. rhenana</i>	Askyn				
	Lower <i>Pa. rhenana</i>	Mendym				
	<i>Pa. jamiae</i>					
	Upper <i>Pa. hassi</i>	Domaniuk				
	Lower <i>Pa. hassi</i>					
	<i>Pa. punctata</i>					
	<i>Pa. transitans</i>	Sargaevo				
	<i>M. falsiovalis</i>	Kyn				

Figure 6. Brachiopod distribution in the F–F interval of the Pechora Platform (Tchernyshev Swell) and Urals. For explanations see Fig. 3.

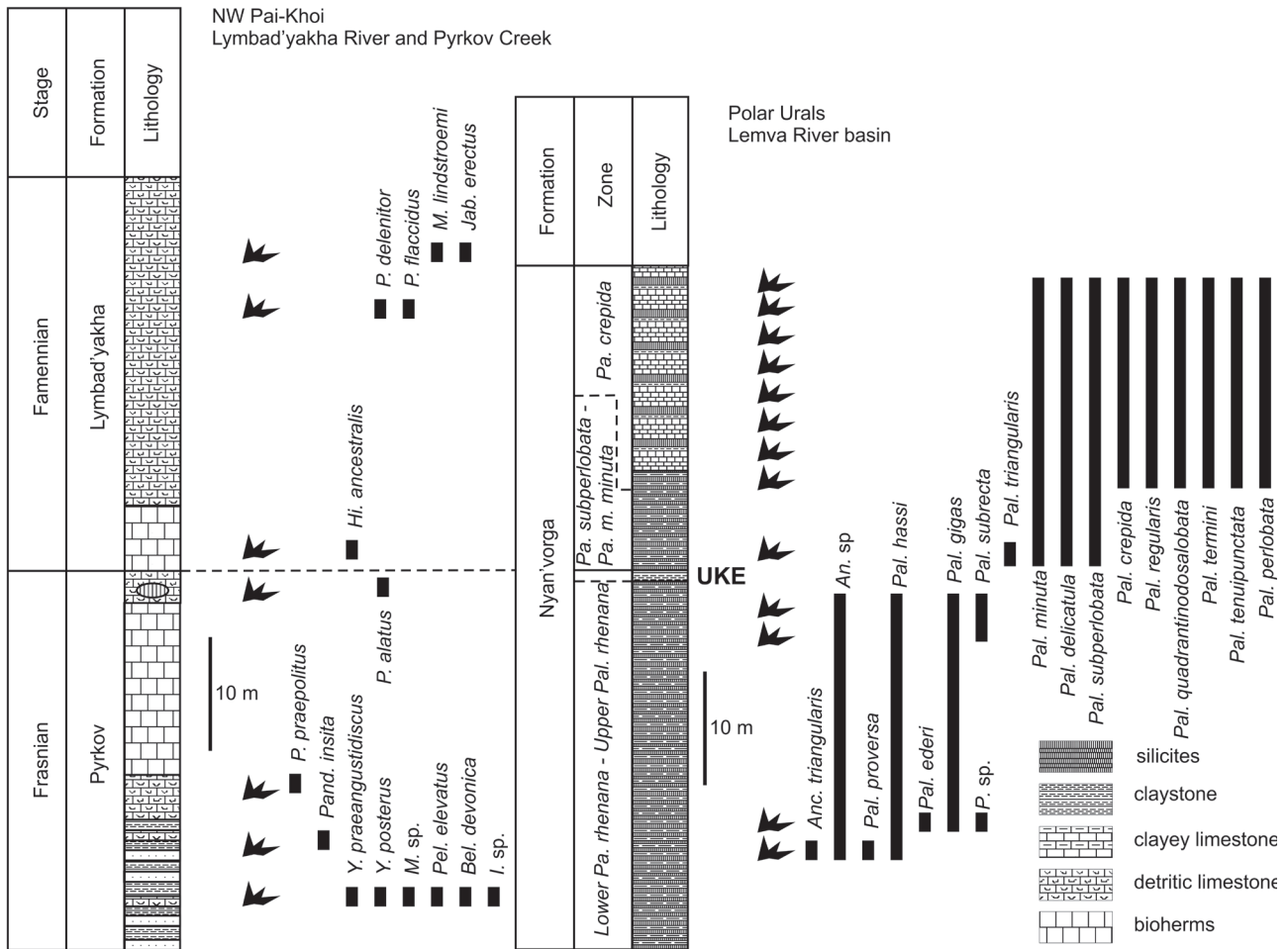


Figure 7. Lithology and conodont distribution in the F–F interval of the isolated carbonate platform (Lymbad'yakha River and Pyrkov Creek) and bathyal (Lemva River basin) sequences of the Pai-Khoi and Polar Urals (based on Zhuravlev *et al.* 2015 and Ovnatanova *et al.* 2017). Abbreviations: *Anc.* – *Ancyrognathus*, *An.* – *Ancyrodella*, *Bel.* – *Belodella*, *Hi.* – *Hindeodus*, *Jab.* – *Jablonnodus*, *Pand.* – *Pandorinellina*, *Pal.* – *Pelekysgnathus*, *Y.* – *Youngquistognathus*. For other explanations see Fig. 2.

Kononova 2008) (Appendix 1). It is notable that oxygen-deficient deep-water deposits span the wide stratigraphic interval that contains the upper Frasnian and the lower Famennian in this region.

Pechora Platform

Shallow-water shelf environment. – Boreholes of the north-western part of the Pechora Platform demonstrate similar successions in the F–F boundary interval. According to the data of Deulin (2006) the uppermost Frasnian, corresponding to Upper *Pal. rhenana* conodont Zone, is represented by bioclastic limestones containing glauconite and thin clay layers. Conodonts within these limestones consist of diverse polygnathids. The upper Frasnian limestones are overlain by dark-grey clays and clayey limestones containing early Famennian conodonts (Appendix 1).

Upper Devonian shallow-water deposits are exposed in the Tchernyshev Swell (eastern part of the Pechora Platform) as well (Tsyganko 2011). Late Devonian brachiopod faunas are known from Sher-Nadeyta River and Bolshaya Synya River sections (Fig. 6). Latest Frasnian brachiopods compose diverse associations (Appendix 2). Early Famennian brachiopods demonstrate less diversity (Pershina 1962).

North of Urals

Deep-water shelf environment. – A well-studied F–F transition section from the deep-water facies is represented by the Syvyu River section located in the Subpolar Urals (Yudina *et al.* 2002). The late Frasnian interval is composed of thin alternation of the dark-grey clayey limestones and limey siliceous shales, containing sponge

spicules, radiolarians, and scarce thin-shelled brachiopods. This interval is rich in conodonts represented by various palmatolepids (Appendix 1). The lowermost Famennian is similar in lithology and is composed of alternation of grey clayey limestones and limey siliceous shales, containing sponge spicules, radiolarians, thin-shelled brachiopods, and conodonts (Appendix 1). A black shale unit corresponds to the Upper Kellwasser Event (Yudina *et al.* 2002). The event is represented by the disappearance of most palmatolepids and polygnathids with the appearance of numerous and diverse representatives of the genus *Icriodus* and some palmatolepids (Yudina *et al.* 2002, Soboleva *et al.* 2018).

Isolated platform environment. – The F–F transition in the isolated carbonate platform facies was studied in the Northern Pai-Khoy Lymbad'yakha River section (Zhuravlev *et al.* 2015, Zhuravlev 2016) (Fig. 7). The uppermost Frasnian in the section is represented by cherty micritic limestones overlying the microbial and algal bioherms of the Pyrkov Formation. The limestone contains rare conodonts belonging to *Polygnathus alatus* Huddle. The lower Famennian disconformably overlies the Frasnian limestone that probably corresponds to the earliest Famennian regression. The successive early Famennian transgression is marked by microbial-stromatoporoid bioherms of the lowermost part of the Lymbad'yakha Formation, containing only *Hindeodus ancestralis* (Dzik) in bioherms, and more diverse association (six taxa) in the overlying bioclastic limestones (Appendix 1). The F–F boundary interval is characterized by interruption in development of the microbial bioherms accompanied by partial erosion of the terminal Frasnian and the lowermost Famennian.

Bathyal environment. – Deep-water bathyal sequences of the F–F transition are represented by successions of the Kharuta River basin, Polar Urals (Ovnatanova *et al.* 2017) (Fig. 7). The terminal Frasnian is composed here by carbonaceous cherty black shales that are barren of conodonts. The overlying lowermost Famennian, containing conodonts of the *Pal. subperlobata*–*Pal. minuta minuta* zones, is composed of greenish-grey clayey cherts and cherty shales (Ovnatanova *et al.* 2017). Black shale (carbonaceous cherty shales) sedimentation probably corresponds to the Kellwasser Event.

Siberia

Northern Siberia

Deep-water shelf environment. – The F–F transition in the northern Siberia region is well studied in the basin facies

only. The representative sections are located in the Taimyr Peninsula (Domba River section, Yolkin *et al.* 2006) and in the Lena River mouth (Stolb section, Yazikov *et al.* 2013) (Fig. 8).

The F–F interval in the Domba River section (73.435100° N, 82.455725° E) contains alternating grey shales and dark-grey micritic limestones with radiolarians. Shales contain lime concretions that yielded entomozoids, bivalves, and small brachiopod shells. The limestones contain earliest Famennian conodonts of *Pal. subperlobata*–*Pal. glabra pectinata* zones (Yolkin *et al.* 2006) (Appendix 1).

The Lena River section (71.953671° N, 127.159098° E) represents a basinal facies with clayey-carbonate sedimentation and increased palaeoseismicity (Yazikov *et al.* 2013). The F–F boundary beds contain mixed carbonate-volcaniclastic deposits (Fig. 8). The terminal Frasnian and lowermost Famennian deposits yield numerous brachiopods (Krylova 1959, 1962; Yazikov *et al.* 2013) (Appendix 2).

Latest Frasnian conodonts are unknown in this succession, but the early Famennian conodonts are represented by palmatolepids and icriodontids (Yazikov *et al.* 2013) (Appendix 1). A layer of black carbonaceous shales 70-cm-thick is considered as mark of UAE (Fig. 8).

North-eastern Siberia

Shallow-water shelf environment. – The Frasnian–Famennian transition in the shallow-water open shelf facies is known in the western part of Kolyma Uplift, Yasachnaya Rives basin section (64.507694° N, 151.230489° E) (Gagiev 2009) (Fig. 8). The upper Frasnian in this section is represented by clayey limestones with claystone and siltstone layers grading to clayey micritic laminated limestones. The deposits yield shallow-water conodonts marking Lower *Pal. rhenana*–*Pal. linguiformis* conodont zones (Appendix 1). Brachiopods were mentioned from the terminal Frasnian in the Yasachnaya and Eastern Khandyga Rivers sections, as well (Alekseeva 1967, Alekseeva *et al.* 1996) (Appendix 2).

The unit of clayey micritic laminated limestones in the upper part of this interval probably corresponds to the latest Frasnian (UKE) transgression. Overlying alternation of lime sandstones and claystones (5-m-thick), grading into alternating siliceous claystones and siltstones, corresponds to the earliest Famennian regression. These deposits contain numerous conodonts, which are characteristic of *Pal. subperlobata*–*Pal. termini* conodont zones (Appendix 1). The early Famennian brachiopods were found in the Khandyga River section (Alekseeva *et al.* 1996) (Appendix 2).

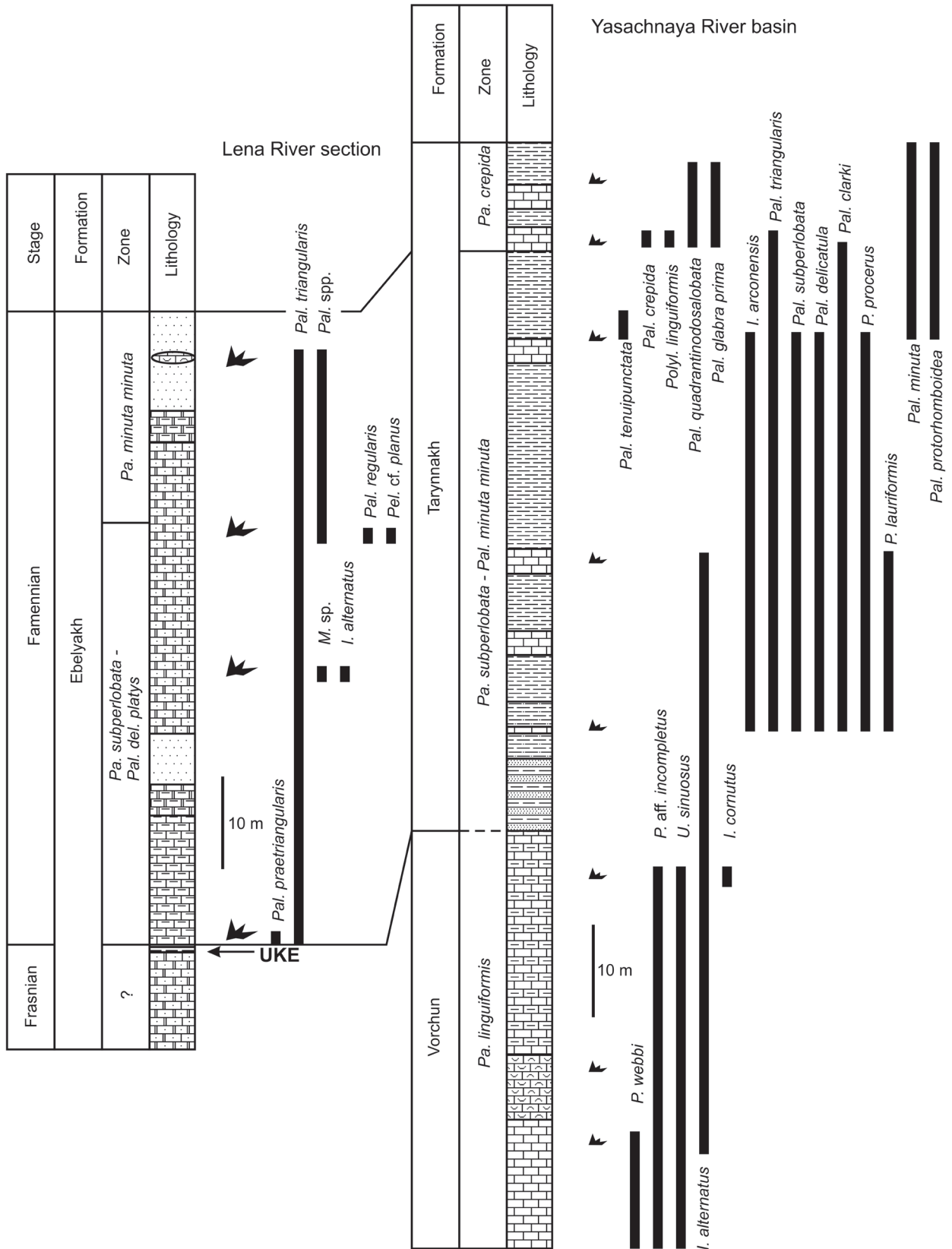


Figure 8. Lithology and conodont distribution in the F–F transition in northern Siberian sequences (based on Yazikov *et al.* 2013, and Gagiev, 2009). For explanations see Fig. 7.

Deep-water shelf environment. – The deep-shelf succession of this region was reported by Gagiev (2009) in the Burgali-Kamenka section (64.271122° N, 153.660630° E) (eastern part of the Kolyma Uplift). The terminal Frasnian in this section contains alternating sandstones and dark-grey shales with conodonts of the *Pal. linguiformis* conodont Zone (Appendix 1). The lowermost Famennian is represented by dark-grey limey and silty shales with lenses of fine-grained limestones containing the early Famennian conodont associations (Appendix 1). In addition, late Frasnian–middle Famennian (*Pal. linguiformis*–*Pal. marginifera marginifera* zones) tuffs and volcanoclastic deposits, as well as late Frasnian (Upper *Pal. rhenana* conodont Zone) local basalts in the Vorchun Fm., are known in the eastern part of the Prikolymian Uplift, NE Siberia. The Kedon Fm., composed of Middle–Upper Devonian rhyolitic and subalkaline volcanic rocks and basalt sheets, is widespread in the Omolon Uplift of NE Siberia (Gagiev 2009).

Facies and biota changes at the F–F transition

Shallow-water sequences commonly demonstrate disconformities and hiatus at the F–F boundary (Aleksiev *et al.* 1996). Subsequent transgression caused start of the shallow-water sedimentation at the *Pal. minuta minuta*–*Pal. crepida* conodont zones. In case of continuous F–F sequences (*e.g.* Yasachnaya River section, Kolyma Uplift, Siberia) the terminal Frasnian UK transgression is marked by a unit of clayey, micritic, laminated limestones.

In the deep-water facies, including troughs on the shelf, the UAE is marked by black shale (carbonaceous cherty shales, cherts, or laminated limestones) sedimentation followed by grey clayey cherts and cherty shales intercalating with calciturbidites. Some northern Siberia sequences (*e.g.* Lena River section) contain volcanoclastic deposits as well, but not in the narrowed F–F interval.

Conodonts

The F–F transition demonstrates weak palaeolatitude gradient in changes of conodont associations. Slightly lower conodont diversity observed in the shelf basins of Siberia is due to poor sample coverage: there are very few papers dealing with conodonts from the North Siberian deposits of this age.

The deep-water and open shelf successions of all the regions under consideration demonstrate conodont associations composed mainly of cosmopolitan species of *Palmatolepis*. The shallow-water successions as a rule

possess stratigraphic gaps (unconformity) comprising uppermost Frasnian (*Pal. linguiformis* Zone) and lower part of the Famennian (*Palmatolepis subperlobata*–*Pal. triangularis* zones). The conodont associations dominated by *Polygnathus* and *Icriodus* show a diversity decrease during the late Frasnian. The early Famennian conodonts are represented mainly by species of *Icriodus*, cosmopolitan species of *Polygnathus* (*e.g.* *Polygnathus brevilaminus*), and specific taxa characterized by their conform elements (*Mitrellataxis* and *Jablonnodus*) (Fig. 9).

Globally the gradual decrease in conodont diversity occurred during the Late *Pal. rhenana*–*Pal. triangularis* interval (Ziegler & Lane 1987, Schülke 1998). The Frasnian conodont taxa, including *Ancyrodella*, most species of *Palmatolepis*, *Polygnathus*, *Icriodus*, and *Ancyrognathus*, became extinct. The dramatic decrease in conodont diversity occurred in the *Pal. linguiformis* conodont Zone when about 50% of conodont species disappeared and at the start of the *Pal. subperlobata* conodont Zone when about 70% of conodont species became extinct (Ziegler & Lane 1987). The early Famennian recovery of conodont diversity began at the *Pal. delicatula platys* conodont Zone preceding the radiative phase in the *Pal. minuta minuta* conodont Zone (Ziegler & Lane 1987).

The recovering conodont communities in the Famennian shallow-water facies are very specific and partly endemic. Icriodontids of *Icriodus iowaensis* group, *Mitrellataxis*, and *Jablonnodus* dominate the unique associations. It is notable that the recovery faunas demonstrate extremely wide ranges of $\delta^{13}C_{org}$ in conodont elements of *Icriodus* (from -27.9‰ to -23.1‰), *Mitrellataxis* (from -27.9‰ to -23.6‰), and *Jablonnodus* (from -28.1‰ to -23.1‰). The high variability of carbon isotope composition in conodont organic matter suggests unstable trophic relations in the post-crisis shallow-water ecosystems, probably due to rapid expansion of survivors into vacant ecospace (see also Sandberg *et al.* 1988, Racki *et al.* 2002, Zhuravlev & Smoleva 2018). Appearance of icriodontids in deep-water associations seems to be the result of their post-crisis ecological expansion into the niches of eliminated taxa (biofacies telescoping of Sandberg *et al.* 1988, compare Huang *et al.* 2018), or transport of the shallow-water conodont elements to deep-water environment by intensive calciturbidite currents in the early Famennian eustatic lowstand.

Brachiopods

Late Devonian strata of northern Laurussia are characterized by taxonomically diverse and abundant brachiopods, in contrast to the mid-latitude sequences of Siberia, which contain few brachiopods (West Siberia, northern Siberia, north-eastern Siberia) or do not contain them at all (east

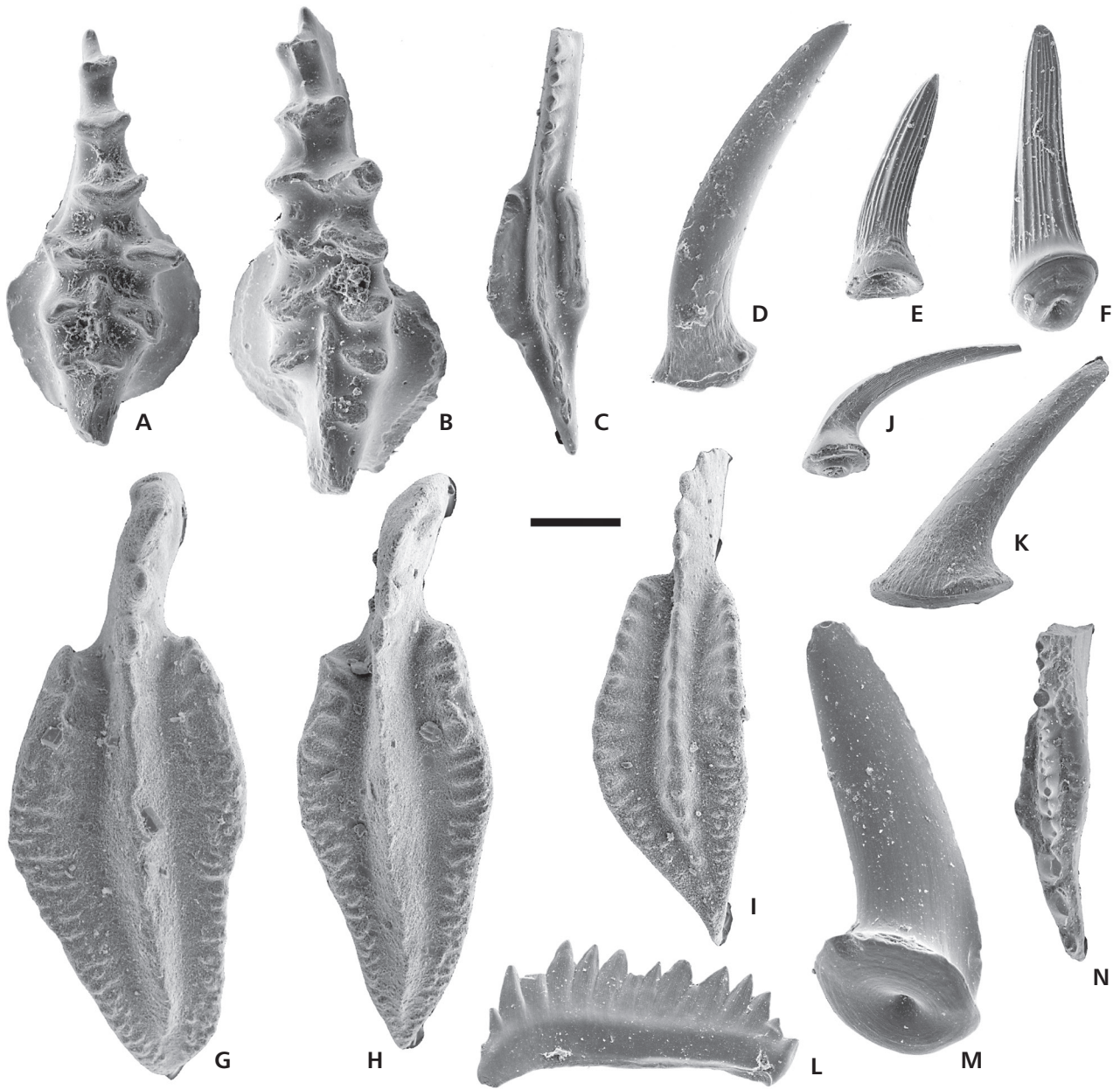


Figure 9. Characteristic conodonts from the F–F transition interval of the Voronezh Uplift, East European Platform. • A – *Icriodus iowaensis iowaensis* Youngquist et Peterson 1947, specimen 713/1, Zadonsk Fm., lower Famennian, Kamenka Quarry. • B – *Icriodus iowaensis ancylus* Sandberg et Dreesen 1984, specimen 713/2, Zadonsk Fm., lower Famennian, Kamenka Quarry. • C, N – *Polygnathus brevilaminus* Branson et Mehl, Zadonsk Fm., lower Famennian, Kamenka Quarry; C – specimen 713/3; N – specimen 713/23. • D – *Jablonnodus erectus* Dzik 2006, specimen 713/7, Zadonsk Fm., lower Famennian, Russkiy Brod Quarry. • E, F – *Mitrellataxis conoidalis* Dzik 2006, Zadonsk Fm., lower Famennian, Russkiy Brod Quarry; E – specimen 713/8; F – specimen 713/10. • G, H – *Polygnathus colliculosus* Aristov 1985, Livny Fm., upper Frasnian, Kamenka Quarry; G – specimen 713/20; H – specimen 713/17. • I – *Polygnathus reitlingeræ* Ovnatanova et Kononova 2008, specimen 713/19, Livny Fm., upper Frasnian, Kamenka Quarry. • J – *Jablonnodus oistodiformis* Dzik 2006, specimen 713/16, Livny Fm., upper Frasnian, Kamenka Quarry. • K, M – *Mitrellataxis circularis* (Wang et Wang 1978), Zadonsk Fm., lower Famennian; K – specimen 713/21, Kamenka Quarry; M – specimen 713/11, Russkiy Brod Quarry. • L – *Mehlina kielcensis* Dzik 2006, specimen 713/13, Zadonsk Fm., lower Famennian, Russkiy Brod Quarry. Scale bar is 0.2 mm.

of the Altai-Sayan region). Therefore, the Late Devonian deposits of western Siberia (Kuznetsk Basin), with the most complete of brachiopod successions (Fig. 10), are important for the analysis of the brachiopod turnover

during the F–F crisis interval in the northern mid-latitudes. These brachiopod faunas were studied in detail (Rzhonsnitskaya 1968, 1975; Rzhonsnitskaya *et al.* 1998; Modzalevskaya *et al.* 2013).

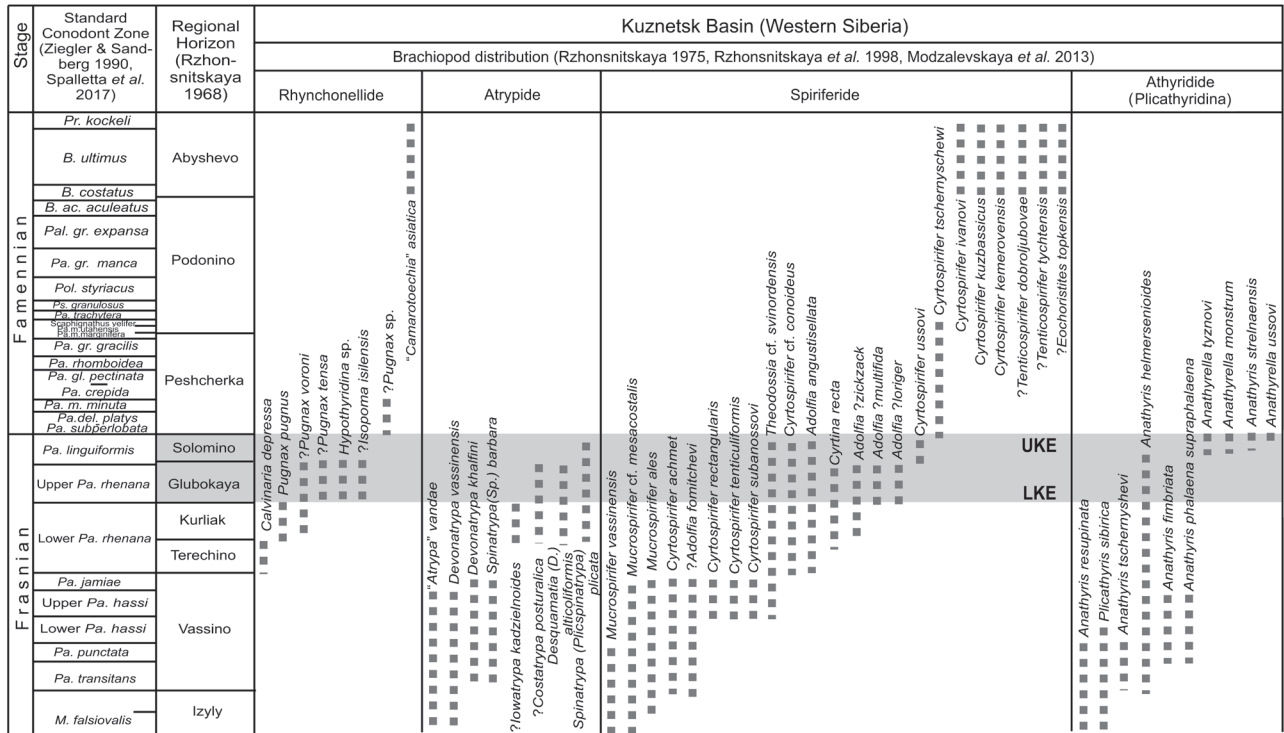


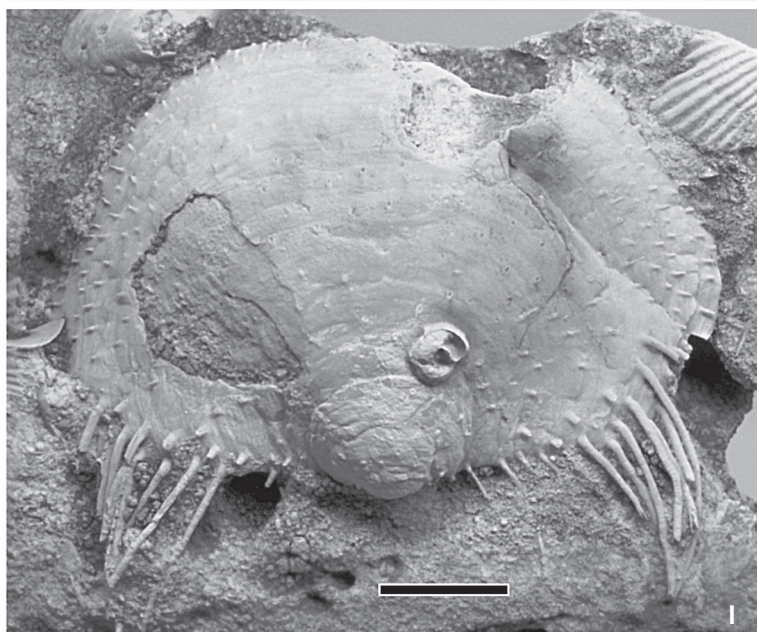
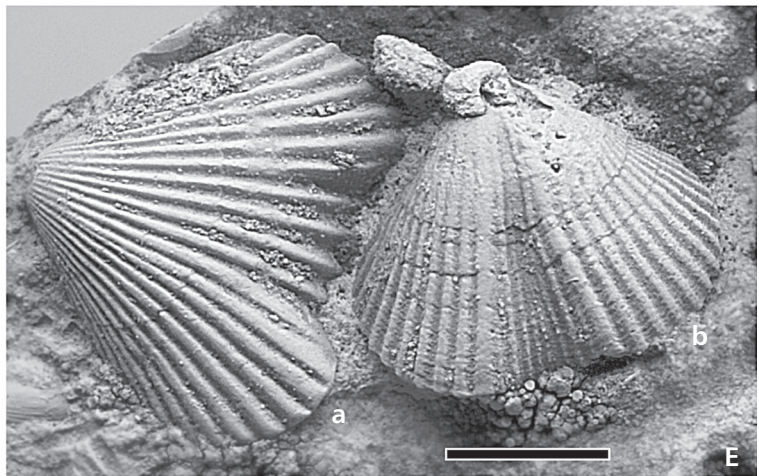
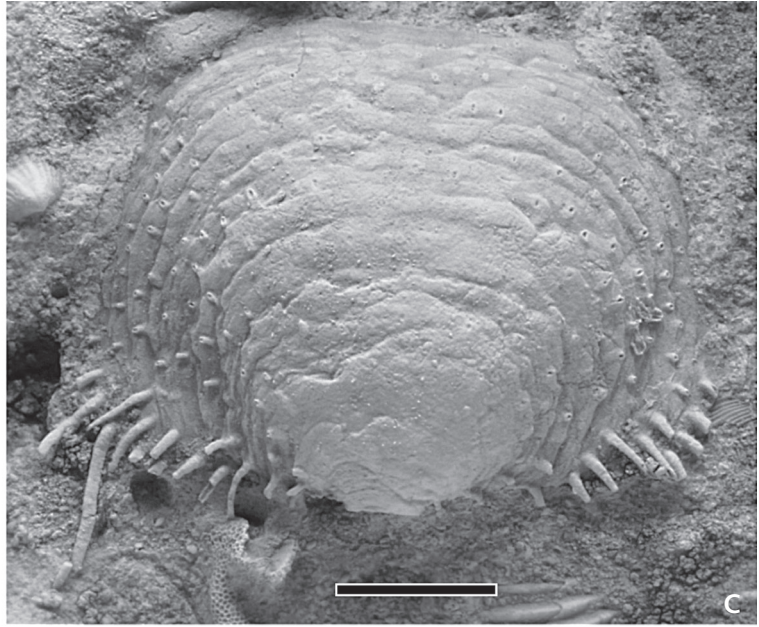
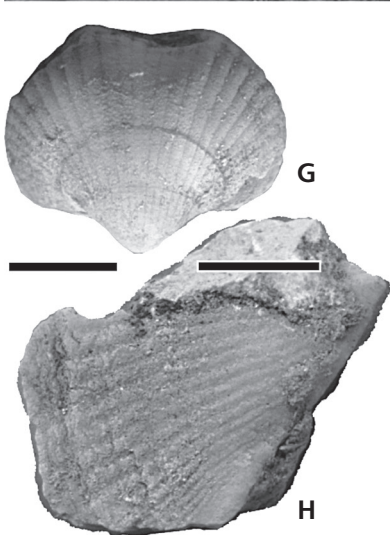
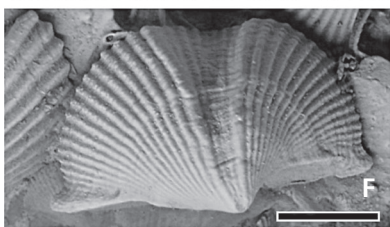
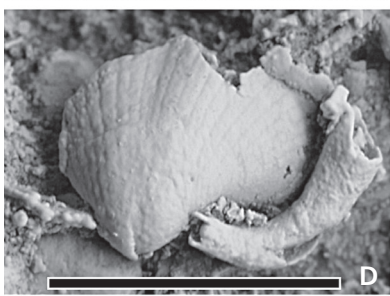
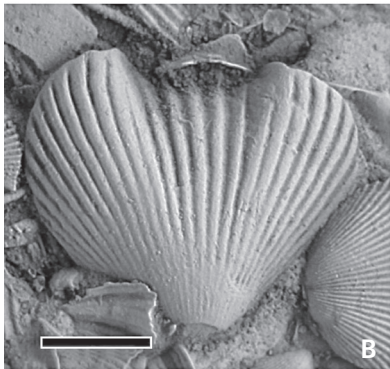
Figure 10. Brachiopod distribution in the F–F interval of the Kuznetsk Basin (West Siberia). For explanations see Fig. 3.

Most informative are the late Frasnian and early Famennian brachiopod sequences of north-eastern Laurussia located in the East European Platform (EEP), Pechora Platform, and Urals. In the central regions of the EEP and Volga-Ural area the late Frasnian (*Pal. linguiformis* conodont Zone) brachiopod fauna is extremely depleted and represented by two taxa: *Cyrtospirifer tribulatus* and *Theodossia* sp. (Figs 5, 11). This situation differs significantly from the contemporary brachiopod fauna of the western slope of South Urals and the north-eastern Pechora Platform (Tchernyshev Swell) (Fig. 6). The late Frasnian brachiopod association of SW Urals is more diverse and contains 15 species of *Gypidula*, “*Hypothyridina*”, “*Pugnax*”, *Desquamatia*, *Radiatrypa*, *Costatrypa*, *Pseudoatrypa*, *Spinatrypa*, *Iowatrypa*, *Theodossia*, *Warrenella*, *Cyrtospirifer*, *Adolphia*, and *Cryptonella* (Abramova 1999). This association is close to those of the Tchernyshev Swell (Fig.6) (Perschina 1962). The late Frasnian *Iowatrypa*, *Costatrypa*, *Radiatrypa*, and *Desquamatia* are common in SW Ural, north-western

Pechora Platform, and West Siberia (Kuznetsk Basin) (Fig. 10), and they were reported from the shallow-water sequences of the southeastern Laurussia (South Poland, Holy Cross Mountains) (Racki & Baliński 1998, Baliński 2002). *Iowatrypa* and *Costatrypa* are known from the Ardennes; *Desquamatia*, *Radiatrypa*, *Iowatrypa*, and *Costatrypa* were reported from China as well (Racki 1998b).

The late Frasnian brachiopod associations of northern Laurussia (EEP, Pechora Platform, Urals, and Novaya Zemlya) and Siberia contain cyrtospiriferids and theodossiids. In the EEP and Novaya Zemlya species of *Theodossia* occur in almost the entire middle and late Frasnian interval (*Pal. punctata*–*Pal. linguiformis* conodont zones) (Nalivkin 1947, Rzhonsnitskaya 1988, Bezgodova 2015). In Arctic Siberia the representatives of *Theodossia* are distributed in the late Frasnian deposits of the Lena, Kulymbe, Kotuy, and Maimecha river basins (Krylova 1962). In contrast to the cosmopolitan *Cyrtospirifer*, the distinctive *Theodossia* was limited to northern Laurussia

Figure 11. Characteristic brachiopods from the F–F transition interval of the Voronezh Uplift, East European Platform (Russkiy Brod Quarry). • A, F – *Cyrtospirifer zadonicus* Ljaschenko 1959, Zadonsk Fm., lower Famennian; A – specimen 713/25; F – specimen 713/31. • B – *Ripidiorhynchus huotinus* (Verneuil 1845), specimen 713/26, Zadonsk Fm., lower Famennian. • C, I – *Donalossia multispinosa* (Sokolskaja 1948), Zadonsk Fm., lower Famennian; C – specimen 713/27; I – specimen 713/34. • D, G – *Theodossia* sp., Zadonsk Fm., lower Famennian; D – specimen 713/28, [a – *Ripidiorhynchus huotinus* (Verneuil 1845), specimen 713/29], [b – *Cyrtospirifer zadonicus* Ljaschenko 1959, specimen 713/30]; G – specimen 713/32. • H – *Cyrtospirifer tribulatus* Ljaschenko 1959, specimen 713/33, Livny Fm., upper Frasnian. Scale bar is 5 mm.



and Siberia. The late Frasnian *Theodossia* from South Poland (Baliński 2002) and South China (Ma *et al.* 2006) needs revision, as well as “*Theodossia*” *hungerfordi* from the Lime Creek Formation (Iowa, North America). However, true *Theodossia* probably occur in the late Frasnian of western Canada (southwestern Laurussia) (McLaren *et al.* 1962).

The Frasnian brachiopod faunas of western Siberia (Kuznetsk Basin) contain diverse and abundant plicathyridines; the endemic species of *Anathyrella* are typical for the late Frasnian sequences of this area only (Fig. 10). Nowhere else in the basins of the northern and southern hemispheres are plicathyridines recorded in the terminal Frasnian, but rather in the lower and middle Frasnian (Mottequin *et al.* 2016).

The late Frasnian sequences of the eastern Pechora Platform and South Urals contain *Warrenella*, which are also known from the South Poland, Belgium, and North America. The globally distributed (South Poland, France, Australia, New Mexico) epiplanktonic chonetid *Retichonetes armata* was found in the terminal Frasnian of the Stolb Island section (Lena River, Arctic Siberia) (Yazikov *et al.* 2013).

The early Famennian brachiopod faunas of the EEP are poorly developed. In the Central region of the EEP and Volga-Ural areas, the early Famennian deposits contain nine species of *Schuchertella*, *Plicochonetes*, *Chonopectus*, *Donalosisa*, *Productella*, *Paromoeopygma*, *Ripidiorhynchus*, and *Cyrtospirifer* (see Ljaschenko 1959, Appendix 2). According to data of Abramova (1999), the coeval brachiopod faunas from SW Ural are represented only by four species (Appendix 2). The concurrent brachiopods from the Kuznetsk Basin (West Siberia) are represented by six species (Rzhonsnitskaya 1968) (Appendix 2).

The early Famennian sequences of northern Siberia are poorly characterized by brachiopods except at the Stolb section (Lena River). The brachiopods from this section have very poor preservation, and therefore they are difficult to be reliably identified (Appendix 2). Among them, *Parapugnax markovskii* is known from early Famennian strata of the SW Urals, Pai-Khoi, and northern Siberia. *Cyrtospirifer tchernyschewi* is widely distributed in the Arctic regions of Russia and in Kazakhstan. Thus, the late Frasnian and early Famennian brachiopod assemblages of low and middle latitudes of the northern hemisphere have numerous common elements that indicate similar habitats.

The detailed study of the oxygen and carbon isotope ratios in the Kosoy Utyos section (Kuznetsk Basin, West Siberia) shows the presence of a carbon isotopic anomaly in the early Famennian mid-latitude deposits. The higher $\delta^{13}\text{C}_{\text{carb}}$ values in the Kosoy Utyos section, as compared with the equatorial sections, might be due to the lower temperatures of the depositional basin (Izokh

et al. 2009). Cooling pulse may occur across the F–F boundary interval (Copper 1998, Averbuch *et al.* 2003, Riquier *et al.* 2016, Huang *et al.* 2018), which led to the final extinction of the late Frasnian tropical brachiopod faunas and the emergence of taxa more resistant to the low temperature regime during the earliest Famennian. Therefore, the climatic change should have affected tropical and mid-latitude faunas in different degree, finally producing clear palaeolatitudinal gradient in diversity and taxonomical composition. Copper (1998) supposed that the main causes of the disappearance of the tropical order Atrypida at the end of the Frasnian were a cooling event and a regressive episode. Decrease in size of some shells of adult brachiopods may be a consequence of the temperature drop. The “Liliput” phenomenon among early Famennian brachiopods in south Poland was reported by Baliński & Racki (1999). The late Frasnian small forms of *Theodossia* are known in the Voronezh Uplift (EEP) sequences. Modzalevskaya *et al.* (2013) reported small athyrididines from the early Famennian recovery interval of the Kuznetsk Basin, as well as Krylova (1959) from the F–F interval of the Stolb Island (northern Siberia). Small size of adult brachiopod forms can also be associated with poorly oxygenated environments. However, evident record of UKE anoxia is recognized in few of the above-mentioned domains, such as the Stolb Island (Lena River) section (Yazikov *et al.* 2013).

Discussion

The bathyal sequences of the tropical realm contain poor associations of the pelagic conodont fauna in both the upper Frasnian and lower Famennian (Rodríguez-Cañero & Martín-Algarra 2014, Ovnanatova *et al.* 2017). The associations comprise cosmopolitan species over the Laurussia and Siberia realms. Numerous conodonts in the deep-water deposits are known just from the calciturbidites and represent reworked, taphonomically enriched and mixed associations. Subautochthonous deep-water conodont associations known from the siliceous and shale deposits are taxonomically poor and composed of cosmopolitan palmatolepid species. Palaeolatitudinal trend in composition of the deep-water conodont associations is not clear. Generally conodonts demonstrate higher diversity in the tropical realm in both crisis and post-crisis intervals, and in shallow-water and deep-water environments (Fig. 12). The decrease in diversity of the associations at mid-latitudes may be due to lack of data on the sections of Siberia and north-eastern Eurasia. Simple statistical analysis demonstrates contingency in the conodont diversity changes at the F–F boundary in the low and middle latitudes ($\text{Chi}^2 = 4.9014$, $p = 0.17916$, degrees freedom = 3).

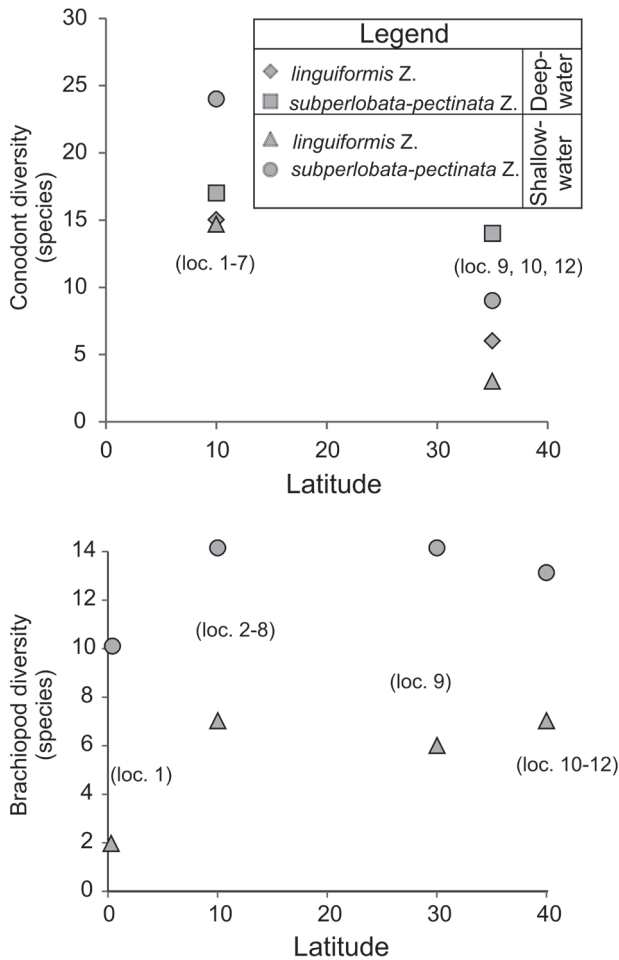


Figure 12. Conodont and brachiopod diversity in F–F boundary interval over the facies and palaeolatitudinal gradient in the northern hemisphere (NE Laurussia and Siberia). Numbers in parentheses refer to localities in Fig. 1.

Low and middle latitude brachiopods in the northern hemisphere demonstrated a generally similar evolutionary trend during the late Frasnian and early Famennian. Significant taxonomic reduction of the brachiopod associations occurred in the KW Crisis mainly due to a decrease in speciation rates, not elevated extinction rates (Stigall 2010). The earliest Famennian (recovery) associations were of low diversity and consisted of Productida, Rhynchonellida, and Spiriferida, similar to those of the southern hemisphere (Baliński & Racki 1999). Approximately the same taxonomic framework is characteristic of the early Famennian of central Hunan (Ma *et al.* 2002). It seems that cyrtospiriferids and rhynchonellids, such as late Frasnian and early Famennian representatives of *Ripidiorhynchus* from the EEP (Sokiran 2002), were invasive taxa characterized by broad environmental tolerance (see also Stigall 2012, 2013). In South Polish carbonate shelf, persistent competition from

expansive productid-cyrtospiriferid-athyrid associations is highlighted by Racki (1998b). It is notable that shelly benthos shows a low latitudinal selectivity in F–F extinction and recovery (Fig. 12) that suggests low influence of the climatic changes on the extinction pattern (Reddin *et al.* 2019).

Thus both the brachiopods (benthos) and conodonts (nekton) demonstrate weak or absence of obvious palaeolatitudinal gradient in F–F extinction and recovery in the northern hemisphere. This suggests low influence of the fluctuations in climate and regional circulation pattern on the fauna diversity changes at the F–F boundary interval. This conclusion is supported by data on the Late Devonian marine phytoplankton. The phytoplankton demonstrates high similarity over the “Boreal Realm” comprising eastern Laurussia and Siberia (Shen *et al.* 2018).

Eustatic fluctuations, which were regionally disturbed by tectonics (Hallam & Wignall 1999), cannot be considered as a global trigger of the biotic changes. In general perspective, it seems that the latest Frasnian decrease in fauna diversity in the Siberian and north-eastern Laurussia realms was caused by environment changes triggered by volcanic eruptions in the Vilyui LIP, associated with palaeorift system (Kiselev *et al.* 2006). Other East European LIPs and diverse volcanism recorded in successions of the Omolon Uplift (Gagiev 2009, Kravchiński 2012) should also be noted. The paroxysmal effusive activity promoted climate destabilization, and ultimately led to turnover in global oceanic circulation towards stagnation and anoxia (Ernst & Youbi 2017, Racki *et al.* 2018). On the other hand, overall correspondence of carbonate facies setting and benthic/nektonic biota of the both studied continents is a noteworthy implication from this study. Thus, the assumed cataclysmic impact of large-scale flood basalt and kimberlite eruptions is difficult to recognize in litho- and biofacies specificity in the regional scale, even if supported by presence of the carbonate-volcaniclastic deposits in the most proximal Lena River section (Yazikov *et al.* 2013) as well as carbonate-siliciclastic and volcaniclastic deposits with gypsum evaporates of the Vilyuchan Formation in the Vilyuy Depression (Rusetskaya & Belenitskaya 1990).

Conclusions

(1) Generally conodonts demonstrate higher diversity in the tropical realm in both KW Crisis and post-crisis intervals, both in shallow-water and deep-water habitats, paired with contingency in the diversity changes at the F–F boundary over the low to middle latitudes of the northern hemisphere. Palaeolatitudinal trend in composition of the conodont associations is also not very clear.

(2) Coeval brachiopod faunas of low and middle latitudes have numerous common elements. They show low latitudinal selectivity in F–F extinction and recovery, that suggests surprisingly moderated ecological effect in the shelly benthos of the rapid climatic shifts during the KW Crisis, with probable exception of the Lilliput effect. Cyrtospiriferids and rhynchonellids, such as *Ripidiorhynchus* from the EEP, were likely invasive taxa.

(3) Summarizing, high similarity of the composition and stratigraphic succession of nektonic (conodonts) and benthic (brachiopods) biota, which dwelt the low- and mid-latitude realms during the F–F biotic crisis, suggests low environment gradients in the northern hemisphere (Fig. 12). Carbonate sedimentation dominantly developed in the shallow-water basins of different latitudes, which implies low temperature and precipitation variations between 10° S and 40° N. The biotic and facies patterns suggest that global causes of the biotic crisis were partly affected by local and regional environment changes, but surprisingly not when they were driven by so catastrophic trigger as flood basalt eruptions of the Viluy LIP.

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Appendix 1. List of conodont taxa in the late Frasnian and early Famennian.

East European Platform, Voronezh Uplift (Zatoń *et al.* 2014; new data)

Latest Frasnian: *Polygnathus krestovnikovi* Ovnatanova, *P. makhlinae* Kirilishina et Kononova, *P. krutoensis* Kirilishina et Kononova, *P. unicornis* Muller et Muller, *P. azigomorphus* Aristov, *P. colliculosus* Aristov, *P. webbi* Stauffer.

Early Famennian: *Palmatolepis subperlobata* Branson et Mehl, *Polygnathus brevilaminus* Branson et Mehl, *P. aff. P. izhmensis* Kuzmin, *P. aspelundi* Savage et Funai, *P. subnormalis* Vorontsova et Kuz'min, *P. ex gr. P. tigrinus* Kuzmin et Melnikova, *P. ovatus* Helms, *Mehlina fitzroyi* (Druce), *Meh. kielcensis* Dzik, *Icriodus iowaensis* Youngquist et Peterson, *I. cornutus* Sannemann, *Mitrellataxis conoidalis* Dzik, *Mit. circularis* (Wang et Wang).

East European Platform, Volga-Ural Uplift (Ovnatanova & Kononova 2008)

Latest Frasnian: *Palmatolepis foliacea* Youngquist, *Pal. subrecta* Miller et Youngquist, *Pal. nasuta* Muller, *Pal. juntionensis* Han, *Pal. praetriangularis* Sandberg et Ziegler, *Ancyrodella ioides* Ziegler, *Polygnathus brevis* Miller et Youngquist.

Early Famennian: *Palmatolepis subperlobata* Branson et Mehl, *Pal. linguiloba* (Dzik), *Pal. triangularis* Sannemann, *Pal. platys* Ziegler et Sandberg, *Pal. delicatula* Branson et Mehl.

Pechora Platform (Deulin 2006, Tsyganko 2011)

Latest Frasnian: *Ctenopolygnathus brevilamiformis* (Ovnatanova), *Polygnathus aequalis* Klapper et Lane, *P. brevis* Miller et Youngquist, *P. churkini* Savage et Funai, *P. imparilis* Klapper et Lane, *P. krestovnikovi* Ovnatanova, *P. planarius* Klapper et Lane, *P. politus* Ovnatanova, *P. unicornis* Muller et Muller.

Early Famennian: *Icriodus alternatus* Branson et Mehl, *I. cornutus* Sannemann, *I. iowaensis* Youngquist et Peterson, *Pelekysgnathus inclinatus* Thomas, *Mehlina* sp., *Polygnathus tigrinus* Kuz'min et Melnikova.

North of Urals (Yudina *et al.* 2002, Tsyganko 2011, Ovnatanova *et al.* 2017, Soboleva *et al.* 2018)

Latest Frasnian: *Polygnathus decorosus* Stauffer, *Palmato-*

lepis subrecta Miller et Youngquist, *Pal. hassi* Muller et Muller, *Pal. bogartensis* (Stauffer), *Pal. timanensis* Klapper, Kuz'min, Ovnatanova, *Pal. kireevae* Ovnatanova, *Pal. juntianensis* Han, *Pal. nasuta* Muller, *Pal. rhenana* Bischoff, *Pal. mucronata* Klapper, Kuz'min et Ovnatanova, *Pal. brevis* Ziegler et Sandberg, *Pal. ederi* Ziegler et Sandberg, *Pal. linguiformis* Muller, *Pal. semichatovae* Ovnatanova, *Pal. boogardi* Klapper et Foster, *Ancyrodella* sp. (originally diagnosed as *Ancyrodella nodosa*).

Early Famennian: *Icriodus alternatus* Branson et Mehl, *I. deformatus* Hun, *I. aff. I. helmsi* Sandberg et Dreesen, *Palmatolepis praetriangularis* Ziegler et Sandberg, *Pal. triangularis* Sannemann, *Pal. clarki* Ziegler, *Pal. protorhomboidea* Sandberg et Ziegler, *Pal. delicatula* Branson et Mehl, *Pal. quadrantinodosalobata* Sannemann, *Pal. minuta* Branson et Mehl, *Ctenopolygnathus brevilamiformis* (Ovnatanova) (originally diagnosed as *Polygnathus angustidiscus*).

Northern Pai-Khoi (Zhuravlev *et al.* 2015, Zhuravlev 2016)

Latest Frasnian: *Polygnathus alatus* Huddle.

Early Famennian: *Hindeodus ancestralis* (Dzik), *Polygnathus delinitor* Drygant, *P. auriformis* Drygant, *P. flaccidus* Helms, *Mehlina lindstroemi* Matveeva, Zhuravlev, Eremenko, *Jablonnodus erectus* Dzik, *Pandorinellina* sp.

Northern Siberia, Taimyr Peninsula (Yolkin *et al.* 2006)

Early Famennian: *Palmatolepis glabra pectinata* Ziegler, *Pal. glabra prima* Ziegler et Huddle, *Pal. subperlobata helmsi* Ovnatanova, *Pal. subperlobata subperlobata* Branson et Mehl, *Pal. minuta* Branson et Mehl, *Pal. quadrantinodosalobata* Sannemann.

Lena River (Yazikov *et al.* 2013)

Early Famennian: *Palmatolepis triangularis* Sannemann, *Pal. praetriangularis* Ziegler et Sandberg, *Pal. regularis* Cooper, *Pal. sp.*, *Icriodus alternatus alternatus* Branson et Mehl, *Mehlina* sp., *Pelekysgnathus* cf. *Pel. planus* Sannemann.

Northeastern Siberia, western part of the Kolyma Uplift (Gagiev 2009)

Latest Frasnian: *Polygnathus webbi* Stauffer, *P. aff. P. incompletus* Uyeno, and *Uyenognathus sinuosus* (Szulczewski)

Early Famennian: *Polygnathus brevilaminus* Branson et Mehl, *P. aspelundi* Savage et Funai, *P. procerus* Sannemann, *P. lauriformis* Dreesen et Dusar, *Palmatolepis triangularis* Sannemann, *Pal. subperlobata subperlobata* Branson et Mehl, *Pal. subperlobata helmsi* Ovnatanova, *Pal. delicatula* Branson et Mehl, *Pal. clarki* Ziegler.

Northeastern Siberia, eastern part of the Kolyma Uplift (Gagiev 2009)

Latest Frasnian: *Palmatolepis* cf. *Pal. hassi* Muller et Muller, *Pal. “gigas”* Miller et Youngquist, *Pal. cf. Pal. linguiformis* Muller, *Pal. sp.*, *Pal. praetriangularis* Ziegler et Sandberg, *Ancyrodella* sp. (reported by Gagiev 2009 as *Ancyrodella nodosa*)

Early Famennian: *Mehlina lindstroemi* Matveeva, Zhuravlev, Eremenko (reported by Gagiev 2009 as *Polygnathus norrisi*), *Pal. triangularis* Sannemann, *Pal. subperlobata* Branson et Mehl, *Pal. delicatula* Branson et Mehl, *Pal. clarki* Ziegler, *Pal. tenuipunctata* Sannemann, *Pal. minuta minuta* Branson et Mehl, and *Pelekysgnathus serratus* Jentzsch.

Appendix 2. List of brachiopod taxa in the late Frasnian and early Famennian.

East European Platform, Voronezh Uplift (Ljaschenko 1959; new data)

Latest Frasnian: *Cyrtospirifer tribulatus* Ljaschenko and *Theodossia* sp.

Early Famennian: *Schuchertella koscharica* (Nalivkin), *?Plicochonetes nanus* (Verneuil), *Chonopectus elcicus* (Nalivkin), *Donalosisa multispinosa* (Sokolskaja), *D. koscharica* (Sokolskaja), *Productella herminae* Frech, *Paromoeopygma koscharica* (Nalivkin), *Ripidiorhynchus huotinus* (Verneuil), *Cyrtospirifer zadonicus* Ljaschenko.

Pechora Platform (Perschina 1962, Tsyganko 2011)

Latest Frasnian: *Gypidula askynica* Nalivkin, *Chonetes* sp., *Hypothyridina* sp., *Radiatrypa magnitica* (Nalivkin), *Desquamatia (D.) alticoliformis* Rzonitskaya, *?Costatrypa posturalica* (Markovskii in Mikryukov), *Adolfia* sp., *Warrenella (W.) koltubanica* (Nalivkin), *Cyrtospirifer markovskii* (Nalivkin), *Theodossia katavensis* (Nalivkin).

Early Famennian: *Ripidiorhynchus* sp., *Plectorhynchella* sp., *Dzieduszyckia baschkirica* (Tschernyschew) *?Leiorhynchus ursus* (Nalivkin), *Pugnax biloba* (Rozman), *Dmitria subrotunda* (Tcherkesova), *Cyrtospirifer* sp.

South Urals (Abramova 1999)

Early Famennian: *Athyris spiriferoides* Eaton, *A. globosa* (Roemer), *Cyrtospirifer* sp., *Parapugnax markovskii* (Yudina).

West Siberia, Kuznetsk Basin (Rzhonsnitskaya 1968)

Early Famennian: *Mesoplica* cf. *M. praelonga* (Sowerby), *M. meisteri* (Peetz), *Athyris angelica* Hall, *A. globularis* Phillips, *Cyrtospirifer tschernyschewi* Khalfin.

Northern Siberia, Lena River (Stolb Island) (Krylova 1959, 1962; Yazikov et al. 2013)

Latest Frasnian: *Retichonetes* cf. *R. armatus* (Bouchard-Chantreaux in de Verneuil), *Athyris* sp., *Mucrospirifer* ex gr. *mucronatiformis* (Khalfin), *Cyrtospirifer* sp., *Adolfispirifer jerejewi* (Tschernyschew), *Theodossia* ex gr. *Th. anossofi* (Verneuil).

Early Famennian: *Mesoplica* cf. *M. meisteri* (Peetz), *Productella* sp., *?Evanescirostrum lenense* Baranov, *Parapugnax* cf. *P. markovskii* (Yudina), *Athyris* sp., *Cyrtospirifer* cf. *C. tschernyschewi* Khalfin, *Mucrospirifer* sp.

Northeastern Siberia (Alekseeva 1967, Alekseeva et al. 1996)

Latest Frasnian: *Productella* sp., *Spinatrypina (Exatrypa) orientalis* Alekseeva et Komarov, *Theodossia yakutica* Sidjachenko.

Early Famennian: *Schuchertella* sp., *Plicatifera* sp., *Momarhynchus indigiricus* Baranov et Sartenaer, *Trifidorostellum aldanicum* Alekseeva, *Cyrtospirifer tschernyschewi* Khalfin, *Cyrtospirifer settedabanicus* Sidjachenko, *Cyrtospirifer communis* Sidjachenko, *? C. zadonicus* Ljaschenko.