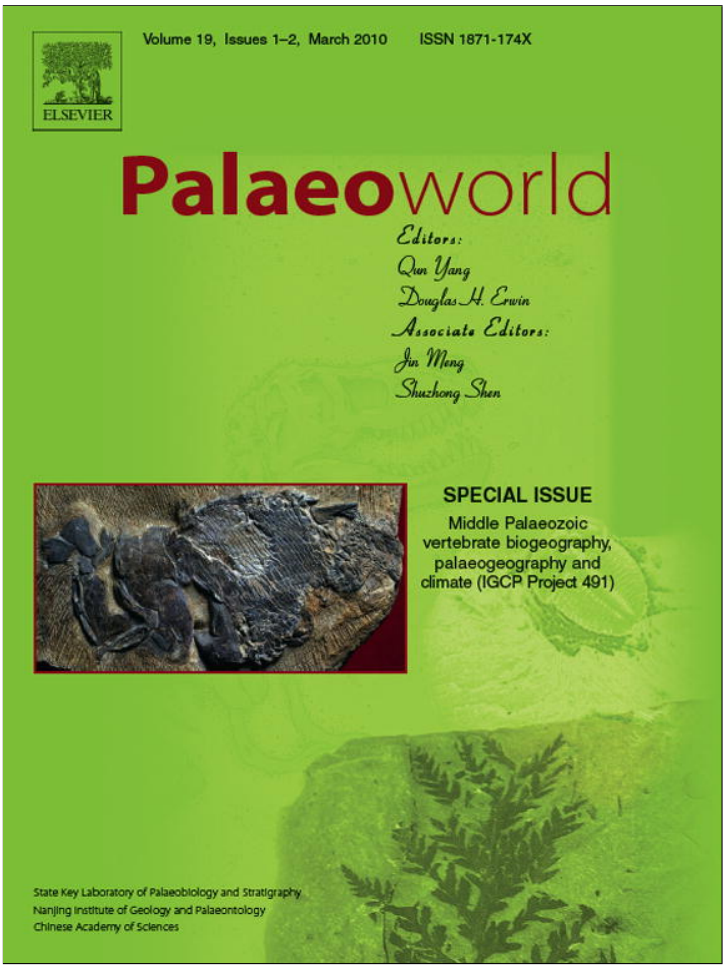

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Research paper

Palaeozoogeographical connections of the Devonian vertebrate communities of the Baltica Province. Part II. Late Devonian

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Abstract

Late Devonian vertebrate communities within the Baltica zoogeographical Province are analysed for intra- and interprovincial connections. Components within the category of provincial endemics are used to assign the communities to a particular zoogeographical province. Marine and continental, presumably freshwater types of vertebrate dispersal are outlined. During the Late Devonian marine dispersal is displayed by ptyctodonts, struniiforms, and some dipnoans, and continental dispersal by psammosteids, acanthodians, and some arthrodires.

Isolation of communities is reflected by predominance of local and provincial endemics; the majority of polydemics and cosmopolitans records wider connections. It is suggested that proportions of endemism-cosmopolitanism significantly correlate with sea-level changes. Augmentation of endemism may result from regressions that increased isolation of faunas. Separation from the main sea basin may have reduced competition, resulting in radiation within limited areas.

Constant faunal interchanges are observed between Baltica and Laurentia, but connections to other provinces are sporadic. Different vertebrate groups indicate varying dispersal capabilities. The cosmopolitans are ptyctodont, arthrodire and antiarch placoderms, chondrichthyans, acanthodians, actinopterygians, and struniiforms. Agnathans and other sarcopterygians show limited dispersal capabilities. Continental and pelagic marine faunas may have interacted by penetration of the members of one fauna into the habitat of another one during favourable periods.

Keywords: Palaeozoogeography; Devonian; Baltica Province; Endemism; Dispersal

1. Introduction

This paper continues the analysis of the vertebrate distribution within the Baltica zoogeographical Province into the Late Devonian presented by Lukševičs et al. (2010) for the Middle Devonian. The dispersal model during the Late Devonian in comparison to the Middle Devonian is exemplified by various agnathan and gnathostome vertebrate groups. The hypothesis on the correlation between the endemic-cosmopolitan composition of the community and sea-level changes is checked. A survey of the interprovincial connections of vertebrate communities is used as a tool for highlighting predominant dispersal directions and clarifying of the role of various vertebrate groups.

2. Methods and terminology

The faunal elements of Late Devonian communities are examined at the generic level for their distribution within zoogeographical districts, provinces, regions, and realms. For explanation of the newly introduced terminology and for the suggested Givetian-Famennian global vertebrate regionalisation, see Lebedev and Zakharenko (2010).

Where available, sedimentological data are used to reconstruct environments. When tracing various dispersal directions we take into account the physico-geographical conditions suggested by earlier authors (Tikhomirov, 1967; Savvaitova, 1977; Sorokin et al., 1981; Rodionova et al., 1995). The most important studied territories (Main Devonian Field and

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Table 1
Early Frasnian vertebrate communities of the Baltica Province. Based upon: Krylova (1973), Vorobyeva et al. (1997), Esin et al. (2000), Valiukevičius and Kruchek (2000), Moloshnikov (2007, 2008) and unpublished author's data.

Local endemics	Provincial endemics	Quasiendemics/didemics	Polydemics	Cosmopolitans	E-C index
Pļaviņas community of MDF (Late *falsiovalis-transitans* Zone interval)					
Rhamphodopsis	*Haplacanthus*	*Psammosteus*	"*Rhynchodus*"	*Ctenurella*	2:2:6:4:9
Platycephalichthys	"*Acanthodes*"	*Plourdosteus*	*Grossilepis*	"*Ptyctodus*"	
		Asterolepis	*Glyptolepis*	*Bothriolepis*	
		Homalacanthus	*Laccognathus*	*Strunius*	
		Eusthenopteron		*Holoptychius*	
		Conchodus		*Latvius*	
				Rhinodipterus	
				Griphognathus	
				Moythomasia	
Timan community of the CDF (Late *falsiovalis* Zone)					
Tartuosteus	*Haplacanthus*	*Psammosteus*	"*Acanthodes*"	"*Ptyctodus*"	1:1:4:3:4
		Plourdosteus	*Glyptolepis*	*Atopacanthus*	
		Asterolepis	*Laccognathus*	*Onychodus*	
		Devononchus		*Holoptychius*	
Timan community of South Timan (Late *falsiovalis* Zone)					
cf. *Nostolepis*	*Haplacanthus*	*Psammosteus*	"*Rhynchodus*"	*Holonema*	3:2:4:3:6
cf. *Diplacanthus*	"*Acanthodes*"	*Plourdosteus*	*Glyptolepis*	*Ctenurella*	
Cheiracanthus		*Devononchus*	*Laccognathus*	*Bothriolepis*	
		Holoptychius		*Atopacanthus*	
				Rhinodipterus	
				Moythomasia	
Ust'-Yarega community of South Timan (*transitans* Zone)					
cf. *Cheiracanthus*	*Haplacanthus*	*Psammosteus*	*Glyptolepis*	*Holonema*	2:2:3:1:5
cf. *Rhadinacanthus*	"*Acanthodes*"	*Plourdosteus*		*Eastmanosteus*	
		Devononchus		*Bothriolepis*	
				Holoptychius	
				Moythomasia	
Ust'-Yarega community of Middle Timan (*transitans* Zone)					
	Haplacanthus	*Psammolepis*	*Homacanthus*	*Ctenurella*	0:1:4:3:7
		Psammosteus	*Glyptolepis*	"*Ptyctodus*"	
		Plourdosteus	*Laccognathus*	*Bothriolepis*	
		Asterolepis		*Holoptychius*	
				Latvius	
				Rhinodipterus	
				Moythomasia	
Vyuchey community of North Timan (?)					
		Psammosteus	*Glyptolepis*	*Bothriolepis*	0:0:2:1:2
		Devononchus		*Holoptychius*	
Styla community of Ukraine, Donets Basin (?)					
		Psammolepis	*Dipterus*	*Bothriolepis*	0:0:1:1:3
				Holoptychius	
				Rhinodipterus	

Central Devonian Field) are abbreviated in the text (MDF and CDF).

3. Dispersal of provincial endemics within the Baltica Province

Analysis of the distribution of provincial endemics includes the geographical positioning of their communities, brief characteristics of the environments and the balance of endemics versus didemics/quasiendemics, polydemics and cosmopolitans. The combination of provincially endemic genera in various districts is used as the main characteristic of the province during the time slice under consideration.

Local endemics provide no information on faunal interchanges, but characterise separate districts. Provincial endemics define the directions of the faunal interchanges between districts and typify the entity of the province during successive chronological periods.

3.1. Upper Devonian

3.1.1. Early Frasnian (Late falsiovalis-transitans time) (Table 1, Fig. 1)

During the early Frasnian the Pļaviņas vertebrate community is distributed in a shallow-water sea in the central and western parts of the Baltic syneclise (MDF). It is widely known as "Snetnaya Gora vertebrate assemblage" (Gross, 1933, 1941, 1942; Ivanov, 1990; Ivanov et al., 2006). The environment changed from lagoonal in the very western part of the basin to tidal and wave-influenced shallow-marine in the eastern part, with rare

Fig. 1. Distribution of vertebrate communities of the Baltica Province during the early Frasnian. Black squares indicate the most important vertebrate localities. Arrows illustrate faunal interchanges between districts; abbreviations by the arrows list the main vertebrate groups participating in the dispersal. Abbreviations: CDF—Central Devonian Field, MDF—Main Devonian Field, ACA—acanthodians, ANT—antiarchs, ART—arthrodires, CHO—chondrichthyans, DI—dipnoans, OST—osteolepiforms, POR—porolepiforms, PSA—psammosteiforms, PTY—ptyctodonts, STR—struniiforms. Base maps for Figs. 1–3 compiled after Vinogradov and Nalivkin (1960), Tikhomirov (1967) and Rodionova et al. (1995).

invertebrates, but still diverse fishes (Tovmasyan and Stinkulis, 2008). Timan fish communities of the CDF and South Timan dwelled in shallow, brackish-water environments, but by the end of this time the freshwater input brought more clastic materials. The Sargay Regional Stage is normal marine, but no vertebrates are known from this time interval (Tikhomirov, 1967; Rodionova et al., 1995). The Ust'-Yarega communities of the South and Middle Timan lived under the maximum marine transgression conditions. In contrast, the Donets Styla Formation placed close to the Ukrainian Island is completely terrigenous, and apart from fishes yields abundant plant remains (Krylova, 1973), suggesting onshore, possibly deltaic or flood plain environments (Table 1; Fig. 1).

In comparison to the Givetian (Lukševičs et al., 2010), early Frasnian communities (Table 1) show the dominance of cosmopolitans and a significant proportion of didemics. Provincialism is characterised by the assemblage composed only of the acanthodians *Haplacanthus* and "*Acanthodes*". This situation contrasts with the late Eifelian (Lukševičs et al., 2010), when the provincially limited acanthodian connection is dominated by wider didemic and polydemic dispersal.

The holonematid *Megaloplax* from South Timan was collected in the locality exposing the deposits of the Lower Frasnian Ust'-Yarega and Middle Frasnian Domanik Formations and its exact origin is unknown. More, A. Ivanov expressed an opinion (2009, pers. comm.) that the holotype specimen belongs in fact to *Holonema*, thus this genus is not used in the current analysis. The ptyctodont placoderm *Rhamphodopsis*, from the Eifelian-Givetian of East Laurentia, survived into the Frasnian in the MDF.

This predominantly cosmopolitan distribution reflects wide dispersal of early Frasnian faunas across the globe. Prevailing faunal connections are traced to Eastern Laurentia (see Section 4.1.1, Section 4.1.2, Fig. 1; Table 8). The basic analysis of this fauna was made by Ivanov (1990) and Schultze and Cloutier (1996).

3.1.2. Middle Frasnian (punctata-jamieae time interval) (Table 2)

The geographical distribution of middle Frasnian communities is similar to the early Frasnian, except that vertebrates reappear in Severnaya Zemlya (Middle-Late Matusevich community) (Table 2).

During punctata Zone (Dubnik time) the MDF basin regressed, followed by a new wide Early hassi Zone (Daugava time) transgression. Lagoonal type hypersaline basins formed in the west, but in the east siliciclastic deposition dominated, with a significant freshwater input from the uplands. The jamieae Zone (Snezha time) evidenced a complete transgression–regression cycle, producing changeable deposits of the shallow sea (Sorokin et al., 1981). The deposits of punctata–Early hassi Zone (Semiluki time) in the CDF are shallow-water marine with normal salinity (Rodionova et al., 1995).

During punctata–Early hassi Zone (Domanik time) a deep-water meridionally directed trough formed in the South Timan. Its deeper parts show evidence of anoxia, but on the lateral shelf parts normal marine conditions persisted, inhabited by a rich shallow-water biota, including vertebrates. Those were sometimes also buried in the deeper parts of the basin (House et al., 2000). The Kraypole community of Middle Timan and the Ust'-Bezmoshitsa community of North Timan also lived in shallow-marine, near-shore environments, as well as the Middle-Late Matusevich community of Severnaya Zemlya (Matukhin and Menner, 1999; Lukševičs, 1999).

The structure of middle Frasnian communities (Table 2) is similar to that of the early Frasnian communities in the dominance of cosmopolitans. The generic composition remains virtually the same as that during the early Frasnian. Provincial endemics include only the acanthodian "*Acanthodes*" and the osteolepiform *Jarvikina*. Their dispersal shows interconnection of the MDF and Timan communities. The connection of both to the CDF is not evident and may be traced only by the didemic arthrodire *Plourdosteus*.

3.1.3. Late Frasnian (rhenana-linguiformis time interval) (Table 3)

The geographical distribution of vertebrate communities during the late Frasnian (Fig. 2) generally remains unchanged from the middle Frasnian. The Pamūšis-Stipinai basin of the MDF with mainly vertebrate fossils was shallow and dominated by sedimentation of sands followed by hyperhaline conditions with only rare occurrence of vertebrates. During linguiformis Zone (Amula time) the shallow sea basin existed only in a restricted area of the western part of the MDF (Sorokin et al., 1981). In all Timan areas, deeper and shallower shelf areas alternated and facies varied from reefal to neritic cephalopod (House et al., 2000). The Lyaiol' community is regarded as a deeper-facies analogue of the Vetlasyan-Sirachoy + Ukhta communities (Esin et al., 2000) (Table 3).

The Voronezh, Evlanovo, and Livny communities of the CDF lived in a shallow-water sea with normal salinity (Rodionova et al., 1995) and are characterised by the absence of provincial endemics (Table 3). No key taxa, such as psammosteids and porolepiforms, are recorded from this district. Arthrodire and ptyctodont placoderms dominated the communities, antiarchs and acanthodians being a rare exception. Dipnoans are few in number with a limited number of genera; *Palaedaphus*, known otherwise from the Famennian of Belgium (Cloutier and Candilier, 1995) is thus a local endemic for the Frasnian in the CDF. Material originally identified as? *Plourdosteus* (Obrucheva and Obrucheva, 1977) from the Voronezh Regional Stage seems to represent a new genus of the family Plourdosteidae.

Another assemblage of Early rhenana Zone (Voronezh time) is known from the Soligalich borehole (northeast of the Moscow syneclise). With *Psammosteus*, *Bothriolepis,* and *Holoptychius*, this grouping is close to that from the MDF, showing an open faunal connection to the western part of Baltica. *Bothriolepis* and *Holoptychius* were obtained from the Evlanovo deposits in the Lyubim borehole of the neighbouring Yaroslavl' Region (Tikhomirov, 1967), also being in accordance with the vertebrate assemblages of the MDF.

The provincial characteristics are based upon the only psammosteid *Obruchevia* known only from the Pamūšis-Stipinai

Table 2
Middle Frasnian vertebrate communities of the Baltica Province. Based upon: Obrucheva and Obrucheva (1977), Lukševičs (1999), Esin et al. (2000), Valiukevičius and Kruchek (2000), Ivanov et al. (2006), Moloshnikov (2008) and unpublished author's data.

Local endemics	Provincial endemics	Quasiendemics/didemics	Polydemics	Cosmopolitans	E-C index
Dubnik community of MDF (*punctata* Zone)					
Parapanderichthys	"*Acanthodes*"	*Psammosteus*	*Gyroplacosteus*	"*Ptyctodus*"	1:2:3:3:8
	Jarvikina	*Plourdosteus*	"*Rhynchodus*"	*Holonema*	
		Asterolepis	"*Dipterus*"	*Eastmanosteus*	
				Bothriolepis	
				Persacanthus	
				Holoptychius	
				Rhinodipterus	
				Moythomasia	
Daugava community of MDF (Early *hassi* Zone)					
Parapanderichthys	"*Acanthodes*"	*Psammosteus*	"*Rhynchodus*"	"*Ptyctodus*"	1:2:3:1:5
	Jarvikina	*Plourdosteus*		*Holonema*	
		Eusthenopteron		*Eastmanosteus*	
				Bothriolepis	
				Holoptychius	
Snezha community of MDF (*jamieae* Zone interval)					
Platycephalichthys		*Psammosteus*		*Holonema*	1:0:3:0:3
		Plourdosteus		*Bothriolepis*	
		Devononchus		*Holoptychius*	
Semiluki community of CDF (*punctata*-Early *hassi* Zone interval)					
Geptolepis		*Psammosteus*	"*Rhynchodus*"	"*Ptyctodus*"	1:0:2:1:4
		Plourdosteus		*Holonema*	
				Holoptychius	
				Moythomasia	
Domanik community of South Timan (*punctata-jamieae* Zone interval)					
Timanosteus	"*Acanthodes*"	*Plourdosteus*	"*Rhynchodus*"	*Eastmanosteus*	3:1:2:2:2
cf. *Cheiracanthus*		*Devononchus*	*Grossilepis*	*Moythomasia*	
cf. *Rhadinacanthus*					
Kraypole community of Middle Timan (*punctata-jamieae* Zone interval)					
	"*Acanthodes*"	*Psammosteus*	*Grossilepis*	"*Ptyctodus*"	0:2:3:1:5
	Jarvikina	*Plourdosteus*		*Bothriolepis*	
		Devononchus		*Persacanthus*	
				Holoptychius	
				Moythomasia	
Ust'-Bezmoshitsa community of North Timan (?)					
	Jarvikina	*Psammosteus*	*Glyptolepis*	*Holonema*	0:1:2:1:3
		Asterolepis		*Bothriolepis*	
				Holoptychius	
Middle-Late Matusevich community of Severnaya Zemlya (?)					
		Psammosteus		?*Eastmanosteus*	0:0:3:0:3
		Asterolepis		*Bothriolepis*	
		Eusthenopteron		*Holoptychius*	

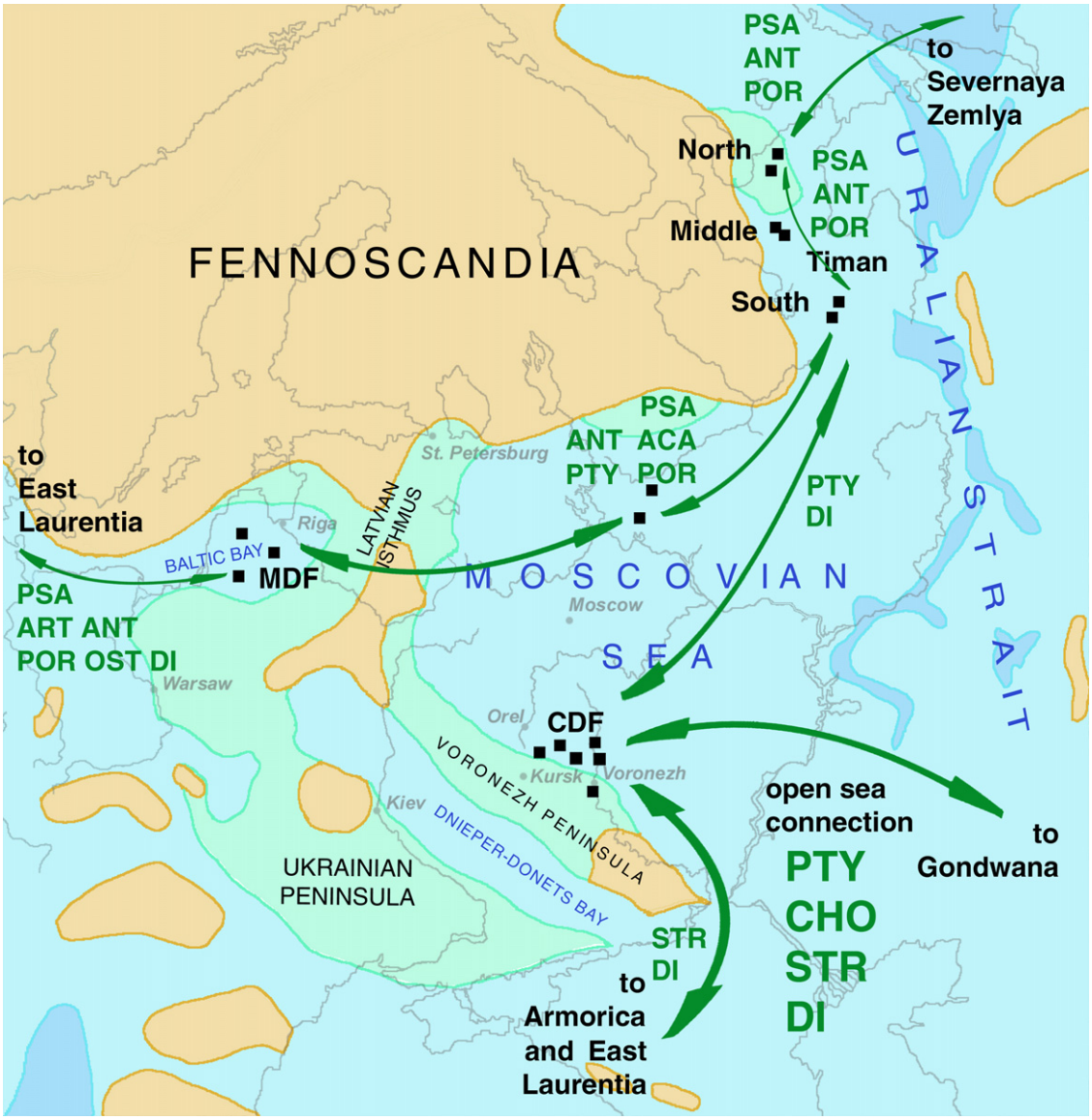


Fig. 2. Distribution of vertebrate communities of the Baltica Province during the late Frasnian. Black squares indicate the most important vertebrate localities. Arrows illustrate faunal interchanges between districts; abbreviations by the arrows list the main vertebrate groups participating in the dispersal. For abbreviations see Fig. 1.

community of the MDF and Kamenniy community of the North Timan, showing a wide range of dispersal but known yet in Baltica only from these areas (Table 3).

Two types of intra- and interprovincial connections are registered for the late Frasnian of the Baltica (Fig. 2): (1) a continental, brackish- or even freshwater connection exemplified by psammosteids (*Psammosteus*, *Obruchevia*), acanthodians (*Devononchus*), and antiarchs (*Bothriolepis*); (2) presumably shallow-water marine, possibly even hypersaline, realised by the ptyctodonts ("*Ptyctodus*", "*Rhynchodus*"), struniiforms (*Strunius*), and dipnoans (*Conchodus*, *Ganorhynchus*). The second type makes clear the presence of some didemics, polydemics and cosmopolitans in the Central Russian faunas, their isolation from the penetration of provincial endemics, typical for the rest of Baltica. The presence of the elasmobranch *Phoebodus*, known otherwise only from the continental shelves, supports this assumption.

Three types of faunas may be established for the late Frasnian within Baltica: (1) Fennoscandian (exemplified by *Psammosteus*, *Obruchevia,* and *Devononchus*), (2) marginal Baltican (exemplified by presence of *Conchodus* and, in contrast, missing *Holoptychius*, which is widely spread in the other parts of Baltica, but is also absent from the Armorican territories), and (3) mixed faunas of Timan, which include the elements of both previous faunas.

3.2. Famennian

3.2.1. Early Famennian (triangularis-rhomboidea time interval) (Table 4, Fig. 3)

Early Famennian communities are documented from the same districts as previously, but in Severnaya Zemlya the vertebrate record is the last in the Devonian section, and no vertebrates of this age are known from Middle and North Timan. A marine

Table 3
Late Frasnian vertebrate communities of the Baltica Province. Based upon: Esin et al. (2000), Valiukevičius and Kruchek (2000), Krupina (2004), Matukhin and Menner (1999), Moloshnikov (2002), Obruchev (1959), Obrucheva (1962), Zakharenko (2007) and unpublished author's data.

Local endemics	Provincial endemics	Quasiendemics/didemics	Polydemics	Cosmopolitans	E-C index
Pamūšis-Stipinai community of MDF (*rhenana* Zone)					
Walterilepis	*Obruchevia*	*Psammosteus*	*Grossilepis*	"*Ptyctodus*"	3:1:3:2:3
Platycephalichthys		*Asterolepis*	"*Dipterus*"	*Bothriolepis*	
Obruchevichthys		*Devononchus*		*Holoptychius*	
Amula community of MDF (*linguiformis* Zone)					
		Psammosteus		*Bothriolepis*	0:0:2:0:2
		Devononchus		*Holoptychius*	
Voronezh community of CDF (Early *rhenana* Zone)					
		"*Plourdosteus*"	"*Rhynchodus*"	"*Ptyctodus*"	0:0:2:1:2
		Ganorhynchus		*Bothriolepis*	
Evlanovo community of CDF (Late *rhenana* Zone)					
Omalosteus		*Conchodus*		"*Ptyctodus*"	2:0:1:0:3
Palaedaphus				*Phoebodus*	
				Strunius	
Livny community of CDF (*linguiformis* Zone)					
			"*Rhynchodus*"	"*Ptyctodus*"	0:0:0:1:1
Vetlasyan-Sirachoy community of South Timan (Early *rhenana* Zone)					
	"*Acanthodes*"	*Psammosteus*		*Holonema*	0:3:3:0:6
	cf. *Cheiracanthus*	*Devononchus*		*Eastmanosteus*	
	cf. *Rhadinacanthus*	*Conchodus*		"*Ptyctodus*"	
				Bothriolepis	
				Holoptychius	
				Moythomasia	
Ukhta community of South Timan (Late *rhenana-linguiformis* Zone interval)					
	"*Acanthodes*"	*Psammosteus*		*Eastmanosteus*	0:3:4:0:3
	cf. *Cheiracanthus*	"*Dinichthys*"		*Bothriolepis*	
	cf. *Rhadinacanthus*	*Devononchus*		*Holoptychius*	
		Glyptopomus			
Lyaiol' community of South Timan (Early *rhenana-linguiformis* Zone interval, deep-water analogue of the Vetlasyan-Sirachoy and Ukhta communities)					
	"*Acanthodes*"	*Psammosteus*	*Protacrodus*	*Eastmanosteus*	0:1:4:1:4
		?*Brachydeirus*		*Bothriolepis*	
		Devononchus		*Phoebodus*	
		Laccognathus		*Moythomasia*	
Kamenniy Ruchey community of Middle Timan (Early *rhenana* Zone)					
		Psammosteus	*Glyptolepis*	*Holoptychius*	0:0:1:1:1
Kamenniy community of North Timan (Early *rhenana* Zone)					
	Obruchevia	*Plourdosteus*		*Holonema*	0:1:1:0:2
				Bothriolepis	
Vavilov community of Severnaya Zemlya (?)					
		?*Psammosteus*		*Bothriolepis*	0:0:1:0:2
				Holoptychius	

Table 4
Early Famennian vertebrate communities of the Baltica Province. Based upon: Obruchev (1958), Vorobyeva (2004), Obrucheva, E.D. (1983), Obrucheva and Obrucheva (1977), Ivanov and Lukševičs (1994), Matukhin and Menner (1999), Esin et al. (2000), Valiukevičius and Kruchek (2000), Moloshnikov (2001, 2004, 2008), Beznosov (2009), Beznosov et al. (2004) and unpublished author's data.

Local endemics	Provincial endemics	Quasiendemics/didemics	Polydemics	Cosmopolitans	E-C index
Eleja community of MDF (*triangularis* Zone)					
	Devononchus		*Holoptychius*	*Bothriolepis* "*Acanthodes*"	0:1:0:1:2
Joniškis community of MDF (*crepida* Zone)					
	Devononchus		*Holoptychius*	*Phoebodus* *Ctenacanthus*? *Moythomasia*?	0:1:0:1:3
Kursa community of MDF (*rhomboidea* Zone)					
	Haplacanthus *Cheiracanthus* *Devononchus*	?*Glyptolepis*	*Phyllolepis* *Holoptychius*	*Bothriolepis* *Protacrodus*	0:3:1:2:2
Zadonsk community of CDF (*crepida* Zone)					
Livnolepis *Rossolepis* *Chelyophorus* *Megapomus* *Chirodipterus* *Conchodus* *Jakubsonia*	*Devononchus*	"*Dinichthys*" *Glyptopomus* *Strunius*	*Holoptychius* *Dipterus*	*Remigolepis* *Bothriolepis* *Protacrodus*	7:1:3:2:3
Elets community of CDF (*rhomboidea* Zone)					
Eunemacanthus			*Dipterus*		1:0:0:1:0
Savinobor-Sosnogorsk community of South Timan (*triangularis* Zone)					
cf. *Holodipterus*	*Haplacanthus* *Devononchus* "*Cheiracanthus*"		*Holoptychius*	*Bothriolepis* "*Acanthodes*" *Moythomasia*?	1:3:0:1:3
Malyutka community of Severnaya Zemlya (?)					
				Bothriolepis	0:0:0:0:1

transgression started in the early Famennian, moving from the southeast to the northwest. In the MDF the sedimentation of triangularis Zone (Eleja time) took place within a restricted shelf, and even in the sabkha, gradually changing into a shallow-water marine environment in the course of the transgression. During the later crepida Zone (Joniškis time), carbonate and clay muds were formed in a shallow sea with normal salinity, followed by rhomboidea Zone (Kursa time), also characterised by shallow-water marine conditions (Savvaitova, 1977) (Table 4; Fig. 3).

Terrigenous material actively washed into the Moscovian Sea from the Voronezh Peninsula, as well as from Fennoscandia (Fig. 3), formed large subaquatic deltas during crepida Zone (Zadonsk time), but eastwards the sedimentation type indicates normal marine salinity. The connection of the CDF basin to the Baltic syneclise was blocked by the Latvian Isthmus (Rodionova et al., 1995), but in comparison to the late Frasnian the provincial endemics *Devononchus*, polydemics *Holoptychius* and cosmopolitan *Bothriolepis* appeared in this part of Baltica, suggesting a direct faunistic contact. The dominating element in the Zadonsk community, *Livnolepis zadonica* (H. Obrucheva, 1983) was also found in the Tver' Region of Russia (Moloshnikov, 2004, 2008), extending the dispersal of this fauna to the northwest. The intermediate location of this vertebrate assemblage (*Bothriolepis* and *Dipterus*) on the way to Timan was recorded in the Lyubim borehole (Yaroslavl' Region: Tikhomirov, 1967). During the successive rhomboidea Zone (Elets time) the sediments were mostly formed in the normal marine environments (Rodionova et al., 1995).

The Savinobor community of South Timan (triangularis zone) lived in shallow shelf environments (House et al., 2000), and the Sosnogorsk community (triangularis-crepida Zone interval) occupied shallow-water lagoonal conditions that periodically dried out (Beznosov et al., 2004; Beznosov, 2009).

As during the late Frasnian, the Latvian Isthmus played an important role as a zoogeographical barrier, but became more "transparent", letting pass some vertebrates and obstructing transit for others. This is exemplified by the provincial endemic *Devononchus*, known from all major Baltica districts, and the biogeographically significant placoderm *Phyllolepis*, which did not penetrate to the CDF from the MDF. On the contrary, the Famennian cosmopolitan *Remigolepis*, appearing in Baltica for the first time in the CDF, remains unknown in the MDF. However, both genera coexist and were closely associated in East Greenland (Blom et al., 2007). A direct Baltica–Greenland connection would require either recognition of the freshwater environments as habitats for these vertebrates, and their capability of fluvial dispersal, or recognition of a western passage to Greenland through Scotland. At the same time, the acanthodian type of connection within Baltica is definitely non-

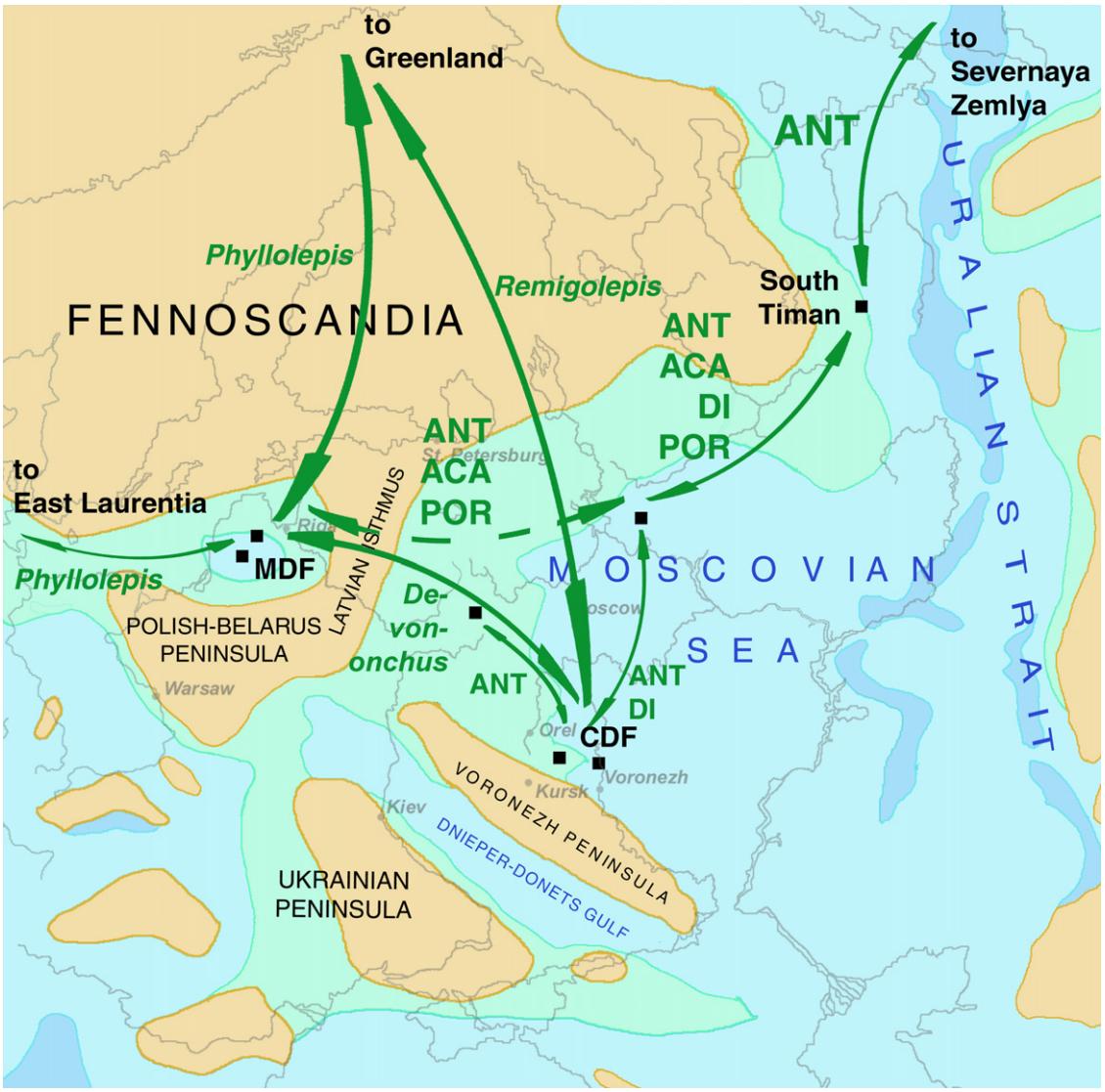


Fig. 3. Distribution of vertebrate communities of the Baltica Province during the early Famennian. Black squares indicate the most important vertebrate localities. Arrows illustrate faunal interchanges between districts; abbreviations by the arrows list the main vertebrate groups participating in the dispersal. For abbreviations see Fig. 1.

marine during the Famennian (in contrast to the late Frasnian and middle–late Eifelian; Lukševičs et al., 2010). It remains unclear, however, whether the MDF–Timan connection characterised by acanthodians, *Holoptychius* and *Bothriolepis*, was a direct one, or used coastal pathways by the southern coast of Baltica.

The low-diversity communities of the MDF and South Timan are characterised by complete or almost complete absence of local endemics (Table 4). In contrast, in the Zadonsk community of the CDF local endemics dominate. The characteristic provincial endemics include the acanthodians *Haplacanthus*, *Cheiracanthus*, and *Devononchus*, comparable to the situation in the early Frasnian.

There are no records of the dipnoans *Chirodipterus* and *Conchodus* elsewhere in the Famennian; most probably the CDF was a refugium for these fishes. The few didemics and polydemics demonstrate predominantly Laurentian affinities.

3.2.2. *Middle Famennian (marginifera-trachytera time interval) (Table 5)*

The middle Famennian communities continued their existence in the MDF, CDF, and South and North Timan. During marginifera Zone (Akmene time) in the MDF, only a few vertebrates are known from almost normal marine environments. In the following trachytera Zone (Spārnene time), the shallow sea gradually regressed, with the formation of shallow-water coastal deposits, including a richer vertebrate assemblage as well as plant remains (Savvaitova, 1977). In the CDF the marginifera Zone (Lebedyan' time) was characterised by normal marine and hypersaline lagoonal aquatic environments. Limited water input continued from the east and south-east; the connection to the Baltic syneclise was still blocked by the Latvian Isthmus; during the trachytera Zone (Optukha time), the territory of the CDF was occupied by a shallow-water lagoonal basins characterised by increased salinity (Rodionova et al., 1995) (Table 5).

Table 5
Middle Famennian vertebrate communities of the Baltica Province. Based upon: Obrucheva, O.P. (1983), Obrucheva and Obrucheva (1977), Esin et al. (2000), Valiukevičius and Kruchek (2000), Lukševičs (2001) and unpublished author's data.

Local endemics	Provincial endemics	Quasiendemics/didemics	Polydemics	Cosmopolitans	E-C index
Akmene community of MDF (*marginifera* Zone)					
Megapomus	*Chelyophorus*	?*Glyptolepis*	*Phyllolepis* *Holoptychius*	*Bothriolepis*	1:1:1:2:1
Spārnene community of MDF (~*trachytera* Zone)					
Platycephalichthys *Cryptolepis* *Conchodus*	*Chelyophorus* *Devononchus*	*Homacanthus* ?*Glyptolepis*	*Phyllolepis* "*Dunkleosteus*" *Holoptychius*	*Bothriolepis* *Protacrodus* "*Acanthodes*"	3:2:2:3:3
Lebedyan' community of CDF (*marginifera* Zone)					
	Chelyophorus		*Holoptychius* *Dipterus*		0:1:0:2:0
Optukha community of CDF (*trachytera* Zone)					
			Dipterus		0:0:0:1:0
Ust'-Pechora community of South Timan (*marginifera-trachytera* Zone interval)					
cf. *Cheiracanthus* cf. *Rhadinacanthus*	*Devononchus*			"*Acanthodes*"	2:1:0:0:1
Pokayama community of North Timan (*marginifera* Zone)					
			Phyllolepis *Holoptychius*	*Bothriolepis*	0:0:0:2:1

The provincial endemics *Chelyophorus* and *Devononchus* characterise the middle Famennian communities, although both are absent from North Timan, and the latter is unknown from the CDF (Table 5). The CDF assemblage is impoverished possibly due to unfavourable salinity in the basin; in South Timan only poorly identified acanthodian scales are recorded, so no zoogeographical conclusions are possible. The presence of the placoderm *Phyllolepis* in the Baltic syneclise and North Timan marks the highest point of its dispersal in Laurussia.

3.2.3. Late Famennian (postera-expansa time interval) (Table 6, Fig. 3)

Carbonate deposits were formed in a shallow-water sea with normal salinity during postera Zone (Piemare time) in the MDF, with sandy deposits closer to the shoreline. During the following expansa Zone (Ketleri time), deposition took place in a low-tidal near-shore environment (Lukševičs and Zupiņš, 2004). During postera-expansa Zone interval (Plavsk time), mostly lagoonal basins occupied the CDF territory, interrupted by locally formed

Table 6
Late Famennian vertebrate communities of the Baltica Province. Based upon: Obruchev (1958), Obrucheva, O.P. (1956, 1962, 1983), Obrucheva and Obrucheva (1977), Krupina (1986, 1999, 2000, 2004), Lebedev (1983, 1995), Lebedev and Lukševičs (1996), Esin et al. (2000), Valiukevičius and Kruchek (2000), Vorobyeva (2004), Lukševičs and Zupiņš (2004), Moloshnikov (2008) and unpublished author's data.

Local endemics	Provincial endemics	Quasiendemics/didemics	Polydemics	Cosmopolitans	E-C index
Piemare community of MDF (*postera* Zone)					
Platycephalichthys	*Chelyophorus*	"*Dinichthys*" *Homacanthus* ?*Glyptolepis*		*Bothriolepis*	1:1:3:0:1
Ketleri community of MDF (*expansa* Zone)					
Ventastega	*Devononchus* "*Cheiracanthus*" *Cryptolepis* *Ventalepis* *Orlovichthys*	*Glyptopomus*	*Holoptychius*	*Bothriolepis* "*Acanthodes*"	1:5:1:1:2
Plavsk community of CDF (*postera*-Early *expansa* Zone interval)					
Tuberospina *Pycnacanthus* *Onychodus* *Holodipterus* *Grossipterus* *Chirodipterus* *Conchodus*	*Chelyophorus* *Devononchus* "*Cheiracanthus*" *Cryptolepis* *Ventalepis* *Orlovichthys*	"*Dinichthys*" *Glyptopomus* *Glyptolepis* *Strunius* *Jarvikia*	*Holoptychius* *Dipterus*	*Bothriolepis* "*Acanthodes*" *Moythomasia*	7:6:5:2:3
Dzhebol' community of South Timan (*postera* Zone)					
	Devononchus			"*Acanthodes*"	0:1:0:0:1

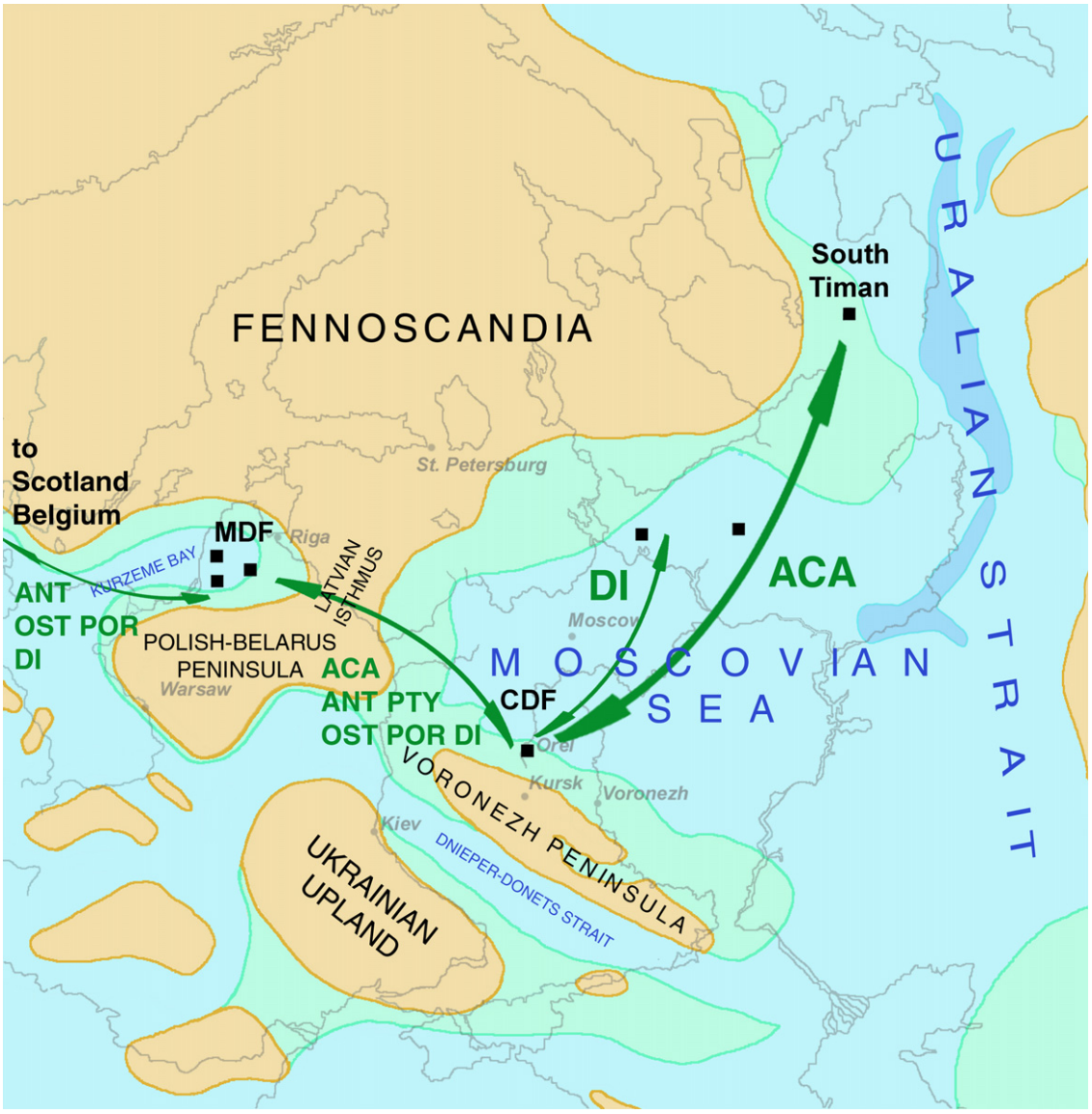


Fig. 4. Distribution of vertebrate communities of the Baltica Province during the late Famennian. Black squares indicate the most important vertebrate localities. Arrows illustrate faunal interchanges between districts; abbreviations by the arrows list the main vertebrate groups participating in the dispersal. For abbreviations see Fig. 1.

river estuaries. These two types of sedimentary environments are bound to each other by a gradual facies transition (Rodionova et al., 1995) (Table 6).

Correlation of the Plavsk Regional Stage and especially its Oryol-Saburovo beds to the upper part of the Ketleri Regional Stage in Latvia (MDF) is controversial as shown by Lebedev and Lukševičs (1996); the accepted dating by conodonts indicates the latter is younger than the former. However, the vertebrate assemblages differ only insignificantly (numerous dipnoans and struniiforms in the former versus the tetrapod *Ventastega* in the latter). This may be explained by the wider temporal range of a single long-lived vertebrate fauna in both areas of the Baltica Province, most probably within the continental basins. This problem is aggravated by the absence of a clear aquatic connection of the basin in western Latvia to the CDF (Fig. 4). Isolated *Dipterus* finds showing the extension of the CDF basin were mentioned by Tikhomirov (1967) from deposits of the same age in the Kostroma and Yaroslavl' Regions. "*Dinichthys*" *machlaevi* Obrucheva (1956) from the CDF is based upon poorly diagnostic material and needs restudy; "*Cheiracanthus*" scales from the Plavsk and Ketleri communities await description, and possibly belong to a new genus.

The provincial endemic assemblage includes the characteristic ptyctodont *Chelyophorus*, acanthodians *Devononchus* and "*Cheiracanthus*", the osteolepiform *Cryptolepis*, the porolepiform *Ventalepis,* and the dipnoan *Orlovichthys*. *Chelyophorus* persists from the middle Famennian, and the acanthodian *Devononchus* characterises Baltica since the middle Givetian. The remaining sarcopterygians distinguish the Ketleri-Plavsk fauna (Table 6).

The Plavsk vertebrates show the dominance of local and provincial endemics while in the Ketleri community provincial endemics definitely prevail. This may indicate stronger isolation of the CDF fauna in combination with more favourable

Table 7
The Latest Famennian vertebrate communities the Baltica Province. Based upon: Savvaitova (1977), Lebedev (1992), Krupina (1987), Lukševičs (1991), Alekseev et al. (1994).

Local endemics	Provincial endemics	Quasiendemics/didemics	Polydemics	Cosmopolitans	E-C index
Šķervelis community of MDF (~Late *expansa* Zone)					
			Holoptychius		0:0:0:1:0
Khovanshchina community of CDF (Late *expansa* Zone)					
"*Cheiracanthus*"		*Strunius*	*Holoptychius*	*Remigolepis*	4:0:1:3:4
Devononchus			*Eusthenodon*	*Bothriolepis*	
"*Chrysolepis*"			*Andreyevichthys*	"*Acanthodes*"	
Tulerpeton				*Moythomasia*	

environmental conditions. Didemics and polydemics emphasise Laurentian affinities (see Sections 4.2.1 and 4.2.2; Fig. 4). Middle Famennian endemism in the CDF is not clearly expressed, whereas the early and late Famennian show strong prevalence of local and provincial endemics.

3.2.4. Latest Famennian (Late expansa time interval) (Table 7)

By the end of the Famennian the habitat for aquatic vertebrates within the Baltica Province was strongly reduced to small areas in the MDF and CDF. During the Late expansa Zone (Šķervelis time) the restricted area in the MDF was a shallow-water partly isolated basin (Savvaitova, 1977), but later its sediments were reworked under subaerial conditions of an arid climate (Stinkulis, 2008) (Table 7).

No vertebrates are recorded from the Ozerki deposits (Middle *expansa* Zone), possibly because of the hypermineralized nature of the basins during this time in the central part of the Russian Platform. During Khovanshchina time (Late *expansa* Zone), sedimentation occurred in near-shore environments under conditions of variable salinity. This basin was influenced by the sea in the south-east of the platform, and by freshwater input from the northern slope of the Voronezh Island (Rodionova et al., 1995; Alekseev et al., 1994).

No provincial endemics may be suggested for this age because it is impossible to compare with other districts (Table 7). Most taxa fall within the polydemic and cosmopolitan categories, showing global, especially Gondwanan, affinities (see Sections 4.2.2 and 4.2.3) and good environmental conditions for faunal interchange.

Two species of a new osteolepidid genus, designed here as "*Chrysolepis*" (sensu Lebedev, 1992), are referred to local endemics.

4. Distribution of didemics/quasiendemics, polydemics, and cosmopolitans within the Baltica Province and globally

This section considers the vertebrate genera found within the Baltica Province classified into the categories of didemics/quasiendemics, polydemics, and cosmopolitans by comparison to their distribution in the other areas of the world during the Late Devonian.

4.1. Frasnian

4.1.1. Didemics/quasiendemics

The psammosteid *Psammosteus*, apart from the Russian Platform, is known from Scotland, Canadian Arctic Archipelago, and Severnaya Zemlya (Blieck et al., 2002), and *Psammolepis* from Arctic Canada (Elliott et al., 2003).

The arthrodire *Plourdosteus* is recorded from the western margin of the Russian Platform (Main Devonian Field: Obrucheva, 1962; and Holy Cross Mountains, Poland: Kulczycki, 1957) and Canada (Denison, 1978). A specimen from Bergisch Gladbach, Germany is attributed to this genus with reservations (Denison, 1978), so further study might require the attribution of this genus to the quasiendemics/didemics.

The widespread antiarch *Asterolepis* occurs in New York State and Nevada (USA), Scotland, and Belgium (Denison, 1978). Its identification in possible Frasnian of Columbia (Janvier and Villarroel, 2000) would indicate connections between Euramerica and Western Gondwana.

Apart from Baltica, the porolepiform *Laccognathus* is known from Canada (Daeschler et al., 2003) and the osteolepiform *Eusthenopteron* from Canada and Greenland (Schultze and Cloutier, 1996).

The Frasnian dipnoan *Ganorhynchus* is recorded from North America (Newberry, 1889) and Belgium (Cloutier and Candilier, 1995); *Conchodus* is known from Poland and Scotland (Kulczycki, 1957; Vorobyeva and Obruchev, 1964).

In comparison to Givetian, the diversity of the didemics remains almost the same. These genera show almost exclusively east Laurentian connections, as during the Middle Devonian (Table 8).

4.1.2. Polydemics

The dental plates of "*Rhynchodus*" are known from the Holy Cross Mountains (Poland), New York State (USA), and Bad Wildungen (Germany). Apart from the MDF, the arthrodire *Gyroplacosteus* was described from the Kuznetsk Basin (Siberia), Poland, and Germany (Denison, 1978).

The antiarch *Grossilepis* is rather widely distributed in the MDF; another species of this genus has been reported from Scotland (Miles, 1968) and Siberia (Obruchev and Sergienko, 1960), but the latter was based on limited material and needs restudy.

Apart from Baltica, the porolepiform *Glyptolepis* is known from Scotland (Ahlberg, 1989), Canada (Schultze and Cloutier,

Table 8
Zoogeographic evolution of non-endemic Late Devonian vertebrates and their faunistic interchanges within the Baltica faunistic Province.

Time	Zoogeographic categories	Vertebrate groups	Prevailing interconnections
Famennian	Quasiendemics/didemics	Acanthodians	Laurentia
		porolepiforms	
		struniiforms	
		dipnoans	
	Polydemics	Phyllolepids	Laurentia
		porolepiforms	Siberia
		osteolepiforms	East
		dipnoans	Gondwana
	Cosmopolitans	Antiarchs	Laurentia
		chondrichthyans	Siberia
		actinopterygians	East Gondwana
			North China
			South China
Frasnian	Quasiendemics/didemics	Psammosteiforms	Laurentia
		arthrodires	
		antiarchs	
		elasmobranchs	
		porolepiforms	
		osteolepiforms	
		dipnoans	
	Polydemics	Ptyctodonts	Laurentia
		arthrodires	Siberia
		antiarchs	
		acanthodians	
		porolepiforms	
		osteolepiforms	
		struniiforms	
		dipnoans	
	Cosmopolitans	Ptyctodonts	Laurentia
		arthrodires	North Gondwana
		antiarchs	East Gondwana
		struniiforms	Siberia
		actinopterygians	Armorica

1996), and Minusa (Obruchev, 1941). The last find is based upon a single scale and needs revision.

The diversity of polydemics increased significantly after the Givetian; antiarchs, acanthodians, and various sarcopterygians were added to the list (Table 8; see also Lukševičs et al., 2010). The distribution of the majority of the polydemic genera included the eastern part of Laurentia and Armorica. *Gyroplacosteus*, *Grossilepis*, and *Glyptolepis* show connections to Siberia. The increase of the polydemics may reflect the general Frasnian increase of diversity (Long, 1993).

4.1.3. Cosmopolitans

The Middle-Upper Devonian ptyctodont placoderm "*Ptyctodus*" is very widely distributed and especially abundant in the shallow-water marine deposits during the Frasnian. It is known from numerous localities in Baltica, Laurentia, East and North Gondwana, and Siberia (Denison, 1978).

The distribution of the arthrodire *Holonema* during the Frasnian includes Laurentia: Eastern USA, Canadian Arctic Archipelago, Scotland; North Gondwana: Iran, Morocco, Afghanistan, Turkey, and East Gondwana: Australia (Schultze, 1973; Denison, 1978; Lelièvre et al., 1993; Janvier et al., 2007).

The antiarch *Bothriolepis* is almost globally distributed in Laurentia: Scotland, Canada, and USA (Denison, 1978); Siberia and adjacent regions (Tuva, Minusa, Kuznetsk Basin, Tien-Shan: Obruchev, 1955; Denison, 1978), Kotel'ny Island (Mark-Kurik, 1974); Kazakhstan (Malinovskaya, 1992); South and North China (Zhu, 2000), and Gondwana: Australia and Antarctica (Young and Long, 2005), Venezuela (Young et al., 2000) and Turkey (Janvier, 1983). Some cosmopolitan species of this genus demonstrate connections between various areas within the Old Red Sandstone continent even on the specific level; for example, *Bothriolepis cellulosa* and *B. panderi* closely resemble *B. canadensis* from Canada (Lukševičs, 2001).

The phoebodontiform elasmobranch *Phoebodus* is very widely distributed during the Frasnian, but its only epicratonic species *Ph. bifurcatus* apart from the CDF is known from Bashkortostan, Timan, and Poland in the Baltica shelves, and in the Armorican Province (Moravia) (Ginter and Ivanov, 1992).

Various species of the acanthodian *Atopacanthus* were discovered in USA and Germany (Denison, 1979); those of the closely related genus *Persacanthus* occur in Iran, Nevada, and Timan (Beznosov, 2002).

Holoptychius was described from Laurentia (Scotland: Ahlberg, 1989, 1992; Canada: Schultze and Cloutier, 1996 and USA: Ørvig, 1957); North Gondwana (Iran: Schultze, 1973), and West Gondwana (Columbia), but this last identification is dubious (Janvier and Villarroel, 2000).

The osteolepiform *Latvius* has been reported from Germany (Jessen, 1966) and New Brunswick, Canada (Greiner, 1977); the struniiform *Strunius* from Poland (Ginter, 2002), Germany (Jessen, 1966), and Iran (Janvier and Martin, 1979). The dipnoan *Rhinodipterus* was discovered in Germany, France, and Belgium (Jessen, 1966; Cloutier and Candilier, 1995), and *Griphognathus* in Germany (Gross, 1956), Nevada (Schultze and Cloutier, 1996) and Australia (Miles, 1977; Andrews et al., 2006).

During the Frasnian the struniiform *Onychodus* was widely spread in North and East Gondwana (Iran: Janvier and Martin, 1979; Afghanistan: Blieck et al., 1982; Turkey: Lelièvre et al., 1993; Australia: Andrews et al., 2006), Laurentia (USA: Elliott et al., 2000; northern France: Cloutier and Candilier, 1995) and Armorica (Germany: Jessen, 1966).

The actinopterygian *Moythomasia* is spread in Armorica (Germany: Gross, 1950) and East Gondwana (Australia: Gardiner, 1984).

The cosmopolitans, including ptyctodonts, arthrodires (*Holonema*), antiarchs, struniiforms, and actinopterygians, demonstrate the maximum diversity in this category during the Middle-Late Devonian (Table 8). *Holonema* changed its status from polydemic to the cosmopolitan; the last three groups remain cosmopolitan since the Givetian. Most of the cosmopolitan connections indicate to Laurentia, Armorica, East and North Gondwana.

4.2. Famennian

4.2.1. Didemics/quasiendemics

Apart from the Baltica Province, the acanthodian *Homacanthus* was recorded from Laurentia (Ohio, USA: Denison, 1979).

The Famennian record of the porolepiform *Glyptolepis* includes localities in Laurentia (France: Cloutier and Candilier, 1995). Apart from the Baltica, *Glyptopomus* is known from Scotland and Belgium (Jarvik, 1950; Cloutier and Candilier, 1995); *Strunius* from Colorado, USA (Ginter, 2001). The dipnoan *Jarvikia* is also known from East Greenland (Blom et al., 2007).

The proportion of didemics strongly decreased in comparison to the Frasnian (Table 8). Arthrodires, chondrichthyans, and antiarchs shifted to the polydemic and cosmopolitan categories. The remaining genera show Laurentian affinities.

4.2.2. Polydemics

The distribution of the phyllolepid placoderm *Phyllolepis* and its relationships to the Famennian zoogeography was earlier mentioned by Lebedev (1985, 2004) and extensively discussed by Young (2006). It was demonstrated that this placoderm is closely associated to the earliest tetrapods. During the Famennian, this fish spread to Laurussia (East Greenland, Scotland, Belgium, Pennsylvania, USA, Latvia; North Timan) from Gondwana (Young, 2006).

Beyond the limits of the Baltica Province the porolepiform *Holoptychius* is known from Laurentia (Greenland, Scotland, Belgium, France: Jarvik, 1972; Cloutier and Candilier, 1995), East Gondwana (Australia: Johanson and Ritchie, 2000) and Siberia (Kuznetsk Basin: Ivanov and Rodina, 2004).

The tristichopterid *Eusthenodon* was previously described from Laurentia: Greenland (Blom et al., 2007), Pennsylvania (Elliott et al., 2000), Belgium (Clément, 2002), and East Gondwana (Australia: Johanson and Ritchie, 2000). It may be present in the Famennian of South Africa, but still awaits description (Anderson et al., 1999).

Numerous finds attributed to the genus *Dipterus* from North America (Eastman, 1907) are dubious and require revision (Friedman and Daeschler, 2006); for the time being the status of this material remains unchanged. *Dipterus* finds from France and Belgium were summarised by Cloutier and Candilier (1995). Obruchev (1940,1960) presented materials from Siberia (Kuznetsk Basin).

Anderson et al. (1994, 1999) illustrated an isolated parasphenoid very similar to that of *Andreyevichthys*; despite insufficiency of the material, this affinity seems obvious. Ginter (2001) figured *Andreyevichthys* juvenile tooth plates from Colorado closely resembling those described by Krupina and Reisz (1999). This genus is conditionally regarded here as polydemic; further studies in South Africa and westerm United States may support or reject this opinion. In the latter case the genus would become a didemic, or a local endemic.

Close connections of the Baltica Province to Laurentia persisted during the Famennian (Table 8). The polydemics demonstrate interrelationships with Siberia, as during the Frasnian, and East Gondwana. The South African link still needs to be supported by further evidence.

4.2.3. Cosmopolitans

The antiarch *Bothriolepis* is one of the frequent cosmopolitan elements in Famennian faunas. It is known from Laurentia: Scotland; Greenland; Pennsylvania, USA, Belgium (Denison, 1978); Siberia: Kuzbass (Obruchev, 1960); East Gondwana (Australia: Young, 1988); China (Zhu, 2000) and South Africa (Anderson et al., 1994).

The antiarch *Remigolepis* is also widely distributed, being found in Laurentia: East Greenland (Blom et al., 2007), Pennsylvania, USA (Daeschler et al., 2003); Scotland (Andrews, 1978); Baltica: Tula Region, Russia (Lukševičs, 1991); East Gondwana: Australia (Johanson, 1997); North and South China: Ningxia, Inner Mongolia, Hunan (Zhu, 2000) and ? Tarim: Kyrghyzstan (Panteleyev, 1992). The last record requires age refinement, being currently defined only as Upper Devonian.

Famennian records of the chondrichthyan *Protacrodus* are numerous and globally distributed. Ginter (2001) regarded this fish as an indicator of shallow-water marine biofacies. Similarly dispersed genera *Protacrodus* and *Phoebodus* were spread in the coastal shelf zones and epicratonic seas of Laurentia: Iowa and Colorado, USA (Gross, 1973; Ginter, 2001), Canada (Ginter and Turner, 1999); Baltica: Poland, Cisurals (Ginter and Ivanov, 2000), Belarus (Esin et al., 2000), Latvia (Ivanov and Lukševičs, 1994); former Armorican territories: Germany (Ginter, 1999),

France (Ginter, 2000) and Italy (Randon et al., 2007); East and North Gondwana: Australia (Young and Turner, 2000), Morocco (Derycke, 1992), Iran (Ginter et al., 2002); Siberia: Kuznetsk Basin (Ivanov et al., 1992) and China: Guizhou and Gansu (Zhu, 2000). Various skeletal fragments of *Ctenacanthus* were found in USA (Zangerl, 1981), Bolivia (Janvier, 2003) and Gansu, China (Zhu, 2000).

Apart from Baltica the actinopterygian *Moythomasia* is recorded in Laurentia (France: Rieman et al., 2002) and North Gondwana (Afghanistan: Blieck et al., 1982; Iran: Long and Hairapetian, 2000).

Only the antiarch *Bothriolepis* persisted as a cosmopolitan after the Givetian. *Remigolepis* became a cosmopolitan as well, but with a smaller area of distribution. The cosmopolitan category became dominated by diversifying chondrichthyans, and to a lesser extent actinopterygians (Table 8).

4.3. Pelagic and continental margin assemblages of the Baltica Province periphery

Research of past decades has documented a number of the Givetian-Famennian vertebrate assemblages in the pelagic facies around the Baltica Province: North and South Urals and Poland (e.g., Ivanov, 1999; Ginter and Ivanov, 2000; Ginter, 2001; Ginter et al., 2002). These assemblages are composed mostly of various chondrichthyan taxa belonging to Phoebodontidae, Protacrodontidae, Omalodontidae, Stethacanthidae, and Symmoriidae. Isolated skeletal parts of acanthodians, struniiforms, and actinopterygians are often found together. As shown by Ginter (2000) and Ginter et al. (2002), these shark-dominated assemblages occupied the continental margins of Laurentia, Armorica, Baltica, and other provinces, and were largely absent from continental or even near-shore communities, thus showing no geographical subdivision. These authors proposed vertical zoogeographical subdivision to distinguish between shallow- and deep-water communities.

However, no separating line can be drawn between the continental and pelagic faunas, as members of one fauna could penetrate to the habitat of another. This is exemplified by invasion of some species of the chondrichthyans *Phoebodus* and *Protacrodus* into shallow-water epicratonic basins of Baltica during the late Frasnian of the CDF and Timan (Table 3), and early Famennian of MDF and CDF (Table 4), during the periods of high transgression.

Assigning such composite peripheral vertebrate communities to one or another province presents difficulties to a palaeogeographer, for example the vertebrate faunas of the Holy Cross Mountains (Poland). The absence of characteristic provincial endemics precludes attribution of these faunas to the Baltica Province. However, during the middle-late Givetian the Baltican-Armorican didemic *Conchodus* and the Laurussian didemic *Glyptolepis* entered the Holy Cross Mountains communities (Kulczycki, 1957; Liszkowski and Racki, 1992; Ivanov and Ginter, 1997). Again, during the middle Frasnian, the Laurussian didemics *Psammosteus*, *Plourdosteus*, and *Eusthenopteron* are known. This may be explained by regressions resulting in shallower seas, making possible the dispersal of continental vertebrates from which they were earlier excluded by deeper water. For the moment, the question on the affinity of this faunal succession to a certain province remains unresolved.

5. General palaeozoogeographical tendencies during the Late Devonian within the Baltica Province

5.1. Zoogeographical evolution of vertebrates

As shown in Table 8, the distribution of various vertebrate groups by the zoogeographical E-C categories during Late Devonian is uneven, perhaps due to ecological constrains of environments (e.g., salinity) or the nature of the animals themselves (e.g., low swimming capabilities). The agnathans (thelodonts and psammosteids), phyllolepid placoderms, porolepiforms, osteolepiforms, and dipnoans never enter the cosmopolitan category (see also Lukševičs et al., 2010).

Other groups originally fall into the lowest E-C category, then flourish (joining all categories), and decrease, like the acanthodians, arthrodires, antiarchs, ptyctodonts, and struniiforms. The decline may be expressed by lowering of the category status, as demonstrated by the last group. Others, like elasmobranchs and actinopterygians, attain their cosmopolitan maxima by the Givetian-Famennian and pass into the Carboniferous. The ingress of the phyllolepids during the Famennian already at the high polydemic level supports Young's (2003, 2006) idea on their spreading to Laurussia from Gondwana.

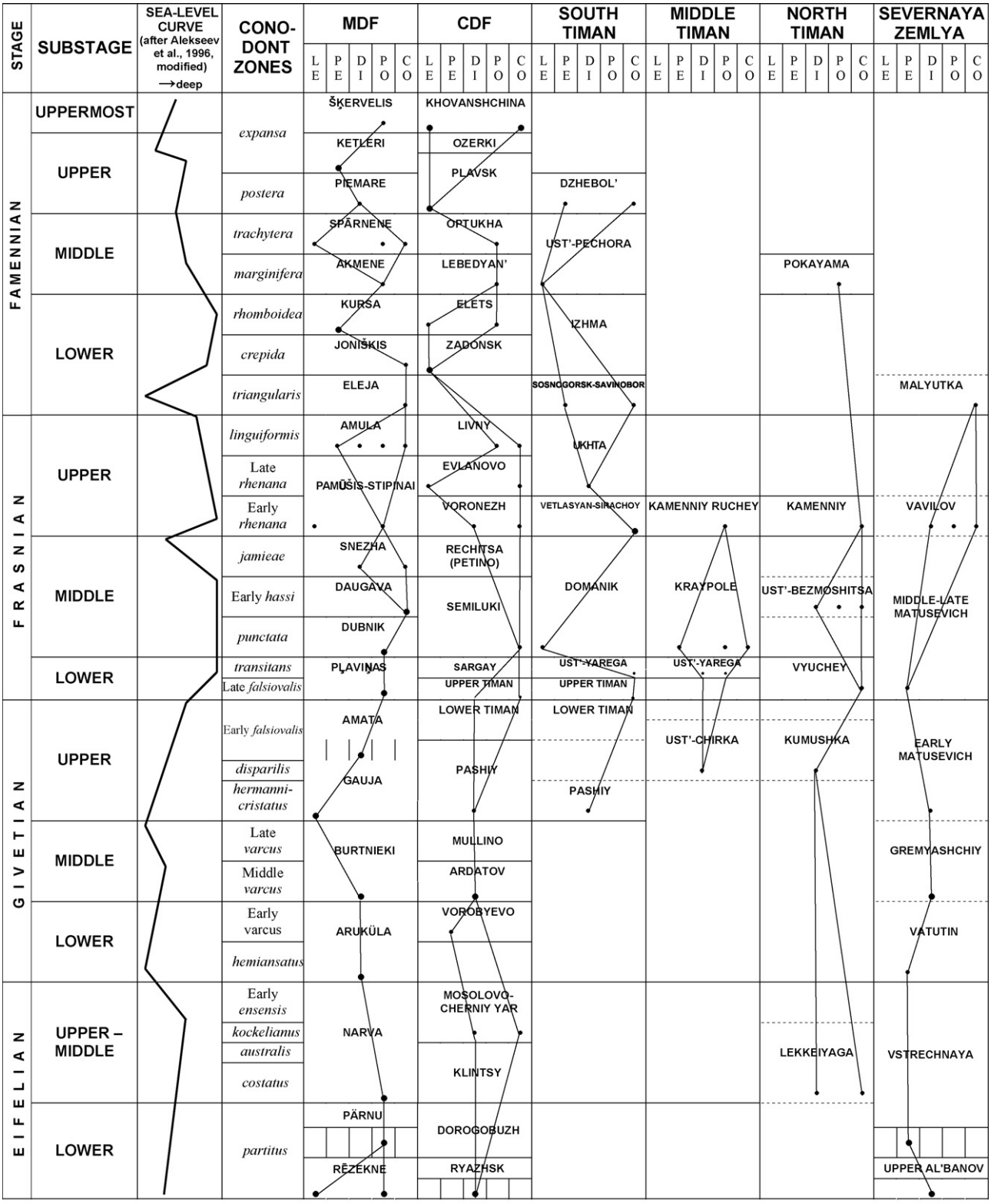
All categories (quasiendemics/didemics, polydemics, and cosmopolitans) attain their maxima during the Frasnian, corresponding to the increase of diversity demonstrated by Long (1993). The quasiendemics/didemics demonstrate their minima during the Famennian, the polydemics during the Givetian, and the cosmopolitans during the Eifelian (Lukševičs et al., 2010). The data on minima are not completely reliable, as each future find would affect the presented result.

5.2. Faunal interchanges of the Baltica zoogeographical Province in space and time

Faunal interchanges between the zoogeographical provinces possibly depend on the proximity of the palaeocontinents, presence of physico-geographical barriers, and eustatic sea-level changes (see Section 5.3). These interchanges may be inferred from the interruptions of earlier established connections. As shown in Table 8, the constant interrelationship between Baltica and Laurentia is not surprising, given the placement of both provinces over the same landmass, the Old Red Sandstone continent. The Armorican connection is also very stable until the dissipation of this province in the Famennian (Lebedev and Zakharenko, 2010), although the connections in the quasiendemic/didemic category are missing.

Interchanges with East Gondwana appear in the Givetian and stay at high (polydemic-cosmopolitan) levels into the Famennian. The North Gondwanan connection appears only during the Frasnian; the West Gondwanan one is almost absent.

Table 9
Distribution of the maxima of the E-C index in the vertebrate communities of the Baltica zoogeographical Province. Large circles—significant meanings, small circles mark insignificant maxima or single records of taxa in the category. Empty boxes stand for missing deposits; labeled empty boxes denote absence of vertebrates in the corresponding formations.



LE—local endemics, PE—provincial endemics, DI—didemics/quasiendemics; PO—polydemics, CO—cosmopolitans.

The connection to Siberia is interrupted during the Middle Devonian, and restored in the Frasnian, but shows no close quasiendemic/didemic associations. A distant South China link is observed only during the Middle Devonian and Famennian in the cosmopolitan category.

5.3. Communities structure, dispersal conditions and sea-level changes

The E-C index based on the suggested endemic-cosmopolitan distributional types presents various combinations. Its structure reflects the isolation rate of the community as demonstrated by the balance of local and provincial endemics, polydemics, and cosmopolitans. Predominance of local and provincial endemics suggests complete or relative isolation of the community not only from the rest of the province, but also from the open sea. The E-C index variation in time reflects changes in faunal isolation/connections of the communities.

Alekseev et al. (1996) published a relative Devonian sea-level curve for the Moscow syneclise, a part of the territory of the East European platform. The analysis of the most important indices (large dots, Table 9) demonstrates approximate correlation of the E-C fluctuations with the sea-level curve.

During the Eifelian the depth of the basin increased. This is reflected by predominance of polydemics and cosmopolitans in the Pärnu, Narva, Mosolovo-Cherniy Yar and Lekkey-Yaga communities.

The Givetian demonstrates a new, very unclearly expressed cycle, and almost all communities show significant endemism-didemism.

During the Frasnian a very strong transgression is interrupted during *jamieae* time. The Pļaviņas, Dubnik, and Daugava communities of the MDF, as well as the Timan and Ust'-Yarega communities of the Timan, correspondingly demonstrate strong polydemism-cosmopolitanism (Tables 1 and 2). Unfortunately, vertebrates of the late Frasnian are poorly known (Table 3), and do not demonstrate a clear picture, showing concentration of both didemics and cosmopolitans (except the Vetlasyan-Sirachoy in the South Timan), although the same tendency is suggested by the data.

In the Famennian the maximum transgression occurred in the Zadonskian-Eletsian interval (*crepida-rhomboidea* zone interval). In contrast, the Kursa and Zadonsk communities exemplify well-pronounced endemism, possibly explained by isolation of the former basin (Fig. 3) and special deltaic environments of the latter. Subsequently the sea-level decreased (Fig. 4); correspondingly the Ketleri-Plavsk fauna shows strong endemism (Table 6). A minor pulse occurred during the Khovanshchinian, as illustrated by cosmopolitanism and endemism at a time of the corresponding community in the CDF (Table 7). However, in this case, local endemism is possibly due to the special habitat in the peculiar coastal environments of the epicontinental sea.

Thus, certain dependence is proposed between the E-C composition of Devonian vertebrate communities and sea-level changes. This observation correlates with the conclusions made by Turner and Young (1997) for the East Gondwanan and Zhao and Zhu (2007) for the Chinese vertebrate faunas. Deepening would result in increased cosmopolitanism, whilst expansion of endemism may be due to regressions, which increased isolation of faunas, and perhaps created advantages for radiation within limited areas.

6. Conclusions

Main results of the present study are summarised as follows:

- subdivisions of community members into E-C categories is an effective tool in zoogeography;
- assemblages of provincial endemics permit assignment of local communities to a particular zoogeographical province;
- dominance of local endemics suggests isolation of the community from the rest of the province, and also from the open sea;
- two types of dispersal are proposed for Devonian aquatic vertebrates: 1. normal marine and 2. continental, presumably freshwater. The first is exemplified by acanthodians during the Middle Devonian, and by ptyctodonts, struniiforms, and some dipnoans during the Late Devonian; the second by psammosteids, antiarchs, and porolepiforms during the Middle Devonian and by psammosteids, acanthodians, and some arthrodires during the Late Devonian;
- E-C index variation in time reflects tendencies of faunal isolation/connections of communities;
- constant faunal interchanges in the didemic/quasiendemic, polydemic, and cosmopolitan categories are observed between Baltica and Laurentia, but connections to other provinces are sporadic;
- various vertebrate groups show different dispersal capabilities. Agnathans (both thelodonts and psammosteids), phyllolepid placoderms, porolepiforms, osteolepiforms, and dipnoans never enter the cosmopolitan category;
- no clear line separates continental from pelagic faunas, as the members of one fauna often penetrate the living area of another;
- the E-C composition of Devonian vertebrate communities generally correlates with sea-level changes. Transgressions resulted in increased cosmopolitanism; augmentation of endemism may be due to regressions causing greater isolation. Separation from the main sea basin may have created reduction of competition, causing radiation within limited areas.

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