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The Middle Devonian fishes of the Baltic States (Estonia, Latvia) and Belarus

With 4 figures and 3 tables

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This is a contribution to IGCP 328: Palaeozoic Microvertebrates

Abstract

An overview of the range of the Middle Devonian fishes from the Baltic states, Estonia and Latvia, and Belarus is given. The Baltic outcrops, in particular, have yielded a rich and diverse fish fauna containing agnathans (heterostracans, osteostracans), chondrichthyans, placoderms, acanthodians, crossopterygians, dipnoans, and actinopterygians. The representatives of some groups (osteostracans, chondrichthyans, palaeoniscoids) which possess an exoskeleton consisting of small elements, are comparatively poorly known and need description. However, acanthodians present an exception here: the scales of these fishes have been thoroughly studied by VALIUKEVICIUS. The acanthodians are out of the scope of this paper, except some species of special interest. Several fish groups, psammosteid heterostracans, placoderms, crossopterygians, and probably dipnoans were represented during the Aruküla and Burtnieki Ages by very large forms. The fish fauna became somewhat less diverse beginning with the Gauja Age and later. Placoderms and some other fishes are close to those known in the Middle Devonian of Scotland, being favourable to the correlation of the sections in these regions. The data on the Middle Devonian fishes in Belarus are less abundant. Still, they show some differences with the Baltic faunas of the same age. The Eifelian of Belarus has yielded phlyctaeniid arthrodires, in the late Eifelian (Gorodok Regional Stage) occur various chondrichthyans; both in the Eifelian and Givetian the occurrences of ptyctodonts and palaeoniscoids are common.

Keywords: Middle Devonian, fishes, stratigraphical range, Estonia, Latvia, Belarus, correlation

Introduction

The information on the Middle Devonian fishes presented in this paper comes from two Baltic States, Estonia and Latvia, and from Belarus. Estonia and Latvia have been known for a long time as the classical outcrop areas of the Middle Devonian terrigenous and carbonate rocks (Fig. 1). The rocks are exposed on river banks or lake shores, on the shore of the Baltic Sea, also in the quarries for mineral resources: clay in Estonia and Latvia, and in these for oil shale in NE Estonia. Natural exposures in particular as well as numerous boring cores, have yielded rich fossil fish material. The fossil fishes have been studied since the first half of the 19th century. Detailed stratigraphical subdivision has been elaborated based on palaeontological, lithological and mineralogical data. These have been published in many papers and several monographs: of the more recent ones can be listed SOROKIN (1981), VALIUKEVICIUS et al. (1986), KURSS (1992), LYARSKAYA & LUKSEVICS (1992), VALIUKEVICIUS (1994), KLEESMENT (1994, 1995) and KLEESMENT & MARK-KURIK (1997). In comparison with Estonia and Latvia, in Lithuania the Middle Devonian outcrops and the fish specimens collected from them are more limited, and the data from this territory are based mainly on the material from boring cores. Also, there is one stratigra-

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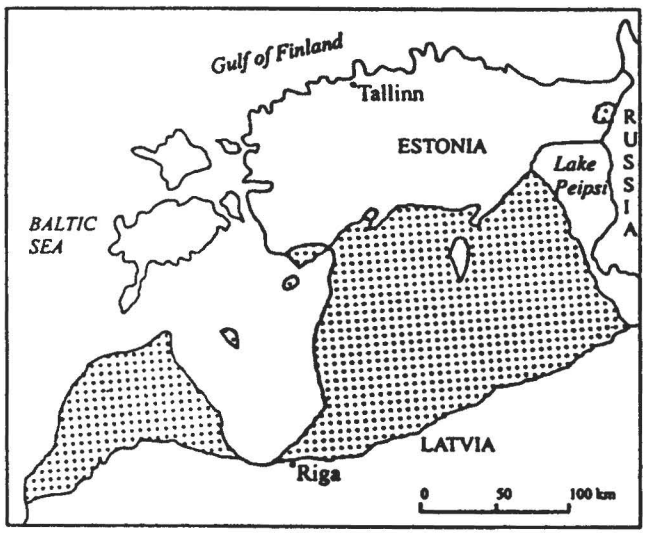

Fig. 1: Middle Devonian outcrop area (spotted) in Estonia and Latvia. Simplified after GRIGELIS (1982).

phical unit, the Sventoji Formation (NARBUTAS 1994) that is distinguished, instead of two formations – the Gauja Formation (with two members) and the Amata Formation known in Latvia and Estonia. For above reasons, the data from Lithuania are, with a few exceptions, not included into the present overview. The information on the Middle Devonian fishes from Belarus comes exclusively from boring cores, and is not very rich either. Some local units are rather poorly characterized by fishes. But the information including both the published data by VALIUKEVICIUS et al. (1995) and the unpublished ones by A. IVANOV (pers. comm., 1997), and by the author of the present paper, is worth to be presented.

All Middle Devonian fish taxa are considered here, except most of the acanthodians as their range and zonation have already been given in quite a number of papers (VALIUKEVICIUS 1988, 1994, 1995, VALIUKEVICIUS et al. 1986, 1995, VALIUKEVICIUS & KRUCHEK, this volume) and a monograph (VALIUKEVICIUS 1985). Yet, the index species and some other, rare acanthodians are listed all right, and the acanthodian zonation is shown. The range of the Middle Devonian fishes from Estonia and Latvia (Tables 1-3) is based on the published data (GROSS 1942, SOROKIN 1981, MARK-KURIK 1997, LYARSKAYA & LUKSEVICS 1992), and on the unpublished information (P.E. AHLBERG and E. LUKSEVICS, pers. comm., 1997).

Stratigraphical framework

The Middle Devonian in Estonia and Latvia includes presently six local stratigraphical units: the Pärnu, Narva, Aruküla, Burtnieki, Gauja, and Amata Formations, which are considered as regional stages (Fig. 2). The Pärnu and Narva Formations are of Eifelian age, the overlying formations belonging to the Givetian. Fig. 2 also shows the Middle Devonian regional stages of Belarus and their correlation with those in the Baltic, as well as the approximate correlation of the regional units with the standard conodont zones and the Eastern European miospore zones. The palynological data are given after AVKHIMOVITCH et al. (1993), G. VAITIEKUNIENE (in the stratigraphical scheme by NARBUTAS et al. 1993), BLIECK et al. (1996) and KÕRTS & MARK-KURIK (1997). The acanthodian zones are presented after VALIUKEVICIUS (1994, 1995) and VALIUKEVICIUS et al. (1995). Two more fish zonations of the Middle Devonian are known in the Baltic, established on the basis of other biostratigraphically important groups: psammosteid heterostracans and placoderms (Fig. 3). The zones of the acanthodians and the psammosteid genus *Schizosteus* are particularly characteristic of the Eifelian. The psammosteids *Pycnosteus* and *Psammolepis*, and the placoderms *Asterolepis*, *Bothriolepis* and *Watsonosteus* have enabled a detailed zonal subdivision of the Givetian.

Both the lower and the upper boundaries of the Middle Devonian, i.e the Emsian-Eifelian and the Givetian-Frasnian boundary have been under discussion for a considerable time. In the north-western and western regions of the Russian (East European) Platform, which include the Baltic states and Belarus, the Emsian- Eifelian boundary coincides, according to RZHONSNITSKAYA & KULIKOVA (1990), with the boundary of the Rezekne and Pärnu Formations, and the Vitebsk and Adrov Regional Stages, respectively. As to the age dating of the Rezekne Formation by MARK-KURIK (1991a), a fossil fish assemblage, consisting mainly of placoderms (*Wijdeaspis*, in particular) and wide interregional correlation, were used. It was concluded that the Rezekne Formation was rather of Emsian than Eifelian age. The conclusion was based on the occurrences of the thelodont *Skamolepis* and the phlyctaeniid arthrodires. The *Skamolepis fragilis* Zone terminates the thelodont and heterostracan zones of the Lower Devonian in Europe and corresponds probably to the *patulus* and *serotinus* conodont zones (BLIECK et al. in press). VALIUKEVICIUS (1988, 1994, 1995) has several times emphasized the appearance in the Rezekne Formation of typical Middle Devonian acanthodian genera and the correlation of this formation as well as the overlying Middle Devonian Pärnu Formation to the common *Laliacanthus singularis* Zone. This view is also expressed in the paper by VALIUKEVICIUS et al. (1995). The Vitebsk Regional Stage which is correlated with the Rezekne Formation is supposed to belong partly to the Eifelian.

The miospore data show that the lower parts of the Vitebsk Regional Stage or Horizon (from Russian 'gorizont') belong to the *Retusotriletes clandestinus* (RC) Zone; in the Urals its upper subzone has yielded conodonts of the *serotinus* Zone (AVKHIMOVITCH et al. 1993). According to the same authors, the upper part of the Vitebsk Stage and the Rezekne Formation correspond to the *Diaphanospora inassueta* (DI) Zone. The latter in the

	Conodont zones	Acanthodian zones	Mio-spore zones	Estonia		Latvia		Belarus	
				Formation	Beds, Member	Formation	Subf., Beds	Reg. Stage	Beds
Frasnian	*falsiovalis**		BI	Pļaviņas		Pļaviņas		Sargaevo	
Givetian	*disparilis*	*Devononchus concinnus*	IM	Amata		Amata	Upper Lower	Lan'	Zhelon' Ubort'
	hermanni-cristatus			Gauja	Lode Sietiņi	Gauja	Lode Sietiņi		
	varcus	*Diplacanthus gravis*	EX	Burtnieki	Abava Koorküla Härma	Burtnieki	Abava Upper B. Lower B.	Polotsk	Moroch' mr_{1-2} Stolin sl_2 sl_1
	hemiansatus			Aruküla	Tarvastu Kureküla Viljandi	Aruküla	Upper Lower		Goryn' gn_{1-2}
Eifelian	*kockelianus**	*N. kernavensis*	RL	Narva	Kernavė Leivu, L_{1-4} Vadja	Narva	Kernavė Leivu Vadja	Kastyukovichi	ks_{1-3}
	australis	*Pt. rimosum*						Gorodok	gr_{1-3}
	costatus	*Ch. estonicus*						Osveya	os_{1-3}
	partitus	*Laliacanthus singularis*	PT	Pärnu	Tamme Tori	Pärnu	Upper Lower	Adrov	
Emsian	*patulus*		DI	Rēzekne	Upper Lower	Rēzekne	Upper Middle Lower	Vitebsk	Lepel' Obol' Drevyaty
	serotinus?		RC						

Fig. 2: Middle Devonian stratigraphy, acanthodian and miospore zones in Baltic (Estonia, Latvia) and Belarus after GOLUBTSOV (1997), LYARSKAYA (1986), LYARSKAYA & LUKSEVICS (1992), KLEESMENT & MARK-KURIK (1997), KURSS (1992), RZHONSNITSKAYA & KULIKOVA (1990), SOROKIN (1996), VALIUKEVICIUS (1994, 1995), and VALIUKEVICIUS et al. (1986, 1995).
Conodont zones after VALIUKEVICIUS (1995). Asterisks show conodont zones recognized in Baltic and Belarus. Miospore zones and subzones after AVKHIMOVITCH et al. (1993) and BLIECK et al. (1996).
B. = Burtnieki, BI = *Acanthotriletes bucerus - Archaeozonotriletes variabilis insignis* Subzone, *Ch.* = *Cheiracanthoides*, DI = *Diaphanospora inassueta* Zone, EX = *Geminospora extensa* Z., IM = *Ancyrospora incisa - Geminospora micromanifesta* Subz., *N.* = *Nostolepis*, *Pt.* = *Ptychodictyon*, PT = *Periplecotriletes tortus* Z., RC = *Retusotriletes clandestinus* Z., RL = *Rhabdosporites langii* Z.; L_{1-4} are beds in the Leivu Member; the Osveya, Gorodok and Kastyukovichi beds have three subdivisions (os_{1-3}, gr_{1-3} and ks_{1-3}), the Goryn', Stolin and Moroch' beds two subdivisions (gn_{1-2}, sl_{1-2} and mr^*_{1-2}).

	Estonia, Latvia		Heterostracan, Thelodont* Zones	Placoderm Zones	Acanthodian Zones
	Formation	Beds, Member			
Frasnian	Pļaviņas			*Bothriolepis cellulosa*	
Givetian	Amata			*B. obrutschewi* *Bothriolepis prima*	*Devononchus concinnus*
	Gauja	Lode Sietiņi	*Psammolepis paradoxa*	*Asterolepis ornata*	
	Burtnieki	Abava Koorküla Härma	*Psammolepis abavica* *Pycnosteus tuberculatus*	*Watsonosteus* *Asterolepis dellei*	*Diplacanthus gravis*
	Aruküla	Tarvastu Kureküla Viljandi	*Pycnosteus pauli* *P. palaeformis*		
Eifelian	Narva	Kernavė Leivu Vadja	*Schizosteus striatus*	*Coccosteus cuspidatus*	*N. kernavensis* *Pt. rimosum* *Ch. estonicus*
	Pärnu	Tamme Tori	*Schizosteus heterolepis*		*Laliacanthus singularis*
Emsian	Rēzekne		*Skamolepis fragilis**		

Fig. 3: Middle Devonian fish zones in Estonia and Latvia after BLIECK et al. (in press, Fig. 6), GROSS (1942), HALSTEAD TARLO (1964), IVANOV & LUKSEVICS (1996), LYARSKAYA (1981a-b), MARK-KURIK (1981, 1993b, 1997), and VALIUKEVICIUS (1994, 1995).
B. = Bothriolepis, Ch. = Cheiracanthoides, N. = Nostolepis, P. = Pycnosteus, Pt. = Ptychodictyon.

western slope of the Urals, contains conodonts of the *patulus* and *partitus* Zones belonging, thus, partly to the Eifelian. As the above data are controversial, the correlation of the regional stratigraphical units at the Emsian-Eifelian boundary and the standard conodont zones has been provided indirectly using the palynological data, and the index species of conodonts come from a distant region (the Urals), it is reasonable for the time being to preserve the boundary in the Baltic between the Rezekne and Pärnu Formations. GOLUBTSOV (1997) mentions that though the age of the Vitebsk Stage is still disputable, this stage could be considered of Late Emsian age. Therefore also of the Lower-Middle Devonian boundary could be placed between the Vitebsk and Adrov Stages.

The problem with the position of the upper limit of the Middle Devonian is similar to that with the lower one as it has not yet completely solved. The conodont occurrences are mentioned in the lower Frasnian Plavinas Formation, but these fossils except one, *Polygnathus pennatus*, have not been listed (VALIUKEVICIUS 1995). Earlier it was mentioned that the conodonts belong to the *asymmetricus* Zone (VALIUKEVICIUS 1994). To establish the Givetian-Frasnian boundary in the Baltic area, the data on conodonts from the Timan-Pechora province and similar fish faunas in the boundary beds of both regions have been used (KUZMIN 1995, 1997, IVANOV & LUKSEVICS 1996). According to IVANOV & LUKSEVICS (1996), the fish assemblage of the *cellulosa* Zone characterizing the Plavinas Formation of the Baltic (in particular its two lower subdivisions) has been established in Middle and South Timan. In the latter region fishes of the *cellulosa* Zone occur together with conodonts of the lower *asymmetricus* Zone in the upper member of the Timan Formation and in the overlying lower member of the Uste Yarega (= Ust'-Yarega) Formation. It can be supposed that the *prima-obrutschewi* Zone corresponding to the Amata Formation could, at least partly, be correlated with the lowermost *asymmetricus* Zone or, according to the present conodont zonation, with the earlier part of the early *falsiovalis* Zone (WEDDIGE 1996). The fish assemblages of the Uste Chirka (= Ust'-Chirka) Formation in Middle Timan and Kumushka Formations in North Timan are very close to that of the Amata Formation, whereas the assemblage from the lower member of the Timan Formation considered as an approximate age equivalent of the above units, resembles more the assemblage of the lowermost part of the Plavinas Formation (Snetnaya Gora Member). SOROKIN (1996) has correlated the Kumushka Formation even with the Gauja Formation. The fishes in the upper member of the Timan Formation (IVANOV & LUKSEVICS 1996) or the Upper Timan Regional Substage corresponding to the beds with *Polygnathus pennatus* (KUZMIN 1997) are much more numerous, and close to those known from the Plavinas Formation.

According to ESIN et al. (this volume), the *cellulosa* Zone (i.e. the Plavinas Formation and its age equivalents in Timan) can be correlated with the *transitans* conodont Zone corresponding to the upper part of the lower *asymmetricus* Zone (WEDDIGE 1996). In this case then the *prima-obrutschewi* fish Zone or the Amata Formation may correspond to the *falsiovalis* conodont Zone or to part of it. ESIN et al. (in press) show that the position of the Givetian-Frasnian boundary could be either at the base or at the top of the Amata Formation. One more position of the boundary, on some level in the Amata Formation, is also probable (IVANOV, pers. comm., 1998). In the recent stratigraphical scheme of Belarus (GOLUBTSOV 1997, Table 4) the Lan' Regional Stage, an age equivalent of the Gauja and Amata Formations, is included into the Givetian. In the text of the same publication this stage is considered as the lowermost part of the Frasnian. This controversy can be explained with differences in age dating of the characteristic "*Estheria* Beds" used for interregional correlation of the sections of Poland, Ukraine and Belarus: in Poland they belong to the Givetian, in Belarus to the Frasnian Lan' Regional Stage. In the above-mentioned scheme and correlation chart (GOLUBTSOV 1997) the Givetian age of the Lan' Stage is preferred.

The miospore data do not give an unequivocal solution to the Givetian-Frasnian boundary problem, either. According to AVKHIMOVITCH et al. (1993) the position of the *Contagisporites optivus-Spelaeotriletes krestovnikovii* (OK) Zone with the *Ancyrospora incisa-Geminospora micromanifesta* (IM) and the *Acanthotriletes bucerus-Archaeozonotriletes variabilis insignis* (BI) Subzones was unclear. The zone could correspond to some conodont zone within a considerable interval from the Givetian *varcus* Zone to the Frasnian *punctatus* Zone. OVNATANOVA et al. (1996) correlated the Timan and the overlying Sargaevo Regional Stages of the East European Platform with the *A. bucerus-Ar. variabilis insignis* (BI) Subzone, considering this subzone as an equivalent of the *falsiovalis* and *transitans* conodont Zones. BLIECK et al. (1996) discovered the miospore assemblage of the *Ancyrospora incisa-Geminospora micromanifesta* (IM) Subzone in the Lode Member of the Gauja Formation of Estonia. This subzone was so far known from the lower portion of the Lan' Regional Stage of Belarus, from the Pashiya Regional Stage and several other units of the East European (Russian) Platform (AVKHIMOVITCH et al. 1993). RODIONOVA & UMNOVA (1997) correlated in the Moscow Basin the earlier part of the *C. optivus-S krestovnikovii* (OK) Zone with the Pashya Regional Stage and the latter unit approximately with the *hermanni-cristatus* and *disparilis* conodont Zones of the Givetian. From this correlation it follows that the Gauja Formation of the Baltic, a probable equivalent of the Pashiya Regional Stage or an equivalent of some upper part of the latter (RZHONSNITSKAYA & KULIKOVA 1990), containing miospores of the *A. incisa-G. micromanifesta* Subzone (IM), may be of Givetian age. It is worth to mention that the Moscow Basin as a region adjacent to the Baltic area and

Belarus seems to be more suitable for correlation and age dating than the distant Timan Pechora province. Valuable data on conodonts come also from the Voronezh region, situated to the south of the Moscow Basin (ARISTOV 1988). In this region the probable Givetian Pashiya and Kynovskii Regional Stages, underlying the Sargaevo Stage or the beds with *Ancyrodella rotundiloba*, are correlated with the *hermanni-cristatus* and lowermost *asymmetricus* Zones. Because of the above discrepancies, in the present paper the Middle-Upper Devonian (Givetian-Frasnian) boundary is considered as corresponding roughly to the boundary of the Amata and Plavinas Formations.

The Eifelian-Givetian boundary in the Baltic is based on the occurrences of the conodonts in the Kernave Member, the upper member of the Narva Formation (VALIUKEVICIUS & OVNATANOVA 1993, VALIUKEVICIUS 1994, 1995). The conodont assemblage containing *Icriodus struvei, Polygnathus linguiformis linguiformis, P.l. alveolus, P. parawebbi, P.* cf. *xylus ensensis, P.* cf. *costatus oblongus* and *Coeloceradontus* species has permitted to correlate the Kernave Member with the uppermost Eifelian *kockelianus* Zone.

The Middle Devonian fishes of the Baltic States and their stratigraphical range

The fishes known from the Middle Devonian of the Baltic area and also from Belarus, characterize the flourishing period of the Devonian fish faunas. Biogeographically, they belong to the eastern part of the Euramerican Province (DINELEY & LOEFFLER 1993). All main fish groups, such as agnathans, placoderms, acanthodians, crossopterygians, dipnoans, and actinopterygians are present and show a great diversity. According to the recent information (Tables 2 A-B, 3), chondrichthyans were also present in the fish assemblages, though they are still very rare and poorly known. Psammosteid heterostracans dominate, but are comparatively rare outside of the North-West of the East European Platform (HALSTEAD TARLO 1964). Numerous placoderms (arthrodires, antiarchs), acanthodians and crossopterygians, particularly porolepiforms and osteolepiforms are frequent. Tesselated osteostracans as well as palaeoniscoids are rather common, but they are represented by microremains, and so is the case with acanthodians. Giant forms occur among the representatives of several groups: psammosteids (*Tartuosteus* and *Pycnosteus* could reach 2.5 m in length), arthrodires (estimated length of *Homostius* and *Heterostius* is over 5 m) and holoptychiids (more than 3 m in length, Per E. AHLBERG , pers. comm., 1997). Very large forms can also be met with among dipnoans, e.g., a *Conchodus* tooth plate discovered in the Aruküla Formation is 6 cm long. A certain decline of the Middle Devonian fish fauna took place in the Gauja Age and further on when the fish assemblages became less variable.

The time of giants did not start from the very beginning of the Middle Devonian. Characteristic for the Pärnu Formation, particularly for the Tori Member (Table 1), are psammosteids of moderate size, *Schizosteus heterolepis* (PREOBR.) and *Psammolepis toriensis* (MARK-KURIK). Osteostracan tesserae occur in this member. A tesselated form from this group of agnathans, *Balticaspis latvica*, has been described by LYARSKAYA (1981a) from Latvia (Talsi boring core, depth 379.4 m). The long ranging actinolepid arthrodire *Actinolepis tuberculata* AG. and antiarch *Byssacanthus dilatatus* (EICHW.) are rather common. Remarkable is the occurrence of rhombic scales of *Porolepis* sp. with bands of very small tubercles and ridges anteriorly to the cosmine-covered surface. GROSS (1942) in the list of the Pärnu (Pernau) fishes mentioned this form as *Porolepis* n.sp.; in Fig.15, one of its scales was determined by him as belonging to *Porolepis posnaniensis* KADE. The crossopterygian genus *Porolepis* is mainly known from the Lower Devonian (ØRVIG 1969).

Of the three subdivisions of the Narva Formation the lower, Vadja and the upper, Kernave Member contain characteristic fish species, whereas the middle, Leivu Member has yielded only longer ranging taxa (Table 1). Among the finds from the Vadja Member, two arthrodires are of note. One of them is a new *Holonema* species (*Holonema* sp.A MARK-KURIK) with an unusual ornamentation consisting of fine tubercles not fused into ridges. The other one, a coccosteid, perhaps belongs to the genus *Protitanichthys*. Recently *Protitanichthys? montanus* was described by OTTO (1997a) from the Eifelian Mühlenberg Formation of Rhineland. OTTO (1997b; pers. comm., 1996) has also reported the occurrence of a tuberculated *Holonema* species from the Eifelian Brandenberg Formation of the same region. The Mühlenberg Formation belongs to the *costatus* conodont Zone, the Brandenberg Formation to the *australis* and lower part of the *kockelianus* Zone (CLAUSEN et al. 1993). The above arthrodires could thus give a possibility to correlate the Baltic section to those in Rhineland and specify the age dating of the Narva Formation.

The Kernave Member is characterized by the psammosteids *Schizosteus striatus* and *Pycnolepis splendens*. Not only isolated tesserae of osteostracans but also skeletal fragments, up to 5 cm long, consisting of these platelets, have been discovered in the Gorodenka locality. The latter is the richest locality of the Kernave Member situated in the north-western part of Estonia. A *Holonema* species (*Holonema* sp.B MARK-KURIK) with a typical holonematid ornamentation consisting of ridges, is common in the same locality. This species is fairly close to *Holonema radiatum* OBR., coming from the Eifelian of the Oviedo region, Spain, and associated with conodonts of the middle and upper parts of the *costatus* Zone (LELIÈVRE et al. 1990). All the coccosteid material, described or mentioned as *Coccosteus orvikui* (GROSS 1940, OBRUCHEVA 1962) and *Millerosteus? orvikui* (MARK-

Tab. 1: Ranges of the Middle Devonian (Eifelian) fishes (mainly macroremains) in Estonia and Latvia, after SOROKIN (1981), MARK-KURIK (1997), LYARSKAYA & LUKSEVICS (1992), and VALIUKEVICIUS (1994). X = occurrence in Estonia; O = occurrence in Latvia; > shows that a taxon occurs in the overlying unit. Index species are in bold characters. Of acanthodians only index species are listed.

Taxa / Formation / Member	Pärnu	Narva		
		Vadja	Leivu	Kernavė
Schizosteus heterolepis (Preobr.)	XO			
Psammolepis toriensis (Mark-Kurik)	XO			
Balticaspis latvica Lyarsk.	O			
Homostius sp.	XO			
Porolepis sp.	X			
Laliacanthus singularis Kar.-Tal.	X			
Thursius talsiensis Vorob.	O			
Gyroptychius? latvicus Vorob.	O			
Hybosteus? sp.	X			
Cheirolepis gracilis Gross	X	X		
Tartuosteus sp.	XO			X?
Dipnoi gen.indet.	X?	X	X	
Cephalaspidida gen.indet.	X	XO	XO	XO >
Osteolepididae gen.indet.	X	X	X	X
Actinolepis tuberculata Ag.	XO	O	O	XO >
Byssacanthus dilatatus (Eichw.)	XO	XO	XO	XO >
Glyptolepis spp.	X	XO	XO	XO >
Holonema sp.A Mark-Kurik		X		
Protitanichthys? sp.n.		X		
Cheiracanthoides estonicus Valiuk.		X		
Onychodus sp.		X		X
Orvikuina sp.		XO	XO	O >
Schizosteus striatus (Gross)		O	O	XO >
Asterolepis estonica Gross		O	O	XO >
Homostius latus Asm.			O	XO >
Coccosteus cuspidatus Miller ex Ag.			O	XO
Ptychodictyon rimosum Gross			X	X>
Thursius fischeri (Eichw.)			O	XO
Gyroptychius? grossi Vorob.			O	O
Dipterus serratus (Eichw.)			O	XO
Orvikuina vardiaensis Gross			O	XO
Cheirolepis spp.			XO	XO>
Pycnolepis splendens (Eichw.)				XO
Pycnosteus sp.				X
Ganosteus sp.				X
Holonema sp.B Mark-Kurik				X
Heterostius? sp.				X
Ptyctodontida gen.indet.				X
Nostolepis kernavensis Valiuk.				X

KURIK 1981), can be regarded as belonging to *Coccosteus cuspidatus* MILLER ex AG. More recent finds show that small plates serving for establishing the species *C. orvikui*, actually belong to juvenile specimens of *C. cuspidatus*. *C. cuspidatus* is a very common arthrodire in the Lower Caithness Flagstone Group, particularly in the Achanarras Limestone and its age equivalents in Scotland, largely referred to as Eifelian (HOUSE et al. 1977, DINELEY & LOEFFLER 1993, YOUNG 1995). One more placoderm fish of the same age known from Achanarras and Edderton, Scotland, is the ptyctodont identified as *Rhamphodopsis* cf. *threiplandi* WATSON (MARK-KURIK 1991b). Its only occurrence, an anterior dorsolateral plate, comes from the Kernave Formation in Lithuania, Taurage boring core, depth 659.85-659.95 m (figured by MARK-KURIK 1977 under the name Ptyctodontida n.gen.). The Kernave Formation has recently revealed another ptyctodont anterior dorsolateral plate from the

Värska boring core (depth 204.3-205.8 m), SE Estonia. This tiny plate cannot be identified at generic level. The bone fragments of the arthrodire *Homostius* met with in the Kernave Member (Gorodenka locality) are sometimes fairly large and massive. The fragments could be confused with those of another giant fish, *Heterostius*. Therefore, the latter was identified in the Narva Formation by GROSS (1942) with some doubt.

The Aruküla Formation is subdivided into three stratigraphical units (KLEESMENT 1994). The two lower ones, *viz.*, Viljandi and Kureküla Beds differ in the occurrences of *Pycnosteus* species (Table 2A). The Viljandi Beds contain *P. palaeformis*, the Kureküla Beds are characterized by *P. pauli*. Both units, as well as the overlying Tarvastu Beds have quite a number of fishes in common, particularly among psammosteids (*Tartuosteus giganteus*, *Ganosteus artus*, *Psammolepis proia*), placoderms (e.g. *Asterolepis estonica, Byssacanthus dilatatus*) and several crossopterygians. The huge arthrodires *Homostius latus* ASM. and *Heterostius ingens* ASM. are equally frequent both in the Aruküla Formation and in the overlying Burtnieki Formation. From an unpublished revision (referred in MARK-KURIK 1992) based on abundant material from many Baltic localities, it appeared that only one species of both genera *Homostius* and *Heterostius* indicated above is valid.

The fishes known so far from the Viljandi Beds are of note. One of them is a very large porolepiform preliminarily determined as Holoptychiidae gen.n.1 by P.E. AHLBERG (pers. comm., 1997). This crossopterygian has been discovered in the collection from the Aruküla caves, one of the oldest known excavation sites near Tartu in Estonia. The same locality and another one (Tähtvere) have yielded bicuspid teeth of very small size belonging to not yet identified chondrichthyans. These teeth somewhat resemble elasmobranch teeth of late Givetian/early Frasnian age from the Southern Hemisphere described by G.C. YOUNG (1982) under the names *Antarctilamna and Xenacanthus*. Among the rather frequent dipnoan tooth plates determined as *Dipterus* spp. there is one specimen which shows a *Rhinodipterus* structure (K.S.W. CAMPBELL, pers. comm., 1997).

From the Kureküla Beds comes a very large dipnoan, *Conchodus* sp., and a rare fish of unclear origin, *Hybosteus*. The rare remains of these fishes and a peculiar acanthodian fin-spine, described under the name *Nodocosta pauli* (GROSS 1940) come from the Tamme locality. This is a rich locality on the eastern shore of Lake Võrtsjärv which, during the excavations in 1993, yielded the single articulated fossil fish from Estonia, a specimen of the acanthodian *Cheiracanthus*(?).

The remain of only one fish can be reported so far as being restricted to the Tarvastu Beds. It probably belongs to the coccosteid *Millerosteus*. The psammosteid *Tartosteus maximus*, characterizing the overlying Burtnieki Formation, in particular its two lower subdivisions, may also occur in the Tarvastu Beds.

The Burtnieki Formation (Table 2 A-B) has revealed two fish faunas which differ rather markedly. The first of both occurs in the two lower subdivisions, Härma and Koorküla Beds, the second is characteristic of the Abava Beds. There are three fishes which are known only from the Härma Beds. One of them is the antiarch *Asterolepis* sp.1 (KARATAJUTE-TALIMAA 1963). The second is a holoptychiid of moderate size, *Glyptolepis* cf. *paucidens* AG., formerly described by VOROBYEVA (1987) as *Paraglyptolepis karksiensis* and reidentified by P.E. AHLBERG (pers. comm., 1997). The listed fossils come from the Karksi locality, Estonia, and so does the third fish, a very large crossopterygian, determined by AHLBERG as Holoptychiidae gen.n. 2.

Quite a number of fishes occur both in Härma and Koorküla Beds, e.g. psammosteids *Pycnosteus tuberculatus* and *Psammosteus bergi*. Among these fishes there are also the arthrodires *Dickosteus*? *markae* and *"Holonema" haermae*. The first of them was preliminarily described as a species of the genus *Coccosteus* (OBRUCHEVA 1962), but it can be regarded with some doubt as a *Dickosteus* species (similarly to *C. grossi* from the Aruküla Formation). *"Holonema" haermae* differs from the other species of the genus in possessing a high median dorsal crest and, quite evidently, belongs to a new genus. The antiarch *Asterolepis dellei* and the dipnoan *Grossipterus crassus* are discovered so far only in the Latvian fish localities. The dipnoan, as well as the psammosteid *Ganosteus stellatus* and arthrodire *Actinolepis magna*, have a longer range. *Ganosteus* fragments with an especially coarse ornamentation occur even in the Sietini Member of the Gauja Formation. Several fishes are common for the Koorküla and Abava Beds, e.g., an undescribed *Byssacanthus* species and the crossopterygians *Hamodus lutkevitshi* and *Panderichthys*? sp. Only from the Koorküla Beds comes probably the acanthodian *Nodocosta* that seems to differ from the Aruküla species, *N. pauli*.

The Abava Beds contain several species in common with the lower subdivisions of the Burtnieki Formation (Table 2 A) and a significant number of fishes that occur only in this stratigraphical unit (Table 2 B). This is why attempts were made to regard these beds as a formation or regional stage (KURIK et al. 1989, MARK-KURIK 1993a). However, the lithological and mineralogical characters have been considered insufficent to give to the Abava Beds a higher rank (KLEESMENT 1995) or even to distinguish them from the Lower Gauja Subformation (KURSS 1992). The psammosteid *Psammolepis abavica* can serve as a good index fossil (Table 2B). The arthrodires *Watsonosteus* and *Livosteus* are highly characteristic of these beds. These very close genera need a thorough revision. It is not excluded that *Watsonosteus* (MILES & WESTOLL 1963) appears to be a junior synonym of *Livosteus* (OBRUCHEVA 1962). One more arthrodire, described by OBRUCHEVA (1962) under the name *Plourdosteus*(?) *panderi*, is now determined as *Eastmanosteus*

Tab. 2A: Ranges of the Middle Devonian (Givetian) fishes in Estonia and Latvia, after SOROKIN (1981), MARK-KURIK (1997), LYARSKAYA & LUKSEVICS (1992), and VALIUKEVICIUS (1994). X = occurrence in Estonia; O = occurrence in Latvia; > shows that a taxon occurs in the overlying unit. Index species are in bold characters.

Formation	Aruküla			Burtnieki			Gauja
Taxa / Beds, Member	Viljandi	Kureküla	Tarvastu	Härma	Koorküla	Abava	Sietiņi
Holoptychiidae gen.n.1 Ahlberg	X						
Rhinodipterus sp.	X						
Chondrichthyes	X						
Schizosteus striatus (Gross)	O	O					
Pycnosteus palaeformis Preobr.	XO	O					
Orvikuina spp.	XO	O					
Cheirolepis spp.	XO	X					
Tartuosteus giganteus (Gross)	XO	XO	XO				
Ganosteus artus Mark-Kurik	XO	XO	XO				
Psammolepis proia Mark-Kurik	XO	XO	O				
Actinolepis tuberculata Ag.	XO	XO	O				
Holonema obrutshevi Mark	XO	O	O				
Dickosteus? grossi O.Obr.	XO	XO	O				
Byssacanthus dilatatus (Eichw.)	XO	XO	O				
Asterolepis estonica Gross	XO	XO	O				
Tartuosteus? luhai Mark-Kurik	O	XO	XO				
Thursius estonicus Vorob.	O	XO	O				
Gyroptychius pauli Vorob.	XO	XO	XO				
Cephalaspidida gen.indet.	X			X			
Homostius latus Asm.	XO	XO	XO	XO	XO		
Heterostius ingens Asm.	XO	XO	XO	XO	XO		
Diplacanthus gravis Valiuk.	X	X	X	X>			
Dipterus spp.	X	X	X	O	O		
Glyptolepis spp.	XO	XO	XO	O	XO	X	
Cheiracanthus sp.		X					
Conchodus sp.		X					
Hybosteus sp.		X					
Pycnosteus pauli Mark		XO	XO				
Nodocosta pauli Gross		X		O	O	O	
Millerosteus? sp.			X				
Tartuosteus maximus Mark-Kurik			X?	XO	O		
Asterolepis sp.1 Kar.-Tal.				X			
Glyptolepis cf. ***paucidens*** Ag.				X			
Holoptychiidae gen.n.2 Ahlberg				X			
Pycnosteus tuberculatus Rohon				XO	XO		
Psammosteus bergi (Obr.)				XO	O		
"*Holonema*" *haermae* Mark				X	O		
Dickosteus? *markae* O.Obr.				XO	O		
Asterolepis dellei Gross				O	O		
Gyroptychius elgae Vorob.				XO	O		
Psammolepis spp.				X	X	X	
Actinolepis magna Mark-Kurik				XO	O	X	
Plourdosteus sp.				O	O	O	
Ganosteus stellatus Rohon				XO	XO	XO	O
Psammosteus spp.				O	O	XO	O
Grossipterus crassus (Gross)				O?	O		O
Nodocosta sp.					X		
Byssacanthus spp.					X	X	
Hamodus lutkevitshi Obr.					XO	X	
Panderichthys? sp.					X	X	

Tab. 2B: Middle Devonian (Givetian) fishes in Estonia and Latvia [continued].

Formation / Taxa / Beds, Member	Burtnieki	Gauja		Amata
	Abava	Sietiņi	Lode	
Psammolepis abavica Mark-Kurik	XO			
Watsonosteus sp.n.?	XO			
Livosteus grandis Gross	O			
Livosteus? sp.	O			
Eastmanosteus cf. *pustulosus* (Eastm.)	O			
Asterolepis essica Lyarskaya	XO?			
Microbrachius cf. *dicki* Traq.	X			
Chondrichthyes?	X			
Osteolepis striata Gross	O			
Laccognathus sp.	X			
Cheirolepis gaugeri Gross	X			
Moythomasia? sp.	X			
Glyptolepis sp.	X	X		
Psammolepis venyukovi Obr.		XO		
Psammolepis heteraster Gross		XO		
Hybosteus mirabilis (Gross)		O		
Bothriolepis sp.		O		
Megadonichthys kurikae Vorob., in litt.		X		
Psammolepis paradoxa Ag.		XO	O	
Psammolepis alata Mark-Kurik		XO	O	
Asterolepis ornata Eichw. sensu Ag.		XO	O	
Laccognathus panderi Gross		XO	O	O
Panderichthys rhombolepis (Gross)		XO	O	O
Glyptolepis baltica Gross		XO	O?	O
Psammolepis undulata (Ag.)		O		XO
Plourdosteus livonicus (Eastm.)		XO		O?
Holoptychius? sp.		O		O
Lodeacanthus gaujicus Upeniece			O	
Latvius sp.n. Upeniece			O	
Eusthenopteridae			O	
Strunius sp.n. Upeniece			O	
Actinistia			O	
Cheirolepis sp.			O	
Psammosteus levis Obr.				O
Psammosteus cuneatus Obr.				O
Psammosteus livonicus Obr.				O
Bothriolepis prima Gross				X?O
Bothriolepis obrutschewi Gross				O
Eusthenopteron obruchevi Vorob.				O
Psammosteus praecursor Obr.				XO >?
Psammosteus maeandrinus? Ag.				XO >
Asterolepis radiata Rohon				XO >
Onychodus sp.				O >
Dipterus sp.				O >

cf. *pustulosus* (IVANOV, pers. comm., 1997). This widely distributed genus has previously not been reported from the Baltic area. Two antiarchs occur: a fairly large species of *Asterolepis*, *A. essica* and one of the smallest representatives of this group, *Microbrachius*. In connection with the former it should be mentioned that the large *Asterolepis* species, *A. essica*, *A. ornata* and *A. radiata* characterize the Abava Beds and the Gauja and Amata Formations. Small denticles (with one or three cusps and long "root") coming from Essi locality, Estonia may belong to a chondrichtyan. Of the crossopterygians the occurrences of *Laccognathus* and *Osteolepis striata* are noteworthy. The very large holoptychiid *Laccognathus* becomes common in the Gauja and Amata Formations.

In *O. striata* the cosmine of the scales is finely striated showing thus an unusual character (GROSS 1942). Both placoderm genera *Watsonosteus* and *Microbrachius* are of much value for interregional correlation, occuring in the John o'Groats and Eday Groups of Scotland (HOUSE et al. 1977) and other regions (MARK-KURIK 1991b).

In the Gauja Formation (Table 2 A-B), the diversity of psammosteids has markedly diminished at the generic level. These heterostracans are very frequent in the lower, Sietini Member but most of them belong to the genus *Psammolepis*. Of the *Psammolepis* species, more common are *P. paradoxa, P. venyukovi* and *P. alata*. The former two species are close in their structure, though their ornamentation is different. *Psammolepis undulata* is also reported from the Gauja Formation, but, actually, is more abundant the overlying Amata Formation. The diversity of placoderms is also small. Among them the coccosteid arthrodire *Plourdosteus livonicus* and antiarchs *Asterolepis ornata* and *Bothriolepis* sp. can be mentioned. *Bothriolepis*, and also *Hybosteus mirabilis* are very rare in the Gauja Formation. *Asterolepis ornata* is one of the most common fossils in both members of this formation. The discovery of hundreds of articulated specimens of *Asterolepis ornata* adult individuals in the Lode clay quarry, Latvia (LYARSKAYA & MARK-KURIK 1972), is one of the most important event in the history of the study of fossil fishes not only in the Baltic but also on the whole East European Platform. After the description of this remarkable material (LYARSKAYA 1981b), the results of several other highly interesting studies were published concerning *Asterolepis* juveniles (UPENIECE & UPENIEKS 1992) and squamation of this placoderm (IVANOV et al. 1996). Equally remarkable is the occurrence in the same locality of the articulated specimens of the acanthodian *Lodeacanthus* (UPENIECE 1996), and two large crossopterygians, *Laccognathus panderi* and *Panderichthys rhombolepis*. The latter has repeatedly been studied (review *in* VOROBYEVA & SCHULTZE 1991). In recent years the number of crossopterygians in the Lode Member has increased, including the representatives of Onychodontidae (*Strunius* sp.n.), Osteolepididae (*Latvius* sp.n.), Eusthenopteridae and Actinistia (UPENIECE 1996; LUKSEVICS, pers. comm., 1997).

The Amata Formation (Table 2B) shows the same tendency of a certain decline of fish diversity as can be observed in the Gauja Formation. *Psammosteus* species become markedly dominant instead of the various species of *Psammolepis*. Of the latter ones *P. undulata* is quite common. The representatives of the genus *Psammosteus* occur in the underlying Burtnieki and Gauja formations (Table 2A) but are still poorly known (except *Psammosteus bergi* from the Burtnieki Formation). *Psammosteus praecursor* and *P. livonicus* are more frequent in comparison with the other species of this genus. As to *Psammosteus maeandrinus*, its occurrence in the Amata Formation is dubious. OBRUCHEV has mentioned that the fragments of *P. maeandrinus* cannot often be distinguished from those of *P. praecursor* (OBRUCHEV & MARK-KURIK 1965). The remains of the antiarch *Asterolepis radiata* are abundant. Two small bothriolepids, *Bothriolepis prima* and *B. obrutschewi* are common (KARATAJUTE-TALIMAA 1966). They are characteristic of the lower and the upper parts of the Amata Formation, respectively. The Amata fish assemblage contains, indeed, several representatives of crossopterygians (*Laccognathus, Panderichthys, Eusthenopteron* etc) and a dipnoan (*Dipterus* sp.). Rich collections of the Amata fishes came from the Pasta Muiza locality on the Daugava River, which was described in detail (VOROBYEVA & LYARSKAYA 1968). In late sixties the locality remained below the water level of the Plavinas power station reservoir.

Correlation with Scotland

As already mentioned, there is a significant number of Middle Devonian fishes that occur both in the Baltic area and in Scotland. The fishes coincide on generic level, and some of them may be identical even on the species level. A correlation chart (Fig. 4) modified after MARK-KURIK (1981, 1991b) and DINELEY & LOEFFLER (1993) is presented to illustrate the similarity of the placoderm faunas of both regions. In the Baltic, the Kernave Member of the Narva Formation is an important unit as it has revealed Scottish forms known from the Lower Caithness Flagstone Group, in particular, from the Achanarras Limestone and its age equivalents. These are *Coccosteus cuspidatus, Rhamphodopsis* cf. *threiplandi* and *Homostius*. The Aruküla Formation and the lower members of the Burtnieki Formation (Härma, Koorküla) contain *Dickosteus*?, *Millerosteus*? and *Homostius* resembling the Upper Caithness Flagstone Group. The Abava Beds, the John o'Groats Group and Eday Beds are characterized by *Watsonosteus* and *Microbrachius*. In the upper part of the Givetian some other fishes are also useful for correlation: the psammosteid *Psammolepis undulata* and the crossopterygian *Laccognathus* (previously described as *Holoptychius decoratus*; P.E. AHLBERG, pers. comm., 1997). The closeness of the large *Asterolepis* species, *A. ornata, A. radiata* and *A. maxima* has been pointed out by KARATAJUTE-TALIMAA (1963). These fishes just are essential components in the assemblages of the Gauja and Amata Formations and the Nairn Beds.

It is worth adding that the Achanarras Limestone and its equivalents in Scotland have been correlated by YOUNG (1995) with the *Hystricosporites reflexus* miospore Interval Zone approximately corresponding to the middle part of the Oppel Zone AD (*Acinosporites acanthomammillatus-Densosporites devonicus*) marked as AD Ref. The Interval zone Ref corresponds to the *Rhabdosporites langii* Zone of Eastern Europe (AVKHIMOVITCH et al. 1993) or to a part of this zone (STREEL & LOBOZIAK 1996). The miospores of the *R. langii* Zone are known to occur in the Kernave Substage

	Conodont zones	Mio-spore zones	Estonia, Latvia			Scotland	
Frasnian	*falsiovalis**	BI	Pļaviņas			Boghole	
Givetian	*disparilis*	IM	Amata		*P. undulata* *A. radiata*	Nairn	*P. undulata* *Asterolepis maxima*
			Gauja	Lode Sietiņi	*Laccognathus* *A. ornata*		*Laccognathus*
	hermanni-cristatus	EX	Burtnieki	Abava	*Watsonosteus* *Microbrachius*	John o'Groats + Eday	*Watsonosteus* *Microbrachius*
	varcus			Koorküla Härma	*Dickosteus?*	Upper Caithness Flagstone Group	*Dickosteus*
			Aruküla	Tarvastu Kureküla Viljandi	*Millerosteus?* *Homostius*		*Millerosteus* *Homostius*
	hemiansatus						
Eifelian	*kockelianus**	RL	Narva	Kernavė	*C. cuspidatus* *R. cf. threiplandi*	Achanarras Lmst	*Coccosteus cuspidatus* *R. threiplandi*
	australis *costatus*			Leivu Vadja	*Homostius*	Lower Caithness Flagstone Group	*Homostius*
	partitus	PT	Pärnu	Tamme Tori	*Homostius*	hiatus?	
Emsian	*patulus*	DI	Rēzekne				

Fig. 4: Correlation of the Middle Devonian of Baltic (Estonia, Latvia) and Scotland, based mainly on placoderms. *A.* = *Asterolepis*, *C.* = *Coccosteus*, *P.*= *Psammolepis*, *R.* = *Rhamphodopsis*. For the other abbreviations, see Fig. 2.

in the East Baltic and in the Gorodok and Kastiukovitchi Stages in Belarus.

The Middle Devonian fishes of Belarus

The data on the Middle Devonian fishes of Belarus (Table 3) are not uniform except for those given on acanthodians (VALIUKEVICIUS et al. 1995). Of the fishes known from the Adrov Regional Stage, an unidentified phlyctaeniid arthrodire and the palaeoniscoid *Cheirolepis sinualis* KAR.-TAL. in litt., as well as fish otoliths are of note. These fossils are not reported from the Pärnu Formation of the Baltic. In the Gorodok Stage the remains of several chondrichthyans such as *Lugalepis multispinata* and *Ohiolepis* etc are noteworthy. Among placoderms occur not only those common in the Narva Formation (*Homostius*?, *Byssacanthus*?) but also a phlyctaeniid and a ptyctodont, belonging probably to new genera. The occurrence *Cheirolepis gracilis* is established in the middle part of the Gorodok Stage. This palaeoniscoid species occurs in the Baltic section somewhat earlier: in the Tori Member, Pärnu Formation, and in the Vadja Member, Narva Formation. A ptyctodont together with the psammosteid *Pycnolepis splendens*? have been met with in the Kastyukovichi Stage, equivalent to the Kernave Member (Fig. 2). The psammosteid *Schizosteus striatus* is identified in the Stolin Beds, thus from a higher level, than in the Baltic. The Stolin Beds have also yielded *Rhynchodus*. This ptyctotont genus has a very wide distribution and a rather long range (Eifelian to Frasnian: DENISON 1978). The antiarch *Microbrachius*? together with the holoptychiid *Laccognathus* and the palaeoniscoid *Cheirolepis gaugeri* indicate that the Moroch' Beds could be correlated with the Abava Beds in the Baltic. The Lan' Regional Stage of Belarus corresponds to the Gauja and Amata Formations (RZHONSNITSKAYA & KULIKOVA 1990, GOLUBTSOV 1997). The assemblage discovered in this stage, particularly the psammosteid *Psammosteus praecursor*, seems to indicate that it coincides with the assemblage of the Amata Formation rather than with that of the Gauja Formation. The occurrences of ptyctodonts and palaeoniscoids almost in all the stratigraphical units of Belarus, the finds of phlyctaeniids in the Adrov and Gorodok Regional Stages and numerous chondrichthyans in the Gorodok Stage (a probable equivalent of the Leivu Member of the Narva Formation) show that in this part of the East European Platform the environmental conditions were somewhat different from those in the northwestern part of the platform, i.e., in the Baltic area.

Conclusions

The rich and variable Baltic Middle Devonian fish assemblages represent the flourishing period of the Devonian fish faunas. In comparison with to the earlier data (MARK-KURIK 1981, LYARSKAYA & LUKSEVICS 1992), the number of species of acanthodians (VALIUKEVICIUS 1994), crossopterygians and palaeoniscoids has increased, and the occurrence of chondrichthyans established. The finds of the representatives of the last group are still rare. Of fish faunas of particular stratigraphical

Tab. 3: Ranges of the Middle Devonian (Eifelian and Givetian) fishes in Belarus, after VALIUKEVICIUS et al. (1995), A. IVANOV (pers. comm.) and E. MARK-KURIK (unpublished data). Of acanthodians only index species (in bold) are listed.
Abbreviations: Ad. = Adrov Stage; O. = Osveya Stage; Gorodok Stage with lower (gr_1), middle (gr_2) and upper (gr_3) beds; Kastyukov. = Kastyukovichy Stage with lower (ks_1), middle (ks_2) and upper (ks_3) beds; Polotsk Stage with Goryn' (gn), Stolin (sl) and Moroch' (mr) beds ; Ln = Lan' Stage; asterisk marks a taxon occurring also in the Lower Devonian Vitebsk Stage; X indicates the taxa reported from the particular stage (beds are not specified).

Stages / Taxa / Beds	Ad.	O.	Gorodok			Kastyukov.			Polotsk			Ln
			gr_1	gr_2	gr_3	ks_1	ks_2	ks_3	gn	sl	mr	
Tartuosteus sp.	O											
Actinolepididae gen.indet.	O											
Phlyctaeniina gen.n.	O											
Laliacanthus singularis Kar.-Tal.	O											
Cheirolepis sinualis Kar.-Tal.,in litt.	O											
Otolithi*	O				O					O		
Cheiracanthoides estonicus Valiuk.		O										
Orvikuina vardiaensis Gross		O		O	O		O	O	O			
Asterolepis sp.*			O		O	O				O		
Ohiaspis? sp.			O	O								
Ohiolepis sp.			O	O								
Byssacanthus? sp.			O	O	O							
Pycnosteus sp.			O	O	O					O		
Homostius? sp.				X								
Ptychodictyon rimosum Gross				X			X		O	O	O	
Lugalepis multispinata Kar.-Tal.				O		O						
Cheirolepis gracilis Gross				O								
Moythomasia? sp.				O						X		O
Elasmobranchii gen.indet.*					O							
Ptyctodontida gen.n.?					O							
Phlyctaeniina gen.n.?					O							
Pycnolepis splendens (Eichw.)?							X					
Nostolepis kernavensis Valiuk.							X					
Glyptolepis? sp.							X					
Gyroptychius sp.							X			O		
Ptyctodontida gen.indet.							X					O
Diplacanthus gravis Valiuk.									O	O	O	
Cheirolepis sp.1 Kar.-Tal.										O		
Schizosteus striatus (Gross)										O		
Coccosteus sp.										O		
Rhynchodus sp.										O		
Dipnoi gen.indet.										O	O	
Cheirolepis gaugeri Gross										O	O	
Glyptolepis sp.										O	O	O
Devononchus concinnus (Gross)										O	O	O
Plourdosteus sp.											O	
Microbrachius? sp.											O	
Laccognathus sp.											O	
Palaeonisci gen.indet.											O	O
Psammosteus praecursor Obr.												O
Plourdosteus livonicus (Eastm.)												O
Plourdosteus? sp.												O
Ctenurella? sp.												O
Bothriolepis sp.												O
Panderichthys sp.												O
Dipteridae gen.indet.												O
Holoptychius sp.												O
Cheirolepis sp.2 Kar.-Tal.												O

units, that of the Lode Member, Gauja Formation, has become significantly richer.

Three different fish zonations have been determined on the basis of biostratigraphically important groups, such as psammosteid heterostracans, placoderms and acanthodians. Acanthodian zones are more numerous in the Eifelian (the Pärnu and Narva Formations), and those of psammosteids and placoderms in the Givetian (from the Aruküla to Amata Formations).

As in the Baltic Middle Devonian the conodont occurrences are rare, the correlation of its subdivisions with the internationally accepted stages and standard conodont zones is complicated. The lower and, particularly, the upper boundary of the series need further clarification in the Baltic.

The fish assemblages of the Kernave Member, Narva Formation and the Abava Beds, Burtnieki Formation, are especially valuable for the correlation with the sections of Scotland and other regions. Several genera and species of placoderms and some other fishes have enabled us to correlate Baltic and Scottish Middle Devonian sections (Fig. 4).

Though the fish finds, particularly those of the macroremains are comparatively rare in Belarus, there are still differences between the Middle Devonian fish faunas of this region and the Baltic area. In the Middle Devonian of Belarus phlyctaeniid arthrodires occur and chondrichthyans and ptyctodonts (Placodermi) are much more common. The assemblage of the Moroch' Beds, Polotsk Regional Stage of Belarus, is close to that of the Abava Beds, Burtnieki Formation of the Baltic. The fishes known from the Lan' Stage resemble those of the Amata Formation. The underlying Gauja Formation (the Lode Member) and the lower part of the Lan' Regional Stage have yielded miospores of the *Ancyrospora incisa-Geminospora micromanifesta* (IM) Subzone.

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