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ON THE ENVIRONMENT OF DEVONIAN FISHES

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Эльга МАРК-КУРИК. О СРЕДЕ ОБИТАНИЯ ДЕВОНСКИХ РЫБ

The deposits of the Old Red Sandstone (ORS) facies, particularly widespread in the Devonian, are traditionally considered as continental. These deposits are mostly clastic (e. g. in the East Baltic and Scotland), containing fish and/or plant remains and few or no invertebrates. However, several authors have expressed the idea of the marine origin of the ORS (Schultze, 1972; Goujet, 1984; Blieck, 1985). In Spitsbergen (Goujet, 1984) the Early Devonian ORS was deposited in near-shore marine environment. The occurring vertebrates are of a very wide geographical distribution and their fossils can be met both in clastic and carbonate deposits; vertebrate-bearing formations reveal lingulids and sometimes the trace fossils *Cruziana* and *Rusophycus* referred to trilobites. As to the East Baltic ORS sections, the lingulids are frequent and they have also been found in the Early Devonian sandstones in the Dniestr Series, Podolia.

The present author has been interested in the environment of the fossil fishes for a number of years, reporting her ideas at several meetings (e. g., in Canberra in 1983 and in Keele in 1989; see also Марк-Курик, Мярсс, 1991). The clastics are known to be poor in fossils except fishes. Sedimentary characteristics of ORS do not always indicate the depositional environment unequivocally. Therefore, the fishes themselves should be used as indicators of their environment. This seems quite natural as fishes are the most highly developed representatives of the Devonian faunas (not considering tetrapods). Moreover, fishes including the primitive ones (Belles-Isles, 1987) were active and powerful swimmers. In the Early Devonian they were of middle size (with the length from 20 to 80 cm), and in the Middle Devonian of large and very large size (from 80 cm to 2 m and over 2 m, respectively).

Solution of environmental problems lies first of all in the comparative analyses of the **whole assemblage**, containing fishes of different size categories, body form and feeding habits. In the Devonian at least the majority of adult fishes, being more than 10 cm in length, did not depend on the ocean currents (see Алеев, 1976) and could migrate freely. The main limiting factors of their distribution were temperature and salinity.

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In the East Baltic, the Middle and lower Upper ORS (from the Pärnu Regional Stage up to the Amata Regional Stage) have been thoroughly studied by Kuršs who established that all formations were of marine origin (see Курше, 1986). But let us still check this, supposing that the fishes were fresh-water ones. In recent rivers the fish faunas change regularly downstream in accordance with changes in the current speed, character of the bottom sediments, water aeration, etc. (Никольский, 1953). In the upstream area the fishes are comparatively small, dorsoventrally compressed, or with a roll-shaped body, and they have several suckers to avoid being transported by strong currents. Downstream larger fishes occur, the number of bottom dwellers decreases and, as the current slows down, suckers become unnecessary. A deep and laterally compressed body form appears. This form prevails in the downstream assemblages, favouring fishes' vertical movement or swimming among water plants. Only predatory fishes are roll-shaped. Bottom-dwelling fishes are rare owing to the muddy bottom and poor aeration of water. Evidently, the same can be said about the lacustrine environment.

	EAST BALTIC		SCOTLAND	
FRASNIAN	AMATA	Plourdosteus livonicus	NAIRN	P.? magnus
	GAUJA	Asterolepis radiata A. ornata		A. maxima
GIVETIAN	ABAVA	Watsonosteus sp. n. Microbrachius cf. dicki	EDAY + JOHN O'GROATS	W. fletti M. dicki
	BURTNIEKI	Dickosteus? markae Gyroptychius elgae	UPPER CAITHNESS FLAGSTONE GROUP	D. threinlandi O. panderi G. milleri T. pholidotus
EIFELIAN	ARUKÜLA	Dickosteus? grossi Osteolepis baltica Gyroptychius pauli Thursius estonicus		
	NARVA KERNAVĖ	Coccosteus cuspidatus? Thursius fischeri Gyroptychius grossi Rhamphodopsis cf. threiplandi	ACHANARRAS LMST.	C. cuspidatus G. agassizi T. moythomasi R. threiplandi
	LEIVU VADJA	Coccosteus sp.	LOWER CAITHNESS FLAGSTONE GROUP	C. cuspidatus T. macrolepidotus
	PÄRNU	Gyroptyhius latvicus Thursius talsiensis	?	
EMSIAN	RĒZEKNE		hiatus	
	ĶEMERI	(with Rhinopteraspis dunensis)	? SARCLET GROUP	

Tentative correlation of the Devonian of the East Baltic and Scotland based on selected fossil fishes. Similar or identical placoderm and crossopterygian taxa are indicated.

It is obvious that the Middle and early Late Devonian fish faunas of the East Baltic do not coincide with any of these recent faunas. There is a great number of dorsoventrally compressed large psammosteid agnathans (body length up to 1.5 m), covered by armour enclosing the gill region. Characteristic are the placoderms (some of them huge: up to 5 m in length, if not more) whose head and the anterior part of the body were flattened. Though there are also numerous other fishes, large and small ones with a variable body form, still none of them has a deep laterally compressed body typical of downstream inhabitants. The most probable environment of these faunas was the comparatively shallow sea with a lot of space for migration, oxygen, food, and a suitable bottom for benthic fishes.

The similarity of the Middle and lower Upper ORS fish faunas in the East Baltic and Scotland has been demonstrated earlier (Марк-Курик, 1981; see also the Figure in this paper). It is noteworthy that in the course of time the number of Scottish "endemics" has considerably diminished. The problem is whether the almost identical faunas could inhabit different environments: lacustrine or fluvial in Scotland (Hamilton, Trewin, 1988) and marine in the East Baltic. Recent fresh water fishes are known to be very sensitive to salinity and never enter the sea. Only rare marine fishes (e. g., some elasmobranchs, salmons among teleosts) are able to migrate into fresh water. This is caused by the fundamentally different physiology in both fish groups. The idea that some Devonian faunas could consist predominantly of euryhaline fishes seems quite improbable. A more reasonable explanation is that the ORS basin of Scotland was permanently connected with the sea. Of marine origin are also the East Greenland Middle ORS deposits which have yielded the giant arthrodire *Homostius* common in the East Baltic and Scotland.

The comparative uniformity of Devonian fish faunas starting roughly from the second half of the Early Devonian and culminating in world-wide distribution of several Late Devonian assemblages and/or genera (e. g. *Bothriolepis*) is evidently the uniformity of the tropical marine environment. If the fish localities are marked on a map of the Devonian world geography, particularly the one by Heckel and Witzke (1979), they will fall mostly between 30° of N and S latitudes. For the Late Devonian and Early Frasnian this has been well demonstrated by Ivanov (Иванов, 1990).

Some comments should be made on the correlation of the East Baltic and Scottish Devonian (Figure) which differs somewhat from an earlier version (Марк-Курик, 1981) both in the stratigraphic and taxonomic aspects. According to a recent subdivision, the Narva Regional Stage consists of three substages: Vadja, Leivu, and Kernavė (Клеесмент et al., 1987). At the Givetian-Frasnian boundary the Abava Formation is distinguished for its specific fish fauna (Курик et al., 1989). Coccosteids in the Vadja and Kernavė substages differ evidently on the species level. *Coccosteus* species from the Kernavė Substage (earlier *C. orvikui* Gross, also *Millerosteus orvikui*) can be considered as *C. cuspidatus*? Miller ex Ag. The other species, *C. grossi* O. Obr. and *C. markae* O. Obr. may belong to the genus *Dickosteus*. In the Kernavė Substage a ptyctodont (Марк-Курик, 1977, Plate VIII Fig. 4) resembling rather closely *Rhamphodopsis threiplandi* Watson, occurs. There is also much similarity between the small and characteristic antiarch *Microbrachius* from the East Baltic and Scotland.

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