TROPHIC RELATIONS OF DEVONIAN FISHES

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ABSTRACT

A Middle Devonian fish assemblage from NE Estonia (Eifelian, Narva Stage), comprising more than 20 fishes and some invertebrates, is analysed from the aspect of trophic relations. It is concluded that many common food items (*e.g.*, several soft bodied invertebrates, arthropods etc.) have been subjected to taphonomic loss. The presence of large and very large flat-bodied fishes (psammosteid heterostracans and the arthrodire *Homostius*), is believed to show that the assemblage came from a shallow marine environment.

KEY-WORDS : FISH ASSEMBLAGE, TROPHIC RELATIONS, MIDDLE DEVONIAN.

RÉSUMÉ

Un assemblage de poissons dévoniens du NE de l'Estonie (Eifélien, Narva Stage) comprenant plus de vingt taxons différents et quelques groupes d'Invertébrés est analysé du point de vue de ses relations trophiques. L'analyse permet de conclure que de nombreuses proies (*e.g.*, plusieurs Invertébrés à corps mou, arthropodes etc) n'ont pas été fossilisés. La présence de grands poissons au corps aplati (Psammostéides, hétérostracés et l'arthodire *Homostius*) indique que cet assemblage de Vertébrés vivait dans un milieu marin peu profond.

MOTS-CLÉS : ASSEMBLAGE DE POISSONS, RELATIONS TROPHIQUES, DÉVONIEN MOYEN.

INTRODUCTION

The aim of the study of trophic relations of ancient fishes, *e.g.,* those from the Devonian, is to help to determine the completeness of fossil assemblages, and to show how the information based on assemblages can be used. This kind of study concentrates our attention on species that could rather easily remain unnoticed because of their preservation type and/or the small number of specimens ; this matter concerns first of all the fishes that are preserved as microremains. There are also several essential species among both producers and consumers which cannot be found as fossils or have been discovered in extremely rare cases only. The most completely known assemblage contributes to identification of the environment in which the fishes lived (Mark-Kurik 1991), and also shows which of the consumers are of more value for this purpose.

Devonian fish assemblages have been considered from the aspect of trophic relations by Novitskaya *et al.* (1983) see also Lebedev (1992) and Luksevics (1992). The listed papers give information on the Early and Late Devonian shallow sea, including estuarine, assemblages. An attempt has been made to analyse a marine Middle Devonian assemblage that is richer in fishes than the assemblages indicated in the above works. It is based on the data from the Gorodenka locality, NE Estonia (for paleogeographical situation see Kurss 1992, Fig. 1b). All fossils come from one bone-bearing bed consisting of reddish-brown fine-grained siltstone, about 0.5 m thick. The locality is the richest one in the Eifelian Kernave Substage of the Narva Stage.

The assemblage (Fig. 1) includes about 20 fishes belonging to the groups typical for the Middle Devonian of the NW part of the East European

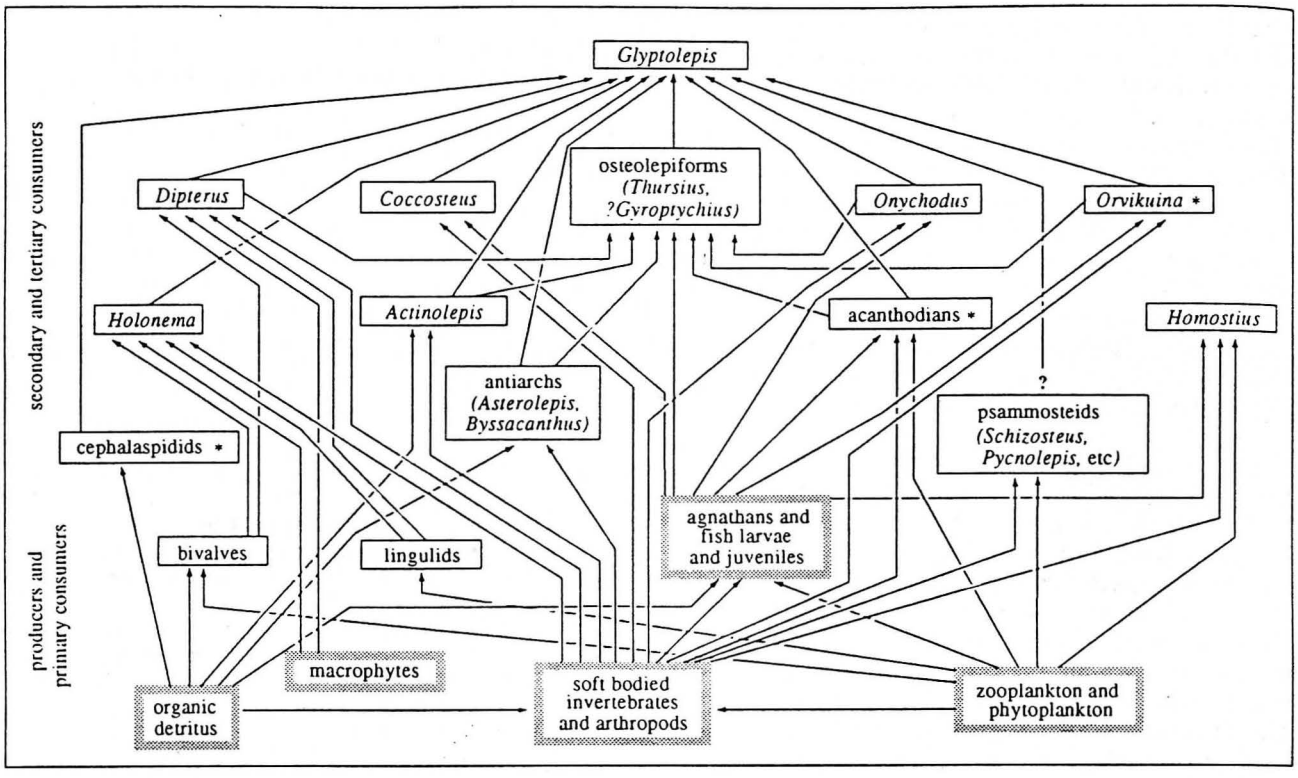

Figure 1 - Proposed trophic relations of a Middle Devonian assemblage from the Gorodenka locality, NE Estonia (Eifelian, Narva Stage, Kernave Substage). The assemblage comprises psammosteid heterostracans (***Schizosteus*** and ***Pycnolepis*** dominating), tesserated cephalaspidids, placoderms (***Actinolepis, Holonema, Coccosteus, Homostius, Asterolepis, Byssacanthus***), acanthodians (climatiids, diplacanthiids, cheiracanthids, acanthodids), crossopterygians (***Glyptolepis, Thursius, ? Gyroptychius, Onychodus***), dipnoans (***Dipterus***) and actinopterygians (***Orvikuina***). Asterisks mark the fishes known by microremains. Of the primary consumers the lingulids and bivalves are preserved as shells and impressions, respectively ; the presence of the other consumers and producers (shaded) is highly probable. *Propositions de relations trophiques d'un assemblage du Dévonien moyen, de la localité de Gorodenka située au nord-est de l'Estonie (Eifélien, étage de Narva, sous-étage de Kernave). L'assemblage est constitué de Psammosteides Hétérostracés (**Schizosteus** et **Pycnolepis**) Céphalaspides tessérés, Placodermes (**Actinolepis, Holonema, Coccosteus, Homostius, Asterolepis, Byssacanthus**) Acanthodiens (climatiidés, diplacanthidés, cheiracanthidés, acanthodidés), Crossoptérygiens (**Glyptolepis, Thursius, ? Gyroptychius, Onychodus**), Dipneustes (**Dipterus**) et Actinoptérygiens (**Orvikuina**). Les astérisques indiquent les poissons connus par des microrestes. Les lingules et les bivalves sont des consommateurs primaires et sont conservés respectivement sous forme de coquilles et en empreintes. La présence des autres consommateurs et producteurs (en ombré) est hautement probable.*

basins. The groups are : heterostracans (psammosteids, 3-4 species), osteostracans (cephalaspidids, 1 species), placoderms (6 species), acanthodians (5-6 species), crossopterygians (4 species), dipnoans (1 species), and actinopterygians (1 species). Of these fishes the cephalaspidids, acanthodians and actinopterygians (palaeoniscoid *Orvikuina*) have been preserved only as microremains, tesserae and scales, but, nevertheless, are very common species in the assemblages. The invertebrates are lingulids and bivalves, the latter being preserved as moulds. Bivalves are reported for the first time from the Gorodenka fish bed locality .

Trophic relations presented here are based on the structure of the mouth and jaw apparatus of agnathans and gnathostomes, as well as on the assumption that these vertebrates were not specialized for one particular diet, but were capable of feeding in different ways as the majority of extant fishes do (Bone & Marshall 1986). This can be illustrated by the feeding mode of the dipnoan *Neoceratodus* that takes frogs, tadpoles, small fishes, snails, shrimps and earthworms as well as some aquatic and terrestrial plant material (Merrick & Schmida 1984). Therefore, it is highly probable that in the Devonian environment analysed, there existed fish food that has not been discovered, *e.g.*, planktonic organisms, soft bodied invertebrates, arthropods, larvae and juveniles of fishes, and organic detritus. There are, still, arthropods (Mysidacea) and juvenile fishes that have been found in most exceptional cases, in

specific clayey rocks of the Baltic basin (Upeniece & Upenieks 1992). Plant macroremains are also known from the different stratigraphical units of the same region (Sorokin *et al.* 1981) so their presence is rather probable. The occurrence of a limited number of invertebrates and the absence of several other food items indicated above, can be explained by **taphonomic loss** as described by Briggs & Kear (1993). When diagenetic mineralization of carcasses of such organisms as polychaetes (Annelida) is late, these marine worms decay almost completely within a month. It is supposed that even such exceptionally well-preserved biota as that of the Burgess Shale has considerably diminished as a result of this loss.

Taphonomic loss concerns first of all producers and primary consumers. Secondary and tertiary consumers include fishes of different size, body form and feeding mode. At least one or two food items have been shown for these fishes on the diagram, though, if this is compared with that in extant fishes, the food chain seems to be greatly simplified. For example, the diet of one only adult herring includes 7 items, but if account is taken of the different earlier stages of the life cycle, the number of items is more than 20 (Barnes & Hughes 1988).

The top consumer is supposed to be the largest predator, *Glyptolepis*. A lower trophic level was occupied by smaller predators and different generalists. It also includes cephalaspidids, the probable detritus eaters. Of much interest are the large psammosteid heterostracans and the arthrodire *Homostius*. They were very common species in the assemblages under consideration. These fishes with their terminal or slightly dorsal toothless mouth were most probably plankton feeders, but could possibly also consume small arthropods, fish fry etc. Large psammosteids, 70-80 cm long and *Homostius* with a length 3-4 m, had dorsoventrally flattened heads and anterior part of the bodies. It is believed that fishes with such body forms, size and feeding mode could inhabit the shallow sea only, and such was the environment from which the whole assemblage came.

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