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Ordovician scolecodonts of the East Baltic and surrounding areas – an overview

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INTRODUCTION

Polychaete worms of the Order Eunicida possessing highly differentiated jaw apparatuses were widespread and taxonomically diversified in the ancient seas forward from the Tremadocian (Underhay and Williams 1995). The elements of jaw apparatuses of these worms, the scolecodonts, are among the most common organic microfossils in the Ordovician shallow-water deposits. In spite of the frequent occurrence, scolecodonts, in comparison with most other fossil groups, have received rather little attention from palaeontologists. That, in particular, is due to complicated taxonomy which involves co-existence of element- and apparatus-based classifications. However, it has been shown in several papers (e.g., Zawidzka 1975, Bergman 1989, Eriksson 1997, Eriksson and Bergman 1998) that rejecting of parataxonomy is possible. It has also been suggested that the extinct apparatus-based species are, in their content, close to Recent species (Kielan-Jaworowska 1966).

Some of the earliest reports on scolecodonts are those from the East Baltic area (Eichwald 1854, Pander 1856). The material collected from the erratic boulders found in Poland, which formed a basis for apparatus-based classification of Ordovician–Silurian jawed polychaetes (Kielan-Jaworowska 1966), originated also from the Baltic area. Ordovician polychaete jaws have been encountered also in Sweden (Bergman 1989), Norway (Harper *et al.* 1984), Poland (Szaniawski 1970) and Estonia (Hints 1998). Outside Europe, Ordovician scolecodonts have been described in great numbers from northern America (Stauffer 1933; Eller 1942, 1969). For other parts of the world, the knowledge of Ordovician scolecodonts is remarkably poor, though their occurrence in particular regions has usually been corroborated.

Thirty years long investigation of Ordovician organic-walled microfossils in Estonia has revealed numerous scolecodonts, preliminarily investigated by Ralf Männil. In recent years the old collections have partly been re-studied by myself (Hints 1998) and several additional sections have been sampled with special interest on polychaete jaws. With few exceptions the material is well-preserved and articulated jaw apparatuses are rather frequently found (on average one apparatus per some hundreds of isolated jaws). In some cases the abundance of scolecodonts in the Ordovician rocks of the East Baltic exceed several thousands in 1 kg of sample.

So far about 120 apparatus-based species of eunicids belonging to some 40 genera and 13 families have been recorded from the Ordovician of the East Baltic. Many species are yet undescribed and therefore below some of the specific names are referred to as *in coll.* The actual number of species will supposedly enlarge, possibly up to several hundreds, when the group will be studied further. All five types of polychaete jaw apparatuses distinguished (for review see Szaniawski 1996) are represented in the collection studied. The most common genera, in terms of the number of species, are *Oenonites* Hinde, *Ramphoprion* Kielan-Jaworowska, *Mochtyella* Kielan-Jaworowska, *Atraktoprion* Kielan-Jaworowska, *Pistoprion* Kielan-Jaworowska and *Pteropelta* Eisenack. Commonly these genera are also most abundant in species.

Most of the material summarized herein is derived from drill core sections of Estonia, but the data available from northwestern Russia, Lithuania and eastern Poland was also taken into account.

Study of the present collection as well as obtainment of additional material from the East Baltic area are currently in progress. Several taxonomic groups need specific study, and certain intervals of the Ordovician are yet inadequately investigated. Therefore the data presented below should be viewed as preliminary analyses rather than solidly based consequences.

STRATIGRAPHICAL DISTRIBUTION AND PATTERN OF TAXONOMIC DIVERSITY

It is a common belief that eunicids are characterized by a relatively low rate of evolution and correspondingly long stratigraphical ranges. They are shown to include some of the so-called living fossils (Szaniawski and Imaiima 1997). Generally my own study has revealed that the majority of the Ordovician species are long-lasting in comparison with many other fossil groups. In a large scale, nevertheless, certain tendencies in the development of the group can be delineated, and numerous relatively short-ranging species occur alongside with those being distributed throughout the Ordovician and most of the Silurian. It should be agreed that scolecodonts may have stratigraphical utility primarily when other fossil groups, which conventionally have provided index forms, are missing in the record, or as a supplement to them.

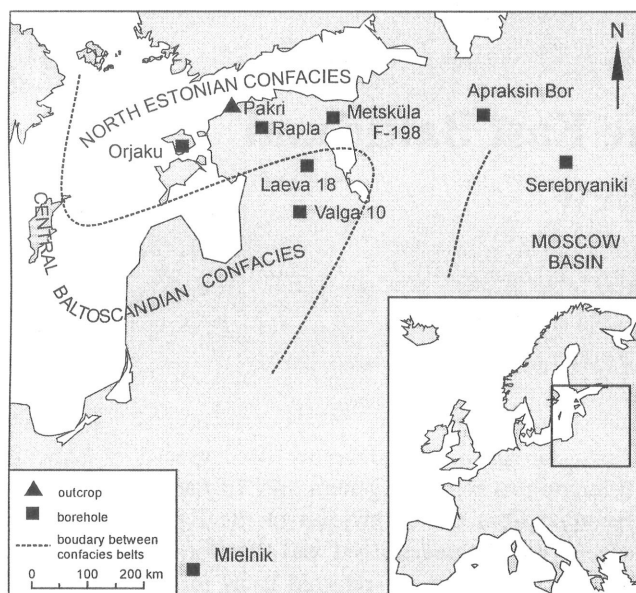


Fig. 1. Sketch map showing the main localities studied. Boundary between the confacies belts after Nölvak 1997.

Some comments on the Ordovician jawed polychaete faunas of particular stratigraphical intervals are as follows:

(1) The oldest scolecodonts are found in the Volkhov Stage, where the abundance and diversity are remarkably low.

(2) The Kunda Stage is characterized by a strong predominance of *Pteropelta gladiata* Eisenack, a species which can be found throughout the Ordovician; the abundance may sometimes be relatively high, but the diversity is low.

(3) Rapidly increasing number of species characterizes an interval from the Lasnamägi Stage to Idavere Substage; several species can be considered as typical of this interval or part of it; ramphoprionids seem to have flourished, their

similarly high percentage is uncommon in overlying strata.

(4) The boundary between the Idavere and Jõhvi substages is distinguished by an increase in mochttyellids and relative decrease in ramphoprionids. Several long-ranging species, including typical elements of Jõhvi-Keila fauna, disappear in the top of the Keila Stage.

(5) In the Oandu-Rakvere-Nabala interval, elements of new fauna appear, partly as replacing older taxa; the assemblages are often predominated by placognath forms, which is usually uncommon in older strata; the average abundance and the assemblage diversity are generally lower than in under- or overlying strata. Some of the appearing taxa being very rare in the Ordovician are typical elements of the Silurian polychaete fauna in Baltoscandia (like *Kettnerites*, *Skalenoprion*, "*Mochttyella*" ex. gr. *trapezoidea*).

(6) Jawed polychaetes of the Porkuni Stage are poorly known in North Estonia. In the southern part of the area, however, a very distinct association has been recovered from the Kuldiga Formation. Since this formation yields the *Hirnantia* fauna, an intriguing question for further study is whether polychaetes may have been part of this cosmopolitan fauna.

(7) Although the Ordovician-Silurian boundary is, with respect to scolecodonts, rather poorly studied, numerous species apparently cross the boundary. There are, however, many forms appearing first in, or never extending to the Silurian.

The large-scale evolutionary pattern proposed for eunicids is mostly based on the stratigraphical ranges of taxa. The present collection enables us to emend stratigraphical ranges of two families. The symmetrionids, so far described only from the Silurian, have now been recovered also from the topmost Ordovician (Porkuni Stage). The archaeoprioids, so far

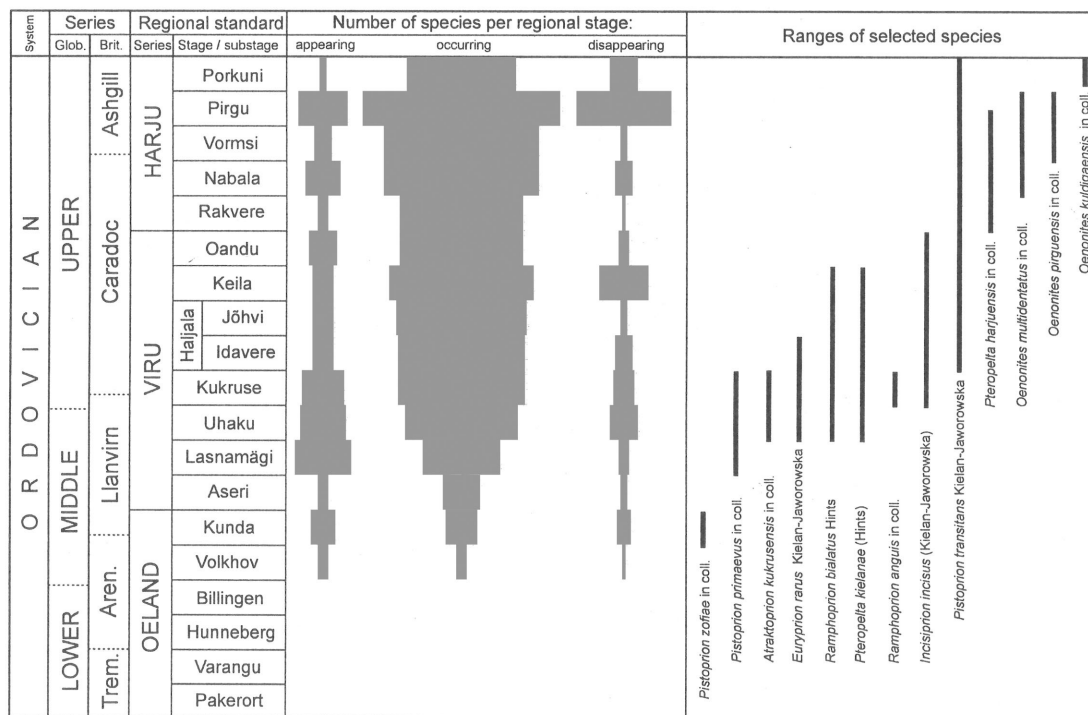


Fig. 2. Dynamics of the taxonomic diversity and stratigraphical ranges of selected species. Stratigraphy is given in accordance with Nölvak 1997.

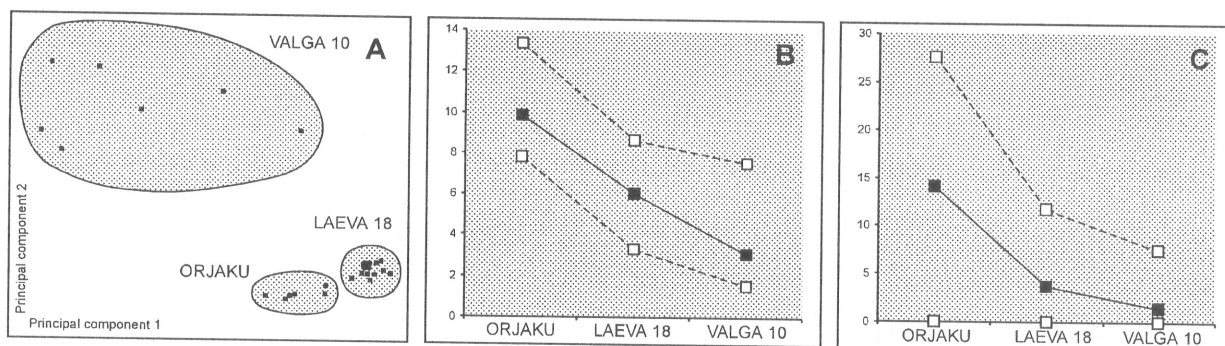


Fig. 3. Differentiation of jawed polychaete assemblages of the Pirgu Stage along the onshore (Orjaku)–offshore (Valga 10) transect. See Fig. 1 for locality map. A – Principal components analyses showing clear differentiation of faunas of three localities. B – scatter plot showing a decrease in the diversity index calculated by Simpson's (1949) formula towards the offshore part of the palaeobasin. Dashed line with white markers stands for minimum and maximum and solid line with black markers for average. C – scatter plot showing decrease in relative abundance (specimens per 100 g sample) towards the offshore part of the palaeobasin. Dashed line with white markers stands for minimum and maximum and solid line with black markers for average.

recorded only from the uppermost Ordovician, occur undoubtedly already at least in the Llanvirn (Lasnamägi Stage) and extend to the lowermost Llandovery.

Since diversification of biotas during the Ordovician is a special object of an ongoing IGCP project, some aspects of diversification of jawed polychaetes should be noted. Main trends in the taxonomic diversity of eunicids in the East Baltic in terms of appearing, occurring, and disappearing species per regional stage are illustrated in Fig. 2. The Volkhov and Kunda stages are characterized by a rather small number of species. The main diversification episode falls into the Lasnamägi–Uhaku–Kukruse interval, where many long-ranging species first appear in the sequence. A high percentage of long-ranging species results in a very continuously widening bar. A slight drop in the number of occurring species in the Oandu and Rakvere stages, together with the disappearance ratio notably higher than the average in the Keila Stage, is most likely an effect of the so-called mid-Caradocian event (see also Meidla *et al.* in the present volume). The number of species achieves its maximum in the Pirgu Stage. The high disappearance rate in the Pirgu Stage and a rather small number of species present in the Porkuni Stage may partly be due to inappropriate preservation of organic microfossils and insufficient knowledge of the Silurian fauna.

The described pattern may not directly reflect the diversification of eunicids in a global scale, which has likely taken place somewhat earlier. That is indicated by the presence of advanced taxa in the Volkhov Stage and discovery of different forms in Tremadocian deposits of other parts of the world (Underhay and Williams 1995; R. Brocke *pers. comm.*). The diversification pattern in the East Baltic may be influenced by the Lower–lower Middle Ordovician climatic conditions prevailed in Baltica, as well as by inadequate fossil record.

GEOGRAPHICAL DISTRIBUTION

The trends in global distribution of Ordovician, as well as other fossil jawed polychaetes are virtually unknown.

However, the scolecodonts from northern America described by Stauffer (1933) and Eller (1942, 1969) show great similarities with those recovered from the East Baltic. Apparently many of the Ordovician jawed polychaete genera, and probably some species were common in Baltica and Laurentia. Genus- or even family-level taxa characteristic of only one of the mentioned regions can nevertheless be observed too.

There are few examples which provide some ideas on the spatial distribution of eunicids in a regional scale.

The scolecodont assemblage recovered from the Nabala–Vormsi interval of the Mielnik drill core, eastern Poland (Fig. 1) is virtually identical to that obtained from the same stratigraphical interval of the Laeva 18 drill core, Central Estonia. Similar approximate abundance and species level composition of the assemblage and, in particular, high percentage of *Polychaetura harjuensis* in coll. have been observed in these considerably distant localities.

Scolecodont assemblages of the Haljala Stage were studied in four drill core sections in North Estonia (see Hints 1998 for details). Layers of the K-bentonites allowed a reliable and very precise correlation of samples from localities several hundreds of kilometres apart. It appeared that the assemblages with extremely stable composition were spread over wide areas during the Haljala time. Certain changes in polychaete faunas, though without major change in species composition, enabled to detect the boundary between the Idavere and Jõhvi substages, which agreed with the initial correlation based on the K-bentonite layers.

The samples from the Haljala Stage of northwestern Russia (Apraksin Bor borehole, see Fig. 1) yielded a scolecodont assemblage very close to that in North Estonia. Similarly, the samples from the Keila Stage from the Serebrjaniki borehole (located in the limits of the so-called Moscow Basin) contained the same species, which have been found in North Estonia.

These examples imply a rather wide regional distribution of particular jawed polychaete assemblages in the East Baltic and surrounding areas. It should be mentioned here, however, that these examples, the last perhaps exclusive, involve only localities from one and the same facies zone, or the so-called confacies belt (Fig. 1).

FACIES DEPENDENCE

Bergman (1989, 1995) and Eriksson (1997, 1998), working on the Silurian material from Gotland, Sweden, argued that many species are strongly dependent on facies, and a rather shallow-water and low water energy environments likely offered the most optimal conditions for the majority of Palaeozoic eunicids.

The conditions determining the suitability of an environment for particular polychaetes change more rapidly along the onshore-offshore profile than parallel to the shoreline. Accordingly, the lateral changes in polychaete faunas are expected to be more distinct along the basin gradient and the degree of facies relationship of extinct jawed polychaetes is therefore most easily detected along the onshore-offshore profile.

A quantitative approach was made with Upper Ordovician scolecodont assemblages of three drill cores (Orjaku, Laeva 18 and Valga 10, see Fig. 1) located in different facies zones (the confacies belts) of the Baltoscandian Palaeobasin. Some of the results for the Pirgu Stage are illustrated in fig. 3. In few words, a remarkable decrease in abundance (which most likely is not a result of differences in deposition rates or preservation) and assemblage diversity (reflecting how many species make up the core of an assemblage, calculated by Simpson's 1949 formula) towards the deeper-water Central Baltoscandian Confacies can be observed. The decrease in diversity indicates that the habitats in the Central Baltoscandian Confacies were likely more stressful for the majority of polychaetes, though there are some species, which demonstrate clear preference for deeper-water conditions. As shown in Fig. 3A, multivariate methods, like principal components, or cluster analyses may prove useful to generalize the differentiation of polychaete faunas and to delineate corresponding biofacies.

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