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# A diverse Hirnantian scolecodont assemblage from northern Estonia and resilience of polychaetes to the end-Ordovician mass extinction

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ABSTRACT

We report the discovery of a rich assemblage of latest Katian and Hirnantian scolecodonts (polychaete jaws) from a new Ordovician–Silurian boundary outcrop in the Reinu quarry, northern Estonia. The recovered polychaete fauna contains at least 40 species attributed to 11 families. Many common taxa appear to range from the latest Katian to the Hirnantian and into the Rhuddanian, indicating the resilience of jawed polychaetes to the end-Ordovician mass extinction. The Reinu assemblage is similar to the coeval faunas known from other Baltic sections, as well as from Anticosti Island, Canada, although with some specific features. The study revealed the highest abundance of scolecodonts in the Ordovician of Baltica, with ca 5400 maxillae per kilogram of rock recorded in the Siuge Member of the Ärina Formation, Porkuni Regional Stage, early Hirnantian.

## Introduction

Jaw-bearing polychaete worms were abundant and diverse inhabitants of Ordovician and Silurian shallow-marine environments, and their resistant jaws constitute a common group of organic-walled microfossils – scolecodonts. The end-Ordovician mass extinction that caused a significant diversity decline among most groups of organisms (Harper et al. 2020) is considered to have had a relatively minor effect on polychaetes (Hints 2000; Hints and Eriksson 2007; Eriksson et al. 2013). However, this notion is mainly based on a broad-scale comparison of Ordovician and Silurian faunas rather than on first-hand studies spanning the extinction interval. The precise response of polychaete worms to rapid changes in climate, environments, and ecosystems has thus far remained poorly understood.

The aim of this paper is to report a recent discovery of a rich fauna of latest Katian and Hirnantian jawed polychaetes from a new Ordovician–Silurian boundary succession in the Reinu quarry, northern Estonia. It provides new insights into the turnover patterns and biogeography of jaw-bearing polychaetes during the end-Ordovician mass extinction.

## Locality and materials

The Reinu quarry is located in northern Estonia, 40 km south of Tallinn (59.08768, 24.74044). The early Silurian limestone of the Varbola Formation (Fm), Juuru Regional Stage (RS), has been quarried for crushed stone production since 2007. The Ordovician–Silurian boundary interval was first exposed in the quarry in 2020. As of 2022, the topmost Pirgu (latest Katian) and the entire Porkuni (Hirnantian) regional stages have been accessible. The Porkuni RS is represented by shallow-marine carbonates of the Ärina Fm, divided into dolostone (Röa Member (Mb)), skeletal grainstone (Vohilaid Mb) and kerogenous limestone (Siuge Mb) and, in places, reef limestone (Tõrevere Mb). The thickness of the formation varies across the quarry, being ca 2.3 m in the main section sampled (Fig. 1). The Ärina Fm is distributed in northern and central Estonia and considered to be primarily early Hirnantian in age, bound by stratigraphic gaps (Meidla et al. 2023). Whereas the basal part of the 11-m-thick Varbola Fm, the Koigi Mb, is likely of late Hirnantian age, the main part of the formation is Rhuddanian (Gul et al. 2021; Meidla et al. 2023).

The lower part of the Reinu section (Fig. 1) was sampled for microfossils in 2020 and 2022, and a total of 25 samples were collected. Additionally, three older conodont samples from the Varbola Fm were examined and the data combined to collectively represent the lowermost Silurian fauna. Acid-resistant microfossils were extracted

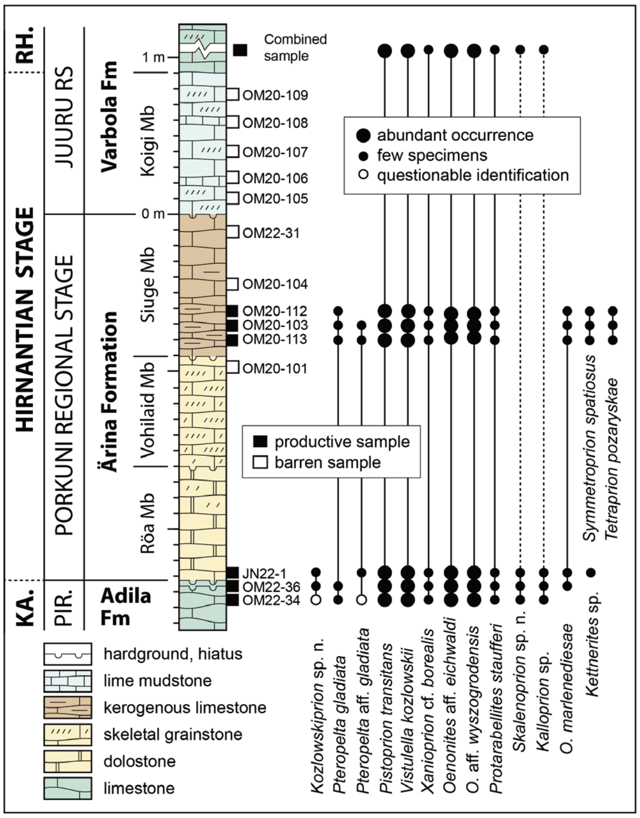


**Fig. 1**. Generalised stratigraphy of the Reinu quarry and distribution of selected late Katian and Hirnantian jawed polychaetes. The uppermost combined sample represents collectively three individual samples from the ca 11-m-thick Varbola Formation. Abbreviations: Pir. – Pirgu Regional Stage; KA. – Katian; RH. – Rhuddanian.

using acetic and hydrochloric acids. Productive samples contained scolecodonts, melanoscleritoids, foraminiferans and rare chitinozoans. The yield of scolecodonts was highly variable: the grainstone intervals turned barren, but the Siuge Mb provided the richest scolecodont sample from the Baltic Ordovician so far, with ca 5400 posterior maxillae per kilogram of rock in sample OM20-113 (3700 specimens/kg according to the counting method explained by Hints 2000). The entire collection from the Reinu quarry contains tens of thousands of scolecodonts. The material is housed at the Department of Geology, Tallinn University of Technology (abbr. GIT).

## Results and discussion

The latest Ordovician polychaete fauna from the Reinu quarry contains at least 40 species attributed to 17 genera and 11 families, and up to 21 species have been identified in a single sample. Quantitative data are available for few samples only, showing high diversity and a relatively even distribution of dominant taxa. For instance, in sample OM20-113, where the highest abundance was recorded, the dominance index (D) is 0.13, the Simpson Diversity index is 0.87, and the Shannon index is 2.3.

Similarly to most other Baltic Ordovician jawed polychaete assemblages studied so far, the Reinu fauna is dominated by polychaetaspids and mochtyellids, followed by polychaeturids, xanioprionids, ramphoprionids and atraktoprionids (Figs 1–2).

**Polychaetaspids** may account for more than half of the specimens and are represented by no less than ten species. *Oenonites* aff. *eichwaldi* (Fig. 2P) and *O*. cf. *wyszogrodensis* (Fig. 2L, M) are the most common ones, occurring in the latest Katian and Hirnantian strata but also ranging into the Silurian. *O. marlenediesae* (Fig. 2N, O) is less abundant but recorded in most samples of Katian and Hirnantian age. A few specimens of *O. zappae* (Fig. 2Q) and *Oenonites* aff. *jennyensis* (Fig. 2K), previously known from the Silurian (Eriksson 1997), were recovered, and several other morphologically distinct species of *Oenonites* are present in the collection, awaiting a systematic description. Polychaetaspids also include rare specimens of a new *Kozlowskiprion* species from the late Katian samples and a questionable find from the Hirnantian.

**Mochtyellids** are strongly dominated by two long-ranging species, *Pistoprion transitans* (Fig. 2A) and *Vistulella kozlowskii* (Fig. 2B, C), which occur in all the productive samples studied. Other mochtyellids are represented by rare specimens of *Mochtyella* ex gr. *fragilis*, *M*. ex gr. *trapezoidea* and *M*. aff. *duplicidentata* (Fig. 2i). Additionally, a few jaws of new mochtyellid genera (Fig. 2H) are present in the collection. Surprisingly, the typical forms of the genus *Mochtyella* common in other latest Ordovician sections of Baltoscandia and Laurentia (such as *M*. ex gr. *cristata* and *M*. ex gr. *polonica*) are missing in the studied collection.

**Polychaeturids** are represented by the genus *Pteropelta*, with the typical *P. gladiata* form and a different form, here tentatively assigned to *P.* aff. *gladiata* (Fig. 2U, V, W). It is usually larger, more elongated and has a narrow, pointed ramus on the right MI. Both forms occur in the late Katian as well as Hirnantian samples, but the elongated form is more typical of the Hirnantian samples. The genus is unknown from the Silurian part of the Reinu succession, but polychaeturids possibly occur in basal Llandovery (Hints and Eriksson 2010; authors' unpublished observations).

**Xanioprionids** are represented in most samples by *Xanioprion* cf. *borealis* (Fig. 2D, E). Additionally, a few jaws of an undescribed xanioprionid were encountered (Fig. 2F). Both types of xanioprionid jaws also occur in the Silurian part of the Reinu succession.

**Ramphoprionids** are rare in all samples, represented by two genera and probably three or four species. *Protarabellites* is present in most samples. The latest Katian samples include typical *P. staufferi*, but in the Hirnantian, most specimens resemble *P. rectangularis* (Fig. 2R). However, transitional forms between the two species have been found. A rare but distinct ramphoprionid in the collection is *P*. aff. *triangularis* (Fig. 2S), with a prominent double fang in the right MI. A single recovered specimen probably belongs to a new species, ancestral to the typical *P*. *triangularis* found in the Silurian (Eriksson 2001). However, some of the left MI elements illustrated by Eriksson (2001, fig. 8:19, 8:23) may represent the same species. In two Katian samples, *Ramphoprion* cf. *gotlandensis* was also identified, and closely similar forms are known from the Silurian (see Eriksson 2001).

**Atraktoprionids** occur in most samples and are represented by at least three different species, of which *Atraktoprion* cf. *major* (Fig. 2Z) is the most common one.

Other taxa include *Skalenoprion* sp. and *Kalloprion* sp. (Fig. 2Y), which are found only in the three oldest samples, but both genera range into the Silurian. Further material is needed for species-level comparison. Paulinitids are rare, probably represented by a single species that also occurs in the Silurian part of the Reinu succession (Fig. 2T).


**Fig. 2**. Selected latest Katian and Hirnantian scolecodonts from the Reinu quarry, northern Estonia. All scale bars correspond to 100 µm. **E, Y** – from sample OM22-36 (Adila Formation, Katian); **G** – from sample OM22-34 (Adila Formation, Katian); **H, S, T** – from sample JN22-1 (Katian/Hirnantian); **Q** – from sample OM20-113 (Siuge Member, Hirnantian); **R, X, Z** – from sample OM20-112 (Siuge Member, Hirnantian); all others are from sample OM20-103 (Siuge Member, Hirnantian). **A** – *Pistoprion transitans*, left MI, GIT 888-1; **B** – *Vistulella kozlowskii*, left MI, GIT 888-2; **C** – *Vistulella kozlowskii*, right MI, GIT 888-3; **D** – *Xanioprion* cf. *borealis*, anterior part of MI, GIT 888-4; **E** – *Xanioprion* cf. *borealis*, posterior part of MI, GIT 888-5; **F** – *Xanioprion* sp., MI, GIT 888-6; **G** – Mochtyellidae gen. nov., left MI, GIT 888-7; **H** – Mochtyellidae gen. nov., left MI, GIT 888-8; **i** – *Mochtyella* aff. *duplicidentata*, right MI, GIT 888-9; **J** – *Lunoprionella*? sp., posterior jaw, GIT 888-10; **K** – *Oenonites* aff. *jennyensis*, left MI, GIT 888-11; **L** – *Oenonites* aff. *wyszogrodensis*, left MI, GIT 888-12; **M** – *Oenonites* aff. *wyszogrodensis*, right MI, GIT 888-13; **N** – *Oenonites marlenediesae*, left MI, GIT 888-14; **O** – *Oenonites marlenediesae*, right MI, GIT 888-15; **P** – *Oenonites* aff. *eichwaldi*, right MI, GIT 888-16; **Q** – *Oenonites zappae*, right MI, GIT 888-17; **R** – *Protarabellites rectangularis*, left MI, GIT 888-18; **S** – *Protarabellites* aff. *triangularis*, right MI, GIT 888-19; **T** – *Kettnerites* sp., right MI, GIT 888-20; **U** – *Pteropelta* aff. *gladiata*, basal plate, GIT 888-21; **V** – *Pteropelta* aff. *gladiata*, left MI, GIT 888-22; **W** – *Pteropelta* aff. *gladiata*, right MI, GIT 888-23; **X** – *Symmetroprion spatiosus*, right MI, GIT 888-24; **Y** – *Kalloprion* sp., left MI, GIT 888-25; **Z** – *Atraktoprion* cf. *major*, right MI, GIT 888-26.

Additionally, sporadic specimens of *Symmetroprion spatiosus* (Fig. 2X) and *Tetraprion pozaryskae*, as well as a few other taxa, have been recovered in the Siuge Mb.

The stratigraphic succession of the Reinu polychaete fauna suggests that turnovers near the base of the Hirnantian were relatively small. Several species that are common in the Adila assemblage (*P. transitans*, *V. kozlowskii*, *O.* aff. *eichwaldi*, *O.* aff. *wyszogrodensis*, *O. marlenediesae*, *P. gladiata*) continue into the Siuge Mb. Even though the lithology of the two units is rather different, the high abundance, taxonomic composition and diversity indicate similarly optimal conditions for many polychaete taxa. Still, certain differences can be outlined. For instance, *Kalloprion* sp., *Skalenoprion* sp., *R*. cf. *gotlandensis* and some mochtyellids are confined to the older assemblage, whereas *S. spatiosus* and *T. pozaryskae* occur only in the Hirnantian strata of the Reinu quarry. Such differences are, however, largely of local significance, as the same taxa are known to have longer ranges in other sections. The Ärina and Varbola assemblages also share many species, but the differences seem to be more significant than near the base of the Hirnantian. First, some new species appear, and the proportion of paulinitids gradually increases in the Varbola Fm.

Polychaeturids have not been found in the Silurian of the Reinu quarry. At present, it is difficult to assess whether the observed changes at the Ordovician–Silurian boundary can be fully attributed to the extinction and recovery or reflect, at least partly, a change in local environments. However, the Reinu collection shows that 20 out of the 40 taxa recorded in the latest Ordovician ranged into the Silurian. Thus, more than 50% of the jawed polychaete species likely survived the end-Ordovician mass extinction.

In the Baltic region, Hirnantian scolecodonts have previously been reported from the Valga (southern Estonia) and Stirnas (western Latvia) boreholes (Hints 2001; Hints et al. 2010), where they occur in the Kuldiga and Saldus formations. The scolecodonts are particularly abundant and diverse in the middle part of the Kuldiga Fm (lower part of the Edole Mb), sharing a number of species with the Reinu assemblage, including the dominant taxa such as *Pistoprion transitans*. However, the composition of polychaetaspids differs at the species level, and other characteristic elements also differ between the Ärina and Kuldiga faunas. For instance, *Mochtyella* cf. *cristata*, *Conjungaspis minutus*, Tetraprionidae gen. et sp. nov. are typical of the Kuldiga fauna, whereas *P. gladiata* is characteristic of the Ärina Fm. The interpretations of age relationships of these stratigraphic units (Meidla et al. 2023) suggest that the mid-Kuldiga interval is younger than most of the Ärina Fm in northern Estonia. We hypothesise that the revealed differences between the Ärina and Kuldiga assemblages are due to the succession of Hirnantian polychaete faunas in time rather than environmentally caused intra-basinal biogeographical differentiation.

Apart from Baltoscandia, taxonomically diverse latest Katian to Hirnantian jawed polychaete faunas are known from Anticosti Island, Canada, the Prague Basin, and the Arabian Peninsula. The Reinu assemblage shows the closest similarity and biogeographical links with the fauna from the Vauréal and Ellis Bay formations of Anticosti Island, Laurentia (Hints et al. 2016). The common species include, e.g., *P. transitans*, *V. kozlowskii* and *P. gladiata* among the dominant taxa. A number of species in the Reinu assemblage are also shared with the latest Katian and early Hirnantian assemblages from the Králův Dvůr and Kosov formations in the Levín section, Prague Basin (Tonarová et al. 2023). However, there are notable differences too. For instance, *Pistoprion* has not been recorded in the Prague Basin before the Llandovery. The latest Ordovician polychaete fauna from central Saudi Arabia, Gondwana (Hints et al. 2015), is the least similar to the Baltic faunas. Overall, such a biogeographical pattern corroborates the conclusions recently outlined by Tonarová et al. (2023).

## Conclusions

The main outcomes of the study are the following:

1. A diverse Hirnantian jawed polychaete fauna was documented for the first time from the shallow-water carbonates of the Ärina Formation.
2. The highest abundance of scolecodonts in the Baltic Ordovician was recorded, reaching 5400 maxillae per kilogram of rock.
3. Polychaete turnovers near the base of the Hirnantian appear to be relatively minor, and many species also range into the Silurian. This corroborates earlier opinions about the resilience of polychaete faunas to the end-Ordovician mass extinction.
4. Palaeobiogeographically, the Reinu polychaete fauna shows the closest similarity with coeval assemblages from Anticosti Island and, to a lesser degree, the Prague Basin, and northern Gondwana.

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