

KARIN TRUUVER

Ostracod associations  
of the Ordovician–Silurian  
boundary interval in Baltoscandia





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## LIST OF ORIGINAL PUBLICATIONS

- I. **Truuver, K.**, Meidla, T., Ainsaar, L., Bergström J. and Tinn, O. 2013. Stratigraphy of the Ordovician–Silurian boundary interval in Östergötland, Sweden, based on ostracod distribution and stable carbon isotopic data. *GFF*, 134(4), 295–308, DOI: <https://doi.org/10.1080/11035897.2012.762550>
- II. **Truuver, K.** and Meidla, T. 2015. A Hirnantian deep-water refuge for warm-water ostracods in Baltoscandia. *Geological Quarterly*, 59(4), 738–749, DOI: <http://dx.doi.org/10.7306/gq.1258>
- III. **Truuver, K.**, Meidla, T. and Tinn, O. 2021. End-Ordovician ostracod faunal dynamics in the Baltic Palaeobasin. *Estonian Journal of Earth Sciences*, 2021, 70(1), 51–69, DOI: <https://doi.org/10.3176/earth.2021.02>
- IV. Meidla, T., **Truuver, K.**, Tinn, O., Ainsaar, L., 2020. Ostracods of the Ordovician-Silurian boundary beds: Jurmala core (Latvia) and its implications for Baltic stratigraphy. *Estonian Journal of Earth Sciences*, 2020, 69(4), 233–247, DOI: <https://doi.org/10.3176/earth.2020.20>

### **Author's contribution:**

**Paper I:** The author analysed the ostracod material (identification, SEM photography and image processing), prepared samples for  $\delta^{13}\text{C}$  analysis and was responsible for data interpretation and writing the manuscript.

**Paper II:** The author analysed the ostracod material (identification, SEM photography and image processing) and was responsible for ostracod and  $\delta^{13}\text{C}$  data interpretation and writing the manuscript.

**Paper III:** The author was responsible for data interpretation and writing the manuscript.

**Paper IV:** The author was responsible for ostracod data interpretation and for complementing the manuscript.

## ABBREVIATIONS

BC	Baltic Carbon
BPB	Baltic Palaeobasin (in Estonian: Balti Paleobassein)
DCA	Detrended correspondence analysis
E	Eastern
FAD	first appearance datum
Fm.	Formation
HB	Geographically widely distributed stratigraphic gap in the uppermost Ordovician
HICE	Hirnantian isotopic carbon excursion
LAD	last appearance datum
N	Northern
O–S boundary	Ordovician–Silurian boundary
RS	Regional Stage
S	Southern
SEM	Scanning electron microscopy
UPGMA	Unweighted pair group method of linkage
W	Western
$\delta^{13}\text{C}$	Stable carbon isotopic signature, ratio of $^{13}\text{C}/^{12}\text{C}$ (parts per thousand)

## INTRODUCTION

The Ordovician Period ended with a glaciation event when large glaciers formed on the Gondwana Supercontinent covering large areas on the Southern Hemisphere. The exact beginning and duration of the glaciation and dynamics of the climate change are both subjects of heated discussion. Brenchley *et al.* (1994) suggested that the glaciation was abrupt and short, lasting about 0.5–1 Ma, and Hallam and Wignall (1997) and Finnegan *et al.* (2011) also support that idea. A number of more recent papers (e.g. Kaljo *et al.*, 2003; Saltzman and Young, 2005; Buggisch, *et al.*, 2010; Rosenau *et al.*, 2012; Sell *et al.*, 2013) suggest that the cooling may have started earlier, around the Sandbian-Katian boundary. Some authors place the beginning of cooling already in the late Early Ordovician (Trotter *et al.*, 2008; Vandenbroucke *et al.*, 2010; Turner *et al.*, 2011).

There has been much debate about what exactly triggered the end-Ordovician cooling. Several explanations have been proposed, e.g. the “classical” organic burial hypothesis (Marshall and Middleton 1990; Brenchley *et al.*, 1994) and the silicate weathering hypothesis (Kump *et al.* 1999). Lenton *et al.* (2012) and Morris *et al.* (2018) suggest that the glaciation was related to the appearance and radiation of the first land plants, whilst Buggisch *et al.* (2010) place the blame on the Deicke volcanic eruption. Still, the true mechanism is yet to be determined.

The end-Ordovician glaciation was accompanied by a prominent extinction event, but its timing and causes are not clear yet and need further investigation. According to the most accepted opinion, the extinction was a sudden event that started at the beginning of the Hirnantian Age. However, some studies (e.g. Kaljo *et al.*, 2008) have shown that it might not have been a very abrupt event but a longer process starting already in the mid-Katian.

Different reasons have been proposed for the extinction. Wilde and Berry (1984) and Marshall and Middleton (1990) place the blame on nutrient-rich but noxious water currents which came from the polar regions and caused an algal bloom and the following rapid eradication of organic matter. A sea level drop intensified organic carbon burial in deep-sea sediments, releasing more and more phosphorus, which in turn increased productivity (Hammarlund *et al.*, 2012). These processes led to severe anoxia by the first half of the Hirnantian Age. Hammarlund *et al.* (2012) also suggest that euxinic conditions prevailed during most of the Hirnantian Age, although the early Hirnantian oceans were seemingly oxygenated. Finnegan *et al.* (2011) linked the mass extinction directly to the Hirnantian glaciation. Rasmussen and Harper (2011) admit the role of climate change in the extinction but place the major blame on the tectonics, namely the closing of the Iapetus Ocean and related loss of marginal-marine habitats suggesting that the glaciation-related sea-level drop only reinforced these conditions. Jones *et al.* (2017) support the hypothesis of volcanic trigger to the extinction but suggest it was the large igneous provinces volcanism that was directly responsible for the climatic changes leading to mass extinctions. Vandenbroucke *et al.* (2015) show that the major Palaeozoic extinctions either coincided



or were directly preceded by an exceptional rise in the amount of dissolved metals in the ocean. They link the increased metal content in seawater with malformations of plankton and suggest it to be at least a precursor of major palaeobiological catastrophes in the Ordovician and Silurian. Long *et al.* (2015) add another cofactor to the long list of the possible extinction inducers, a prolonged (estimatedly ~10 Ma) period of selenium depletion in the ocean. Selenium is a vital element for all animals and most of the plants. Crustal weathering (which is the main source of Se) is reduced during times of low oxygen. That leads to less Se being carried (e.g. by rivers) to the ocean, causing Se-deficiency. Long *et al.* (2015) show strong oceanic Se depletion prior to end-Ordovician, end-Devonian and end-Triassic extinctions. Harper *et al.* (2014) conclude that the aforementioned factors probably acted together to create such long-lasting and heterogeneous extinction event.

Due to their high sensitivity to environmental changes, ostracods were one of the animal groups most affected by this event (Boomer *et al.*, 2003; Tinn *et al.*, 2006; Smith and Delorme, 2010; Rodriguez-Lazaro, J. and Ruiz-Muñoz, F., 2012). Meidla (1996a) compiled a thorough study about the composition and dynamics of the Upper Ordovician ostracod associations of Estonia. The study area was restricted to Estonia as the coeval ostracod data were poor or lacking in several parts of the Baltic Palaeobasin (BPB) (W Lithuania, S Sweden, N Poland).

Carbon stable isotopic ( $\delta^{13}\text{C}$ ) analysis is often used in palaeoenvironmental studies and was included also in this study as an additional correlation proxy for clarifying the distribution of ostracod associations in the Baltoscandian area. The  $\delta^{13}\text{C}$  of marine dissolved inorganic carbon is associated with carbon circulation in ocean water. A positive excursion of  $\delta^{13}\text{C}$  reflects intensified carbon removal from seawater and atmosphere, causing the drawdown of atmospheric  $\text{CO}_2$ , which in turn creates favourable conditions for onset of glaciation (e.g. Ainsaar *et al.*, 2010). The development of the glaciation and the respective regression are reflected in the Upper Ordovician  $\delta^{13}\text{C}$  values in the BPB as a significant positive shift during the first half of the Hirnantian Age, followed by a gradual decline (e.g. LaPorte *et al.*, 2009; Ainsaar *et al.*, 2015; Wang *et al.*, 2019).

Ainsaar *et al.* (2010) compiled a chemostratigraphic subdivision of the Middle and Upper Ordovician carbonate strata of Baltoscandia consisting of 17 chemostratigraphic zones based on distinctive intervals of the  $\delta^{13}\text{C}$  curve (BC1–BC17, “BC”=“Baltic Carbon”). The time-span addressed by this study spans the isotopic zones BC13–BC17 and further up. In N Estonia, BC14 and BC15 are often absent because of the pre-Hirnantian sedimentary gap in this area (Ainsaar *et al.*, 2010); BC16 marks a steep rise in the carbon isotopic values and the beginning of the Hirnantian stable carbon isotopic excursion (HICE). The zone BC16 can be identified in the Taagepera (Brenchley *et al.*, 2003) and Valga-10 and Ruhnu (Ainsaar *et al.*, 2010) sections in S Estonia, in the Riekstini (Brenchley *et al.*, 2003) and Jurmala R-1 (Ainsaar *et al.*, 2004) sections in Latvia and S Swedish Borenshult (Bergström *et al.*, 2012) drill core where isotopic data were available.

The zone BC17 corresponds to the slowly lowering carbon isotopic values on the background of decline of glaciers (Ainsaar *et al.*, 2010). This zone is mostly missing in Estonia. It has been described only in the Valga-10 section in S Estonia (stratigraphically one of the most complete sections in Estonia) and could also be assumed to be partly present in the Taagepera and Tartu-453 sections, as well as in the Jurmala R-1 section in the Livonian Basin.

No comprehensive studies on the ostracod associations of the Ordovician–Silurian transition in the BPB area have been conducted during the last two decades. It is also unknown how changes in the ostracod associations correlate with the changes in  $\delta^{13}\text{C}$  values during the latest Ordovician ecological crisis. These questions and significant changes in the stratigraphy of the Baltoscandian area introduced over the last decade necessitated an extensive study of ostracod associations of the Ordovician–Silurian boundary interval in the ancient BPB.

The specific objectives of this research were:

- Determining the composition of the ostracod associations in the ancient BPB and their geographical range during the time interval from the late Katian up to the earliest Silurian.
- Testing the hypothesis on the earlier start and extended duration of the Hirnantian extinction on ostracods of the BPB.
- Complementing the Hirnantian stratigraphy in Lithuania, S Sweden and N Poland.
- Specifying the relationship between the dynamics of  $\delta^{13}\text{C}$  and changes in ostracod associations in the BPB during the period from the late Katian up to the earliest Silurian.
- Confirming the need for repositioning the Ordovician–Silurian boundary upwards in the Baltoscandian area.

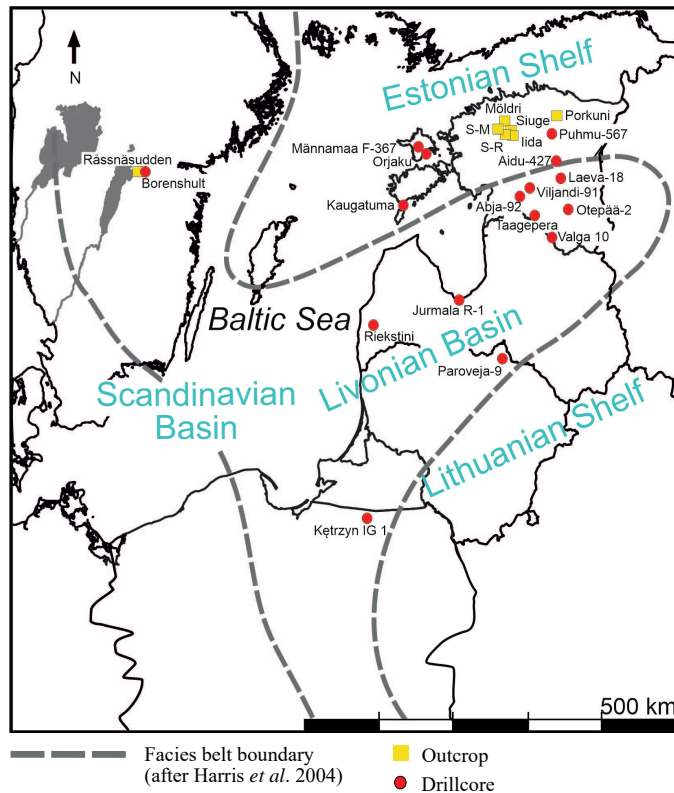
This study aims at testing the following hypotheses:

- the evidence of an earlier (pre-Hirnantian) extinction of the ostracod fauna in the BPB is recorded as a distinct diversity decline that can be distinguished from the sampling bias.
- Principal changes in the composition of ostracod associations were caused by the global ecological crisis in the latest Ordovician and are tied to the specific levels in the  $\delta^{13}\text{C}$  record (and to the specific carbon stable isotopic zones).
- The appearance level of the Hirnantian cold-water ostracod fauna can be used as a characteristic stratigraphic marker in regional biostratigraphy.
- More than one distinct association can be distinguished within the Hirnantian ostracod fauna.
- The distinctive Hirnantian cold-water ostracod fauna can be considered a part of the Hirnantian fauna *sensu lato*.

# BACKGROUND

## Geological setting

In the Late Ordovician, the Baltoscandian area was part of the Baltica Palaeocontinent situated in the southern hemisphere in a close vicinity of the Equator (Fig 6.2b in Torsvik and Cocks, 2017). In the north and east, the continent was surrounded by the Palaeo-Tethys Ocean. In the west, the Iapetus Ocean separated Baltica from the Laurentia Palaeocontinent. The Avalonia Microcontinent was approaching Baltica from the south, causing slow closure of the Tornquist Sea and the related volcanic activity. The Baltoscandian area was situated in the south-western part of the palaeocontinent and was covered with an epicontinental sea deepening in the south-westerly direction. The present N Estonia and E Lithuania comprised the shallowest part of the palaeobasin (Fig. 1; Fig. 2 in Kaljo *et al.*, 2011), being separated by the Livonian Basin – a north-easterly extension of the deeper-water Scandinavian Basin comprising S Estonia, W Latvia, W Lithuania, SE Sweden and northern and north-eastern areas of Poland (Harris *et al.*, 2004; Paper III).



**Figure 1.** Map of the study area and the sections used in this study. S-M, Seli-Metsküla; S-R, Seli-Russalu.

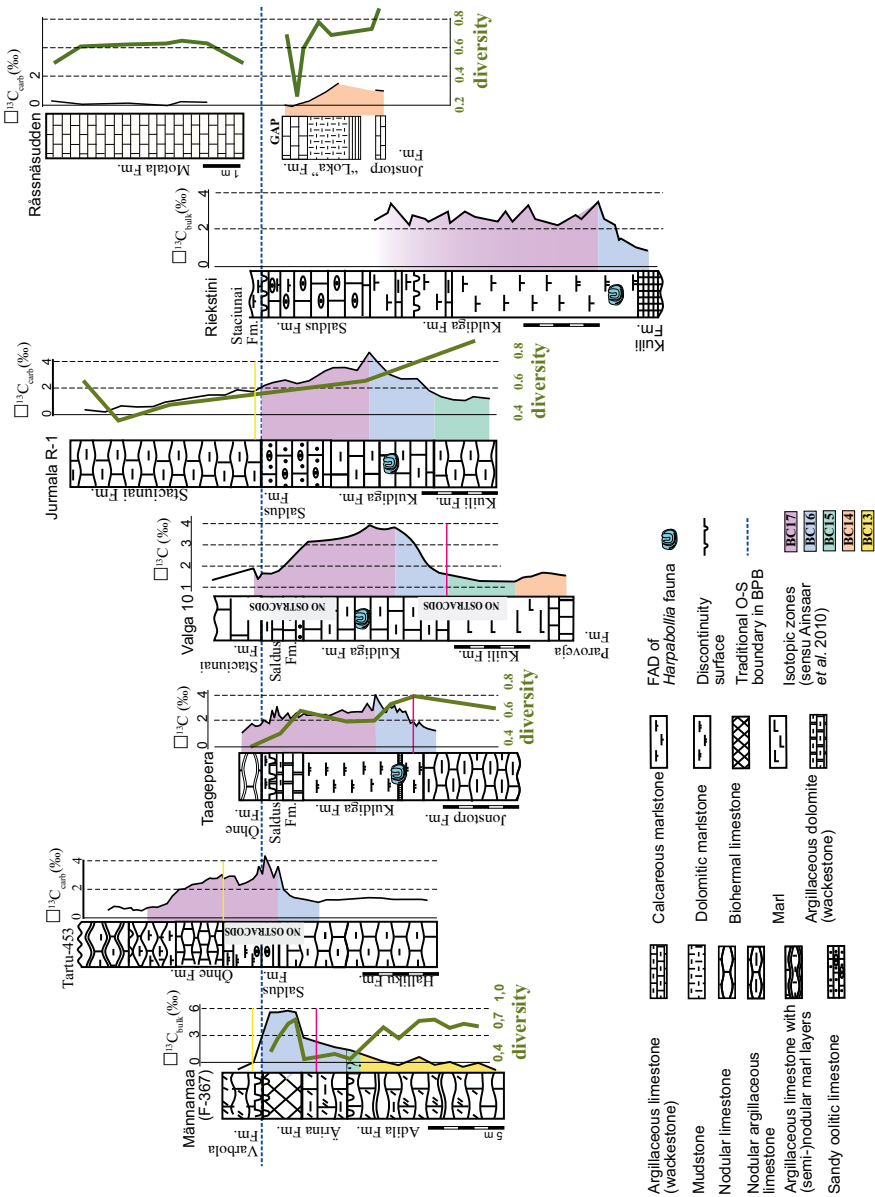
The end-Ordovician world was climatically one of the harshest and most unstable places to live due to the end-Ordovician climate event – the Hirnantian glaciation. It has received an increasing amount of attention over the last couple of decades because of its possible causes but a consensus has not been reached yet. According to the organic burial hypothesis (Marshall and Middleton, 1990; Brenchley *et al.*, 1994), the position of the continents favoured the accumulation of snow and ice in the polar regions. Intensified ocean circulation moved cold, nutrient-rich currents from polar regions into the warmer waters close to the Equator, increasing productivity and accelerating carbon burial. Reduction of dissolved pCO<sub>2</sub> in seawater in turn lowered the atmospheric pCO<sub>2</sub> to levels sufficient for accelerated ice cap formation. Kump *et al.* (1999) introduced the silicate weathering hypothesis according to which the Taconic orogeny that started in the late-middle Ordovician intensified silicate terraine exposure and weathering, lowering marine and atmospheric CO<sub>2</sub> levels enough for the ice caps to form. The proceeding ice albedo effect further supported the glacier formation. Lenton *et al.* (2012) and Morris *et al.* (2018) suggested that the appearance and radiation of the first land plants increased the weathering of silicate rocks, causing a drawdown of atmospheric CO<sub>2</sub>. This was yet reinforced by phosphorus weathering and influx from land to oceans where it enhanced production and organic carbon burial (Lenton *et al.*, 2012). According to Buggisch *et al.* (2010), cooling started after the biggest single volcanic eruption in the Phanerozoic – the Deicke eruption in the late Sandbian. Herrmann *et al.* (2011), Rosenau *et al.* (2012) and Sell *et al.* (2013) disagree with that opinion, relying on δ<sup>13</sup>O (Herrmann *et al.*, 2011; Rosenau *et al.*, 2012), U–Pb analyses and interpretation of more detailed datasets (Sell *et al.*, 2013).

The glaciation-related changes are well documented in the sections of the BPB. The sections used in this study vary in both stratigraphic extent and contiguity.

Bioclastic limestones and dolomites with numerous discontinuity surfaces dominate the Adila Formation in the Estonian Shelf area (Hints and Meidla, 1997a). The Halliku Fm. in the “transitional area” between the Estonian Shelf and Livonian Basin in Central Estonia consists of highly argillaceous limestones and marls (Hints and Meidla, 1997a). The Adila Fm. is overlain by a succession of dolomites, reef limestones and sandy or oolitic limestones designated as the Ärina Fm. These sections are lacking in most of the Hirnantian and the O–S boundary strata and the reef limestones of the Ärina Fm. (Hints and Meidla, 1997b) are overlain by nodular biomicritic limestones with thin marlstone intercalations, the Varbola Fm. (Nestor, 1997).

Within the Livonian Basin, the pre-glacial Jonstorp Fm. (S Sweden) and the Jelgava Fm. (S and W Latvia, W Lithuania; Ainsaar *et al.*, 2015; Paper III) are characterized by brownish-red or grey argillaceous limestones, dolomites and mudstones (Hints and Meidla, 1997a; Brenchley *et al.*, 2003; Paper III) which are occasionally nodular (e.g. Otepää-2 and Taagepera sections, Meidla 1996b; Fig. 1). In the deeper part of the BPB in N Poland, marls and marly limestones comprise the Sasino Fm. and the lower Prabuty Fm. (Paper II). The Jonstorp and Jelgava

**Figure 2.** Changes in the  $\delta^{13}\text{C}$  values and ostracod diversity indices in different parts of the BPB during the late Katian–latest Ordovician. The Diversity indices were calculated for sections where sufficient quantitative ostracod data were available. Blue *H. harparum* ostracod figures mark the FAD of the first typical representatives of the Hirnantian *H. harparum* association in the section. The pink line marks the LAD of the chitinozoan *Spi-nachitina taugourdeui* in the section. The yellow line indicates the first appearance of the traditionally called “Silurian fauna” that is here considered as belonging to the topmost Ordovician. The dark blue dashed line indicates the position of the principal regional dis-conformity in every lithological log. The sections are drawn after Meidla and Tinn (2008) – Männamaa F-367; Meidla (1998) and Bauert *et al.* (2014) – Tartu 453; Meidla (1996b) – Taagepera; Meidla (2001) and Kaljo *et al.* (2008) – Valga-10; Ainsaar *et al.* (2010) – Jurmala R-1; Brenchley *et al.* (2003) – Riekskini and Paper I (Räs-näsudden)



formations are overlain by bioclastic limestones and marls of the Kuldiga Fm. and silty and sandy, occasionally oolitic limestones of the Saldus Fm. (Hints and Meidla, 1997b). Many of these sections either contain one or more sedimentational gaps in the Kuldiga and Saldus formations (e.g. in the Taagepera, Riekstini (Fig. 2), Paroveja-9 (see Paškevičius, 1972) drill cores). Marls of the Prabuty Fm. in N Poland gradually grade into sandstones in the upper part of the formation, marking the peak regression in the late early Hirnantian (Paper III). In Östergötland (SE Sweden), the Jonstorp Fm. is overlain by the Loka Fm. consisting of a succession of greenish calcareous mudstones (unit A in Bergström and Bergström, 1996), grey to white, sometimes mottled reddish, partly oolitic, calcarenitic fossiliferous limestone with rounded clasts of limestone and mudstone (unit B in Bergström and Bergström, 1996) and greenish mudstone (unit C in Bergström and Bergström, 1996). While the Loka Fm. is at least partly present in the Borenshult and Smedsby Gård core sections (Bergström *et al.*, 2012), its presence in the Råsnäsudden section (assumed by the same authors) seems problematic (Paper I).

Nodular, occasionally argillaceous limestones and carbonaceous marlstones of the Öhne and Stačiunai formations overlie the Saldus Fm. in the Livonian Basin comprising S Estonia, W Latvia and W Lithuania (Nestor, 1997; Fig. 1). In N Poland, micritic limestones of the Pasłék Fm. are directly overlying the sandstones of the Prabuty Fm. (Paper II). In S Sweden, the Loka Fm. is overlain by light to dark grey nodular limestones, calcareous mudstones and a few brownish, calcilititic to calcarenitic limestones of the Motala Fm.

## The uppermost Ordovician stable carbon isotope geochemistry

The late Katian  $\delta^{13}\text{C}$  values are relatively low, mostly  $\sim 0$ – $1\text{‰}$ , but start to rise slowly at the very end of the age. A positive shift of  $\delta^{13}\text{C}$  values has been described from carbonates of the latest Ordovician Hirnantian Stage globally (e.g. Finney *et al.*, 1999; Brenchley *et al.*, 2003; Ainsaar *et al.*, 2010, 2015; Mauviel and Desrochers, 2016; Wang *et al.*, 2019). In the BPB, the  $\delta^{13}\text{C}$  values rise to values of up to  $+6\text{‰}$  in the lower half of the Kuldiga Fm. (Ainsaar *et al.*, 2010). The sharp rise in  $\delta^{13}\text{C}$  values is followed by a much more gradual decline in the upper half of the Kuldiga Fm. and in the overlying Saldus Fm. (Fig. 2)

Several studies in the Baltoscandian area and Anticosti Island, Canada, have shown that the decline does not stop at the formerly accepted Ordovician–Silurian boundary – the  $\delta^{13}\text{C}$  values keep falling above that level (e.g. Ainsaar *et al.*, 2010; Mauviel and Desrochers, 2016; Paper III). Stratigraphically one of the most complete sections in Baltica, the Jurmala R-1 core, has yielded gradually decreasing  $\delta^{13}\text{C}$  values (around  $+2\text{‰}$  and  $+1\text{‰}$ ) right above the current position of the former Ordovician–Silurian boundary (Ainsaar *et al.*, 2010). Due to the lack of the zonal graptolites and presence of a geographically widely distributed

stratigraphic gap known as the HB unconformity (Schmitz and Bergström, 2007), the O–S boundary has traditionally been drawn at the lower boundary of the Juuru Stage in Estonia (Bauert *et al.*, 2014; Meidla *et al.*, 2014). Chemostratigraphic data have shown that an upward shift of the Ordovician–Silurian boundary should be considered here (Ainsaar *et al.*, 2010; Männik, 2014; Meidla *et al.*, 2014). On the basis of their high-resolution, detailed  $\delta^{13}\text{C}$  curve from the W coast of Anticosti Island (Canada) spanning the Ordovician–Silurian boundary, Mauviel and Desrochers (2016) mark that although the  $\delta^{13}\text{C}$  curve reaches its pre-Hirnantian (+0.5‰) values a few meters above the present system boundary, the  $\delta^{13}\text{C}$  values continue descending for >50 m above the O–S boundary, suggesting reconsideration of the position and shifting it higher than its current position also in Canada. Kaljo *et al.* (2001) and Ainsaar *et al.* (2010, 2015) show that the basal Silurian  $\delta^{13}\text{C}$  values from various central, W and S Estonian drill cores “fall into the limits of the Porkuni Stage” (Kaljo *et al.*, 2001), reaching up to 2.1‰ and continuing to decline slowly until they reach the pre-Hirnantian values above the traditional Ordovician–Silurian boundary (Fig. 2).

The chemostratigraphic zonation compiled for the Middle and Upper Ordovician carbonate strata by Ainsaar *et al.* (2010) constitutes an independent stratigraphic tool which helps to analyse the chronology of changes in the ostracod associations in BPB.

## **Early Palaeozoic ostracods and their subordinal classification**

Ostracods are tiny crustaceans belonging to the phylum Arthropoda. They have about 0.5–2 mm long calcitic bivalved carapaces which can fossilize easily; soft body remains are rare in Palaeozoic ostracods (Williams *et al.*, 2015).

Ostracods have probably the longest fossil record among all arthropods extending back to the late Tremadocian (Tinn and Meidla, 2004, Meidla *et al.*, 2013, Rodriguez-Lazaro and Ruiz-Muñoz, 2012). Although ostracods were primarily environmental generalists (Williams *et al.*, 2008), they demonstrated environmental differentiation already by the early Middle Ordovician, with low-diversity assemblages inhabiting marginal marine and other stress environments (Meidla *et al.*, 2013). The lower Palaeozoic ostracods were exclusively marine; the first nonmarine species appeared in the Carboniferous only (Smith *et al.*, 2015).

Modern ostracods inhabit all sorts of natural and artificial wet environments from Polar to Equatorial regions. Whilst the first ostracods were endemic, with the first signs of possible cosmopolitanism appearing in the latest Ordovician, there are both cosmopolitan and endemic forms among modern ostracods (Smith *et al.*, 2015).

## Suborders of the order Beyrichiocopa

The ostracod classification used in this study is based on Vannier *et al.* (1989) and Meidla (1996b). The descriptions of suborders are based on Meidla *et al.* (2013), Vannier *et al.* (1989), Meidla (1996b) and Olempska (2012).

Palaeocopa (Fig. 3.1) is the most diversified lower Palaeozoic group of ostracods, considered to be characteristic of stable conditions and carbonate environments. Ostracods belonging to this group display sexual dimorphism which mostly is reflected in the variable adventral structures of carapace (velum, histium and alike). The shells of this group are characterized by various shell structures such as lobes, sulci and marginal structures (Vannier *et al.*, 1989). Palaeocopes strongly dominated the BPB up to the Sandbian and started declining from thereon, but they retained their dominance in the BPB associations until the latest Ordovician.

The suborder Binodicopa (Fig. 3.2) comprises species that are characteristic of high-stress and clastic environments. Their carapace has fewer structural features than the shells of palaeocopes. The main sculptural features comprise two lateral nodes, one of which may have a spine or may be divided into three swellings. Some species have a pseudovelum. Sexual dimorphism is expressed in the shell shape, size or outline, rather than in sculptural or admarginal features.

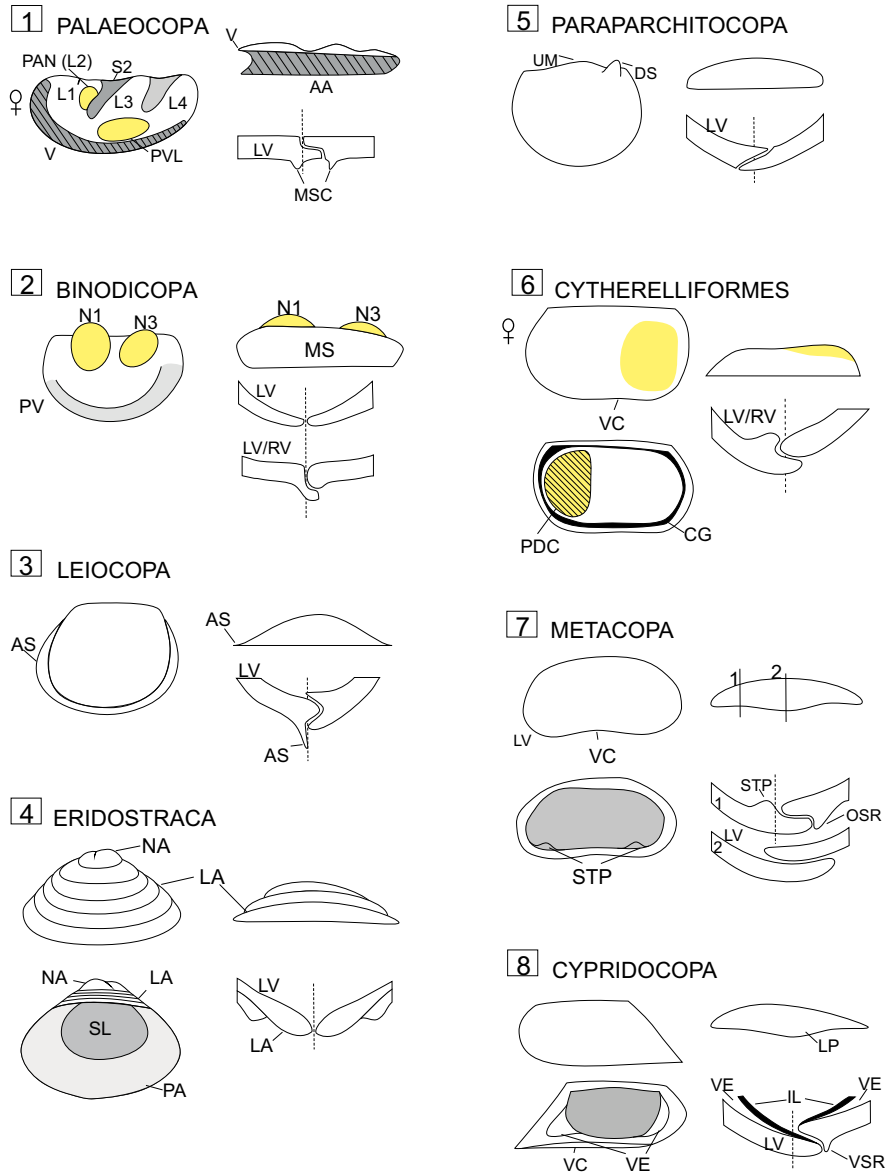
Leiocopa (Fig. 3.3) is a suborder of species that inhabited stable, carbonate environments. The shells are round or slightly elongate and smooth or punctate. Valves are unequal in size, the right valve overlaps the left one and the hinge line is relatively short.

Eridostraca (Fig. 3.4) was a distinctive ostracod group characteristic of stable, carbonate marginal marine environments (Olempska, 2012). A noticeable difference between eridostracans and other ostracod suborders is multilamellar shell, due to very common shell retention that is otherwise very rare in any other Lower Palaeozoic ostracod group. The shells are relatively small ( $\leq 1.5$  mm) and sub-ovate to sub-triangular in lateral view. The umbo often projects above the long and straight hinge line. Some species possess a conspicuous adductor sulcus in later instars, which is covered with valves of earlier instars. Sexual dimorphism has been suggested in some species, with the supposed males being more elongate than the supposed females.

The suborder Paraparchitocopa (Fig. 3.5) contains species that inhabited carbonate environments. Their shells are small, valves oval and smooth, sometimes with a spine in the centrodorsal part of the valve. Sexual dimorphism may occur.

The representatives of Cytherelliformes (Fig. 3.6) are not very common in the studied material. Our data show that they likely preferred carbonate environments. They have small, ventrally slightly convex shell which may have reticulated surface. Dimorphism has been described occurring in the form of broad posterior domiciliary concavity in presumable females.





**Figure 3.** Compilation of the drawings from Vannier *et al.* (1989) showing the main morphological features of ostracod suborders: 1 – Palaeocopa, 2 – Binodicopa, 3 – Leiocopa, 4 – Eridostraca, 5 – Paraparchitocopa, 6 – Cytherelliformes, 7 – Metacopa, 8 – Cypridocopa. AA – admarginal antrum; AS – adventral sculpture; CG – contact groove; DS – dorsal spine; IL – inner lamella; L1-L4 – lobes 1, 2, 3, 4; LA – lamella; LP – lappet; LV – left valve; MS – marginal surface; MSC – marginal sculpture; N1 – anterior node; N3 – posterior node; NA – nauplioconch; OSR – outer stop-ridge; PA – paleola; PAN – preadductorial node; PDC – posterior domiciliary concavity; PV – pseudovelum; PVL – posteroventral lobe; RV – right valve; S2 – adductorial sulcus; SL – sulcament; STP – stop-peg; UM – umbo; V – velum; VC – ventral concavity; VE – vestibulum; VSR – ventral stop-ridge. Parallel striation marks dimorphic feature; yellow colour marks protruding features; grey colour marks depressions.

### Suborders of the order Podocopa

The species of *Metacopa* (Fig. 3.7) were resilient opportunists who managed to survive both in stable and unstable conditions. Their shells are relatively simple and inequivalved, with the left valve being slightly bigger than the right valve. Dimorphism is unknown in this group.

The shells of *Cypridocopa* (Fig. 3.8) are usually very small (<0.5 mm) and elongate, often with distinct vestibula. The left valve is a bit larger and overlaps the right valve.

Ostracods reached high diversity and abundance all over the BPB by the beginning of the Late Ordovician. Although the Baltoscandian ostracod associations suffered in several environmental disturbances during the Late Ordovician (e.g. the late mid-Sandbian Kärddla impact event and the Kinnekulle volcanic eruption) (Vannier *et al.*, 1989 and references therein; Suuroja and Suuroja, 2006 and references therein), their diversity rebounded fast, reaching its peak in the early Pirgu age (Meidla, 1996a).

Meidla (1996b) conducted a thorough study on the Upper Ordovician ostracods of Estonia focussing on the taxonomic description of ostracods and composition of the ostracod associations. His observations show that 95% of the Late Ordovician ostracod species in the BPB belong into two orders: *Beyrichiocopa* (67%) and *Podocopa* (28%). The most prominent suborders in the BPB were *Palaeocopa*, *Metacopa* and *Binodicopa* (Meidla, 1996b), which were followed by the somewhat less common suborder *Leiocopa* and minor occurrences of *Paraparchitocopa*, *Cytherelliformes* and *Cypridocopa* (Paper III). During the latest Ordovician, the diversity and subordinal importance of *Cytherelliformes* grew together with those of *Binodicopa* (Meidla *et al.*, 2013) and *Metacopa* (Vannier *et al.*, 1989). *Binodicopes*, which are characteristic of unstable, clastic environments, were overpowered by more dominant palaeocopes and metacopes until the very end of the era when they for the first time attained strong dominance over all other ostracod groups, due to the Hirnantian glaciation (Meidla, 1996b).

## MATERIAL AND METHODS

### Geological sections investigated in the course of the study

The ostracod material used in this study derives mostly from drill cores, in some cases also from outcrops. The study area covers two facies belts, the shallower Estonian Shelf and deeper Livonian and Scandinavian basins. The Estonian Shelf is represented by six outcrops and five drill cores, the Scandinavian Basin by 11 drill cores, one outcrop and regional overviews of the ostracod distribution in NE and E Poland (Sztejn, 1985, 1989, respectively) (Fig. 1). One of the aims of this study was to complement the data set with new sections from poorly studied areas and extend the previous knowledge on the distribution of biofacies within the BPB.

The Hirnantian Stage has been described in several sections in S Sweden Östergötland, Västergötland, Scania and the Siljan District (Bergström and Bergström, 1996; Koren *et al.*, 2003; Meidla, 2007; Bergström *et al.*, 2011 a, b; Bergström *et al.*, 2012; Bergström *et al.* 2013; Paper I) but most of these studies do include ostracod data. The specific Hirnantian *Harpabollia harparum* ostracod association was described by Meidla (2007) in the material from the Borenhult locality (SE Sweden), obtained from the remaining loose blocks after the end of construction works for sluice to Göta Canal (SE Sweden). The association was found co-occurring on the same rockslabs with abundant other fossil taxa typical of the Hirnantian globally, such as *Stegerhynchus eoborealis* Rong, Jin, Zhan *et Bergström* (2008), *Dalmanella testudinaria* (Dalman, 1828), *Hindella cassidea* (Dalman 1828), *Hirnantia sagittifera* (McCoy 1851), *Normalograptus persculptus* (Elles and Wood, 1907) (Paper I) and several others. The specimens of the *H. harparum* association and *Hirnantia* fauna co-occur also in the Kętrzyn IG 1 drill core in N Poland (Rubel in Modliński *et al.* 2002; Paper II), further confirming that the *H. harparum* ostracod association is part of the cosmopolitan *Hirnantia* fauna *sensu lato*. Since the studied material derives from loose rock slabs, statistical analysis and correlation of the ostracod record with dynamics of the  $\delta^{13}\text{C}$  curve was not possible for the Borenhult locality but several of the blocks demonstrate elevated  $\delta^{13}\text{C}$  values (Paper II). The purpose of studying the ostracod material from the **Råssnäsudden** outcrop was to confirm the presence of Hirnantian strata in Östergötland by obtaining the species of the *H. harparum* ostracod association from this suggested Hirnantian section, together with  $\delta^{13}\text{C}$  data.

The end-Ordovician ostracods of E and NE Poland were studied three decades ago by Stejn (1985, 1989). The ostracod data represented in the mentioned papers were qualitative and generalized over stages and could not be used in statistical analysis, correlation of ostracod data with  $\delta^{13}\text{C}$  values or analysing the first and last appearance datums (FADs and LADs) of the key species. The **Kętrzyn IG 1** borehole in NE Poland was studied in order to update and specify the species composition and distribution pattern of ostracod associations in NE Poland during the latest Ordovician and, if possible, to justify the position of the lower boundary of the Hirnantian Stage in this area.

Not many studies have been conducted on the latest Ordovician ostracods in Lithuania. Two papers by Sidaravičiene (1992, 1996) about Lithuanian Ordovician ostracods are available, but the data are not sufficiently detailed and the Hirnantian seems to be missing in most of the sections she studied. The **Paroveja-9** drill core was incorporated in the present study to provide the latest Ordovician ostracod data obtained for N Lithuania.

Data from the three aforementioned sections were complemented with sections in N Estonia and Latvia to compile a detailed quantitative ostracod database with individual sample resolution covering the entire ancient BPB area.

The stable isotopic data were mainly gathered from numerous previously published studies (Brenchley *et al.* 2003; Ainsaar and Meidla, 2008; Ainsaar *et al.* 2010; Bauert *et al.* 2014) except for  $\delta^{13}\text{C}$  data of the **Rässnäsudden** outcrop material which were collected and analysed for Paper II in the Department of Geology of the University of Tartu, Estonia.

The chitinozoan and graptolite data used as additional biostratigraphic markers in this study were gathered from published papers (Brenchley *et al.* 2003; Kaljo *et al.* 2008; Meidla *et al.* 2014; Nölvak, 2008).

## Laboratory preparation of material and study methods

For ostracod fossils, crushed rock material (fragment size ~2–3 cm) was treated using a standard physical disintegration method with sodium hyposulphite ( $\text{Na}_2\text{S}_2\text{O}_3 \cdot 5\text{H}_2\text{O}$ ), heating and cooling repeatedly. After this, the samples were wet sieved into four fractions (>2 mm, 0.5–2 mm, 0.25–0.5 mm, <0.25 mm) and dried. Ostracods were picked from the dry residue using stereoscopic binocular microscope with amagnification of 16–25x (Tinn and Meidla, 2004; Tinn *et al.*, 2006, 2010).

Published ostracod data and existing collections were used for species identification. Photomicrographs of ostracods for Paper I were taken using a PHILIPS XL30 ESEM TMP scanning electron microscope in the Institute of Physics of the University of Tartu, Estonia. For Papers II and IV, photomicrographs of ostracods were taken using the Zeiss EVO MA15 SEM scanning electron microscope in the Department of Geology, University of Tartu (Paper II). The collection numbers for collections are TUG-1583 for Paper I, GIT-698 for Paper II and TUG-1820 for Paper IV. Collections TUG-1583 and TUG-1820 are deposited in the Natural History Museum, University of Tartu, collection GIT-698 is deposited in the Department of Geology of Tallinn University of Technology, Estonia.

For stable carbon isotopic analysis, about 2 g piece of material was taken from each sample and powdered. The powdered material was analysed using the mass spectrometer Delta V Advantage and (for preparation of gases) GasBench II by Thermo Scientific, using the international standards NBS 18, NBS 19 and LSVEC. The analytical work was conducted in the mass spectrometry laboratory in the Department of Geology of the University of Tartu, Estonia (Paper I).

## Statistical analyses of ostracod associations

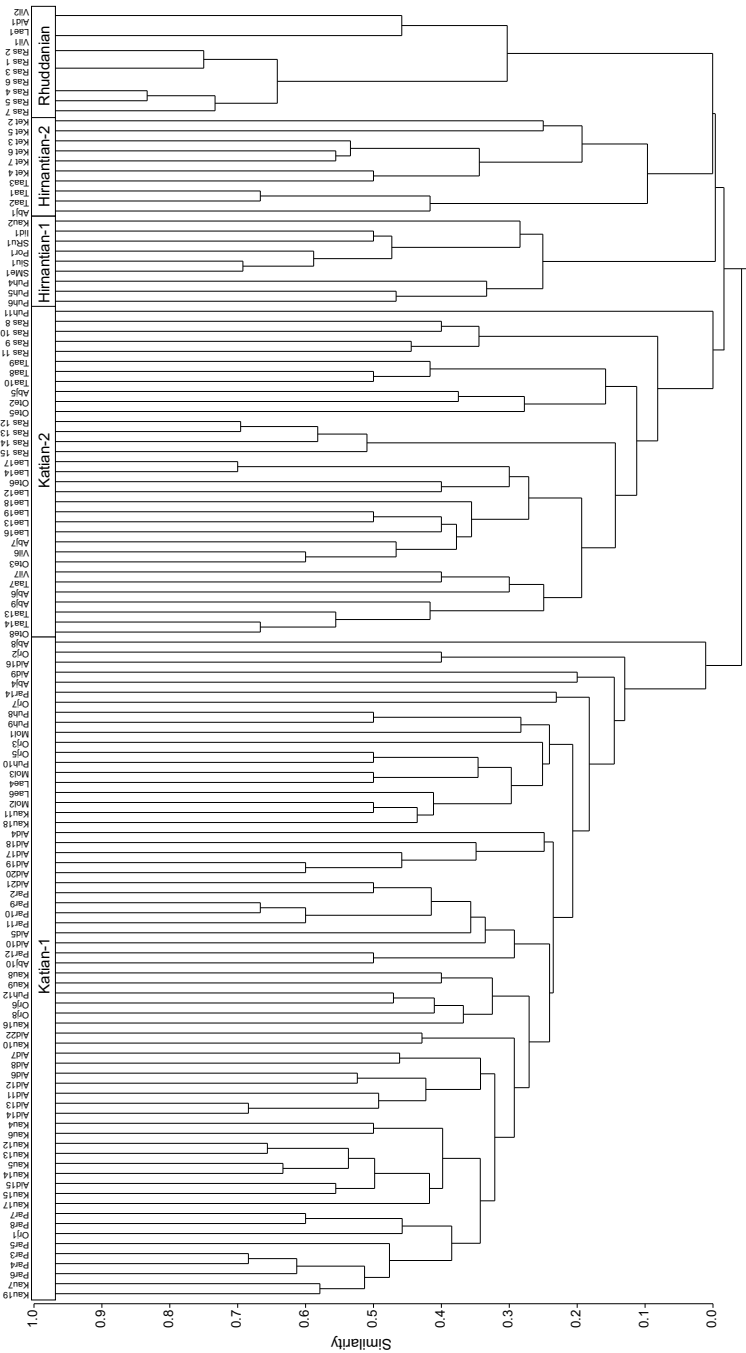
The parent dataset was constructed as data matrix with locality, sample, stratigraphic and species data. The information originated from newly collected data from core sections and outcrops and from relevant literature, which was examined in the course of the compilation of this database (see Fig. 1 for the sections). However, due to different levels of generalization, the latter was not always usable for detailed statistical analyses (see supplementary information of Paper III at <https://doi.org/10.23679/505>).

From this parent dataset we restricted the study to species and samples with more than one sample/taxonomic occurrence. Samples with unduly low diversity were also excluded from the dataset, and, in the final stage of the analyses, also samples with very unstable position. The remaining matrix contains data on 15 983 ostracod individuals/specimens, attributed to 116 species, 71 genera and 9 sub-orders, where the Katian is represented by 103 samples, Hirnantian by 34 samples and late Hirnantian–Silurian transition (late Hirnantian–Rhuddanian, designated as “Juuru” below) by 11 samples. Altogether 148 samples from 20 localities were analysed (Paper III).

For statistical analyses, we used Microsoft Excel 2007 in Papers I–IV and the PAST statistical package version 4.01 (Palaeontological Statistics; Hammer *et al.*, 2001) for Paper III and version 4.03 for Paper IV. The non-metric multidimensional scaling (NMDS) ordination and unweighted pair group method of linkage (UPGMA) cluster analyses were conducted on the presence/absence matrix using the Jaccard similarity index as a distance measure. The UPGMA clustering (also known as average linkage or mean linkage clustering), where the distance between two clusters is defined as the average of all possible distances (Hammer and Harper, 2005), helps to distinguish and illustrate different groups in the dataset and is often used in ecological analyses (Paper III).

The UPGMA analyses resulted in five major clusters (Fig. 4). The clusters, named Katian-1, Katian-2, Hirnantian-1, Hirnantian-2 and Juuru, represent concurrently stratigraphical and biogeographical units (supplementary online data at <https://doi.org/10.23679/505>).

The two biggest clusters, Katian-1 and Katian-2, incorporate taxa/samples of late Katian age. The division of the samples is based on their geographical distribution. The clusters Hirnantian-1 and Hirnantian-2 represent samples/taxa of Hirnantian age, but again, from different parts of the study area. Hirnantian-1 comprises samples of Central and N Estonia, Hirnantian-2 covers the southern part of the study area (Abja-92, Taagepera, Jurmala R-1, Kętrzyn IG 1 drill cores). The cluster Juuru comprises samples from the Laeva-18, Aidu-427, Viljandi-91 and Râsnassuden sections (Paper III).



**Figure 4.** Dendrogram of cluster analysis of the Upper Ordovician–basal Llandoveryan ostracod samples. Clusters Katian-1 and Katian-2 consist of samples containing preglacial associations, clusters Hirnantian-1 and Hirnantian-2 of samples containing species distinctive to the glacial period and the cluster Juuru contains samples yielding the post-glacial survival and recovery faunas. Clusters Katian-1 and Katian-2 comprise samples from the shallower and deeper part of the BPB, respectively. Cluster Hirnantian-1 contains N Estonian uppermost Katian–lower Hirnantian samples and Hirnantian-2 involves the Hirnantian samples from the Livonian Basin.

The biodiversity indices (Shannon index, dominance and evenness) were calculated for all five clusters. While in the Katian and Hirnantian clusters both the dominance and Shannon indices are relatively similar (0.1 to 0.2 and 2.0 to 2.5, respectively), the Juuru cluster shows rather different values ( $d = 0.5$  and  $H = 0.7$ ). The evenness values stay low ( $>0.3$ ) in the Katian clusters and in the cluster Hirnantian-1 but make a considerable leap up to 0.4 in the Hirnantian-2 and further to 0.5 in the Juuru cluster (Paper III).

Detrended correspondence analysis (DCA) was performed on the same dataset, in order to provide an alternative visualization for the Katian, Hirnantian and Juuru ostracod assemblages of the Baltic area. As one of the tools for multi-dimensional data analysis in ecology and palaeontology DCA is discussed in detail by Clapham (2011) and Correa-Metrio *et al.* (2014); see also references therein. It has been argued that the detrending process may yield more accurate and interpretable ordination results, especially for long ecological gradients or in the case of rapid ecological turnover (Clapham, 2011) (Paper III).

## RESULTS

The five clusters obtained with the statistical analyses (Katian-1, Katian-2, Hirnantian-1, Hirnantian-2 and Juuru) contain samples that yielded five distinct ostracod assemblages inhabiting the BPB during the period from the immediate pre-Hirnantian (roughly the 2nd half of the Katian) up to the Juuru Age. The distribution of samples between the clusters is presented in Figure 4. The diversity indices (dominance, evenness, Shannon index), calculated to evaluate and compare the diversity of the five associations, are presented in Figure 5. The distribution of the association is shown in Figure 6. The taxonomic relationship between the associations is presented in Figure 7.

### **Late Ordovician–basal Silurian ostracod associations in the BPB**

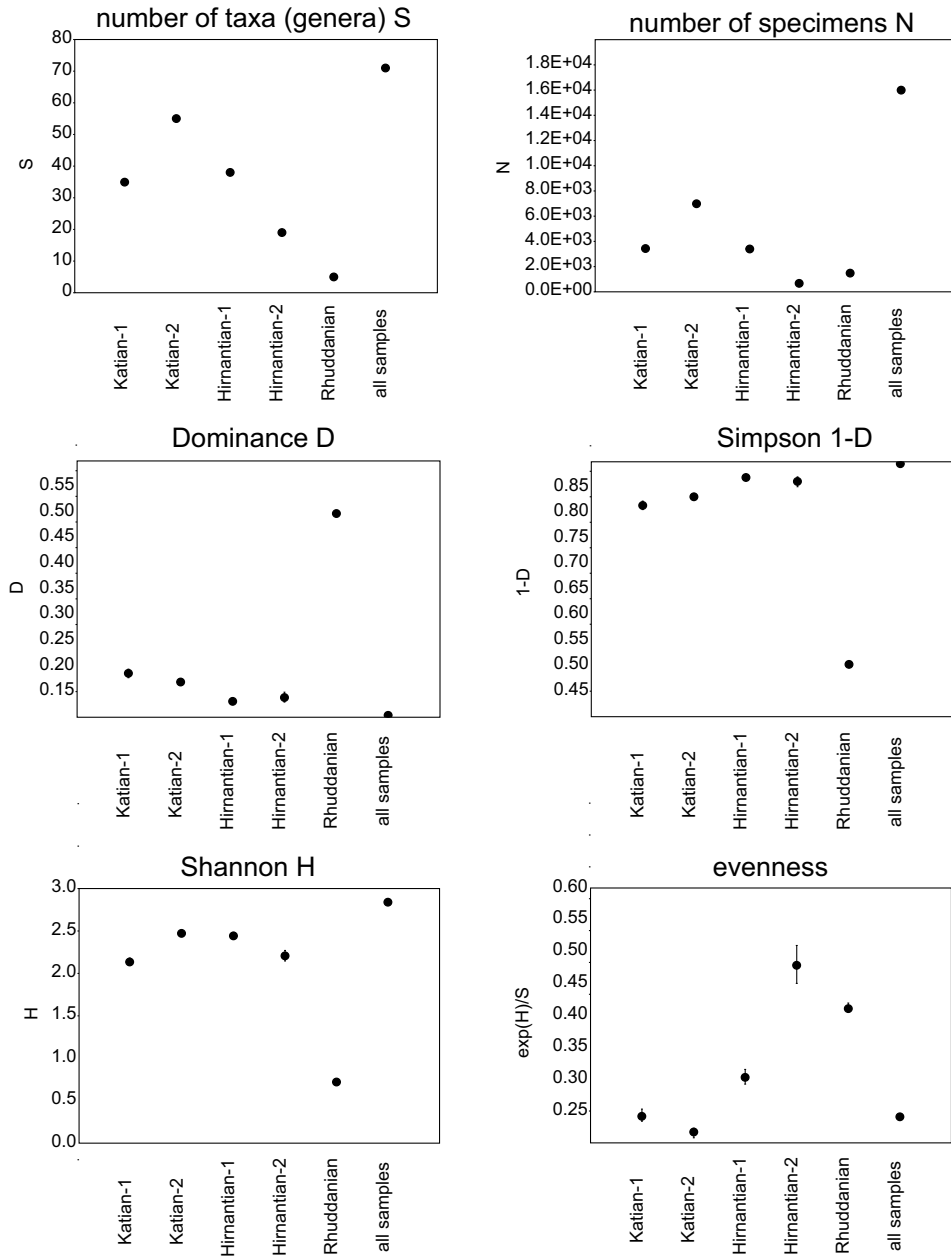
Low generic dominance and high entropy (Fig. 5) suggest that the ostracod associations in both shallower and deeper parts of the BPB were rich and diverse during most of the Katian.

The two biggest clusters, Katian-1 and Katian-2, incorporate taxa/samples of Katian age, whilst the division of the samples is based on their geographical distribution (Fig. 6A and B, respectively).

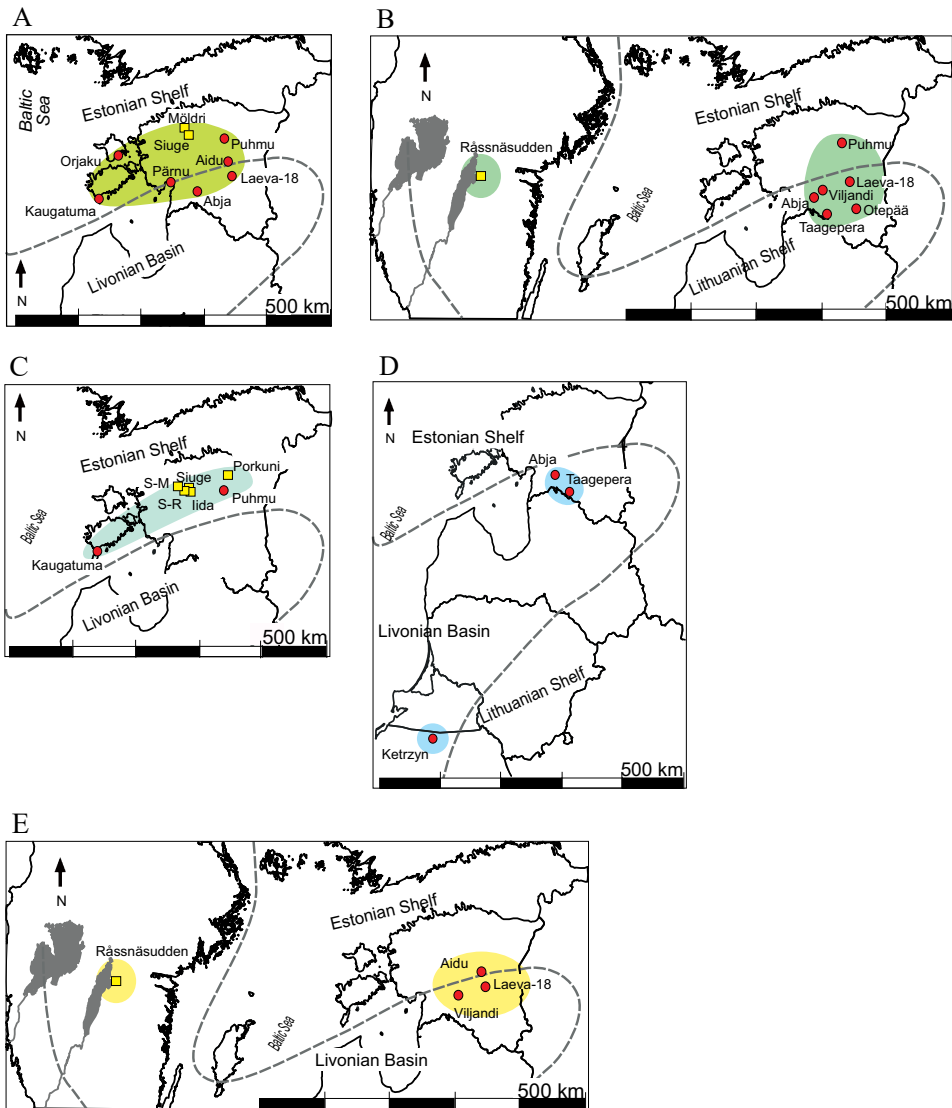
The diversity values show that both of these clusters comprise rich and abundant associations (Fig. 5). The biggest but second most diverse association was formed from the samples which were included in the cluster Katian-1. The samples come from the northern part of Estonia (Fig. 6A) and represent 49 species of five suborders. The proportion of major taxonomic groups within the associations is strongly dependent on the grouping level. In specimen level, metacopes constitute by far the most dominant suborder, followed by palaeocopes, but palaeocopes dominate over metacopes in genus level. Binodicopes, together with eridostracans and paraparchitocopes, form the minority in this cluster (Fig. 7).

The richest cluster of the five, Katian-2, comprises localities/samples from the southern part of the study area (S Estonia and Rässnäsudden Fig. 6B) and encompasses altogether 80 species from eight suborders. The division of samples of Katian age is not strict; both Katian clusters contain samples from the Abja-92, Taagepera and Puhmu-567 sections (Paper III). The majority of ostracod genera belong to Palaeocopa, Metacopa and Binodicopa; leiocope, paraparchitocope, cypridocope, cytherelliform and eridostracan species form the minority of the genera (Fig. 7).





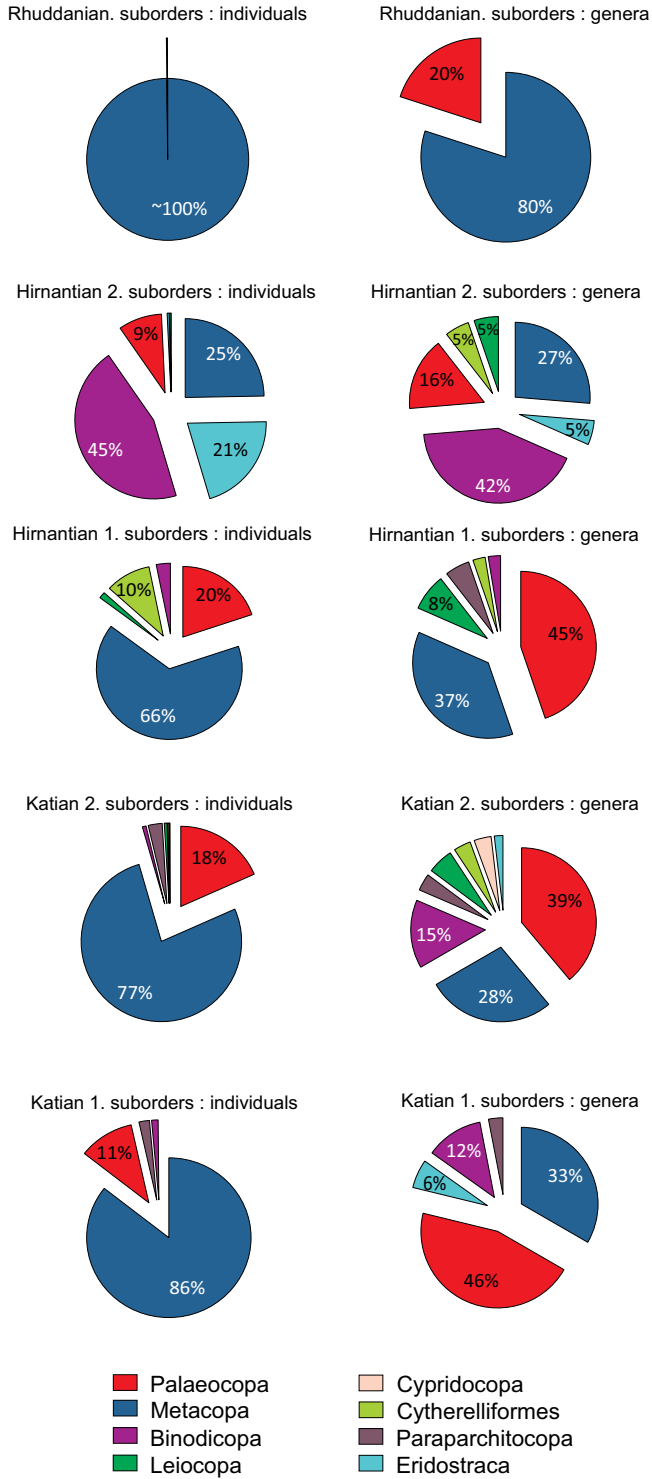
**Figure 5.** Plots displaying different diversity indices (number of taxa, number of specimens, dominance, Simpson and Shannon indices and evenness) for the Katian, Hirnantian and Juuru (Rhuddanian) clusters and for the total dataset.



A - localities containing samples of cluster Katian-1  
 B - localities containing samples of cluster Katian-2  
 C - localities containing samples of cluster Hirnantian-1  
 D - localities containing samples of cluster Hirnantian-2  
 E - localities containing samples of cluster Rhuddanian  
 S-M - Seli-Metsküla  
 S-R - Seli-Russalu

■ Outcrop  
● Drillcore  
 - - - - - Facies belt boundary (after Harris *et al.*, 2004)

**Figure 6.** Distribution areas of ostracod associations corresponding to the clusters Katian-1 (A), Katian-2 (B), Hirnantian-1 (C), Hirnantian-2 (D) and Juuru (E). Due to the nature of the original data, some of the sections and samples were removed from the data matrix in the course of the analysis. Only sections that were retained in the modified data are figured on the maps.



**Figure 7.** Pie charts of the five clusters (Katian-1, Katian-2, Hirnantian-1, Hirnantian-2 and Juuru) demonstrating the relative proportions of individuals per genera and suborders.

The typical “non-Hirnantian“ fauna described in samples of the clusters Katian-1 and Katian-2 occurs in the intervals where the carbon stable isotopic ratio has low values, corresponding approximately to the Baltic Carbon Isotopic Zones BC13–BC15 (Figs 2, 8). The  $\delta^{13}\text{C}$  values are slowly starting to rise in the uppermost part of the Katian Stage. This interval corresponds rather well to the Zone BC15 (Fig. 2; Ainsaar *et al.*, 2010). The Zone BC15 shows slightly rising  $\delta^{13}\text{C}$  values (up to  $\sim 1.5\%$  in its topmost part; Ainsaar *et al.* 2010; Fig. 8, Paper III) before the steep rise of  $\delta^{13}\text{C}$  levels corresponding to BC16 and the global Hirnantian carbon isotopic excursion (HICE). This trend is visible in most of the Baltoscandian sections, e.g. Männamaa (F-367), Taagepera, Valga-10, Jurmala R-1 and Riekstini drill cores (Fig. 2) although BC14 and BC15 are absent in many northern Estonian sections (e.g. the Puhmu-567 and Kaugatuma drill cores; Kaljo *et al.*, 2017 and Brenchley *et al.*, 2003, respectively) due to a sedimentary gap.

The clusters Hirnantian-1 and Hirnantian-2 represent samples/taxa of Hirnantian age, but from different parts of the study area and of slightly different age. The difference between the Hirnantian clusters is also more conspicuous than between the Katian clusters: no sections are represented in both of the Hirnantian clusters.

The cluster Hirnantian-1 is composed of samples from the Ärina Fm. characteristic of Central and North Estonia and is slightly older than material in the cluster Hirnantian-2. Hirnantian-1 is restricted to the Estonian Shelf (Fig. 6C) – it comprises samples of 52 species from six suborders. The taxonomic composition of this association resembles that of the Katian-1 association but is considerably impoverished compared to the latter. The great majority of both the specimens and genera are palaeocopes and metacopes. The binodicopes form a small fraction of the specimens in samples of this cluster but in genus level they still form the third biggest suborder after palaeocopes and metacopes, while cypridocopes and eridostracans are missing here (Fig. 7).

The occurrence of the association of the cluster Hirnantian-1 in the sections is tied to slightly rising carbon stable isotopic values, corresponding approximately to the transition from the topmost Zone BC15 into the lower part of BC16 (Fig. 2).

The cluster Hirnantian-2 comprises samples of Hirnantian age and covers the southern part of the study area (Abja-92, Taagepera, Kętrzyn IG 1; Fig. 6D). It contains considerably poorer ostracod material than the cluster Hirnantian-1 – 25 species from six suborders. Species composition of the ostracod assemblage picked from this material is significantly different from that of any aforementioned association. The relative importance of binodicopes has risen considerably here: close to half of the specimens and genera belong to the suborder Binodicipa. The importance of metacopes has dropped here, but they are still the second largest group at both individual and genus levels. The significance of the palaeocopes is strongly reduced (Fig. 7). The analysis shows high diversity with low dominance and high Shannon and evenness indices (Fig. 5). The association described from the samples forming the cluster Hirnantian-2 is found in the intervals with high and/or gradually lowering carbon stable isotopic ratios comprising the upper part of the Zone BC16 and unit BC17 (Fig-s 6, 8).

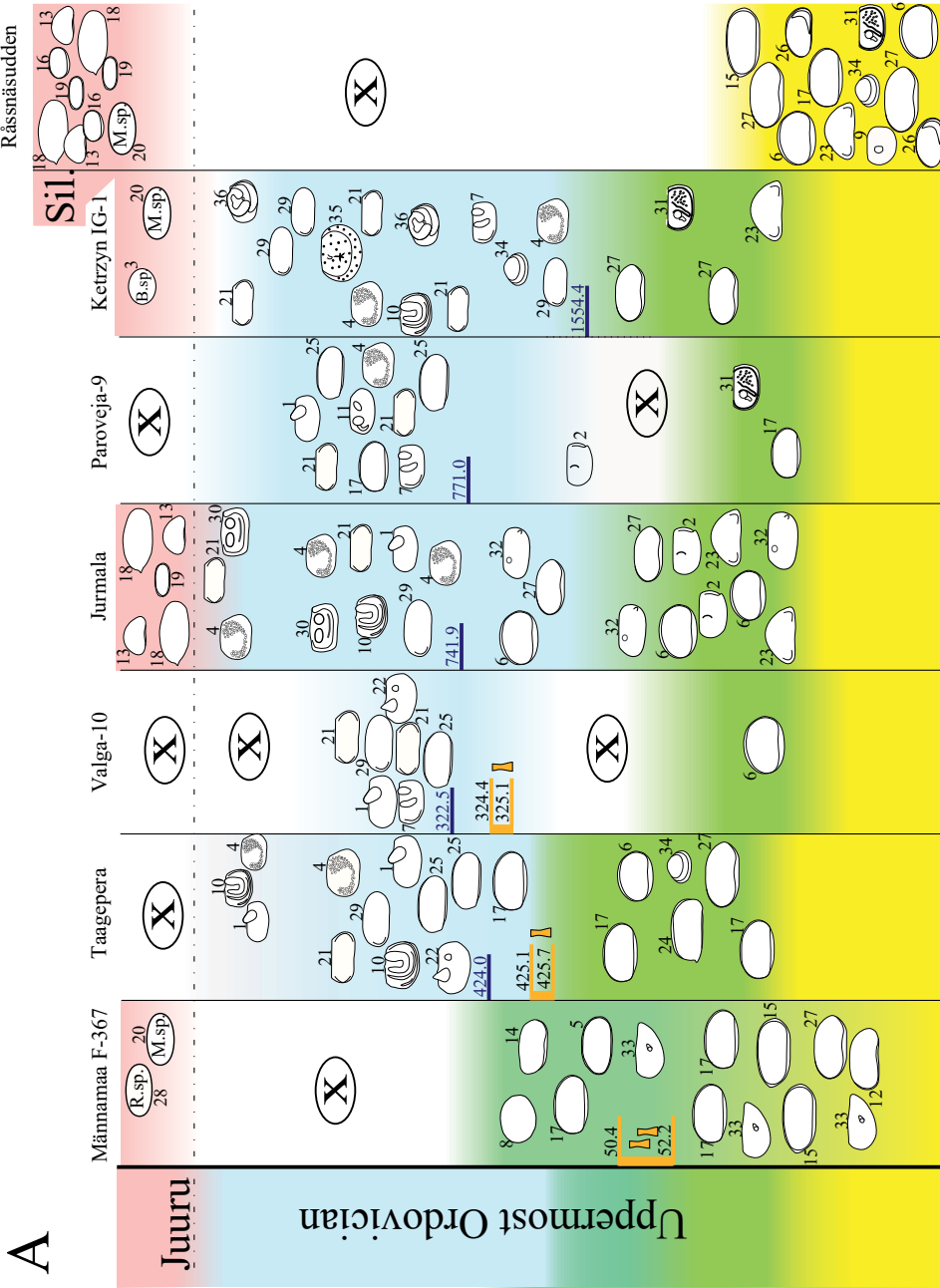
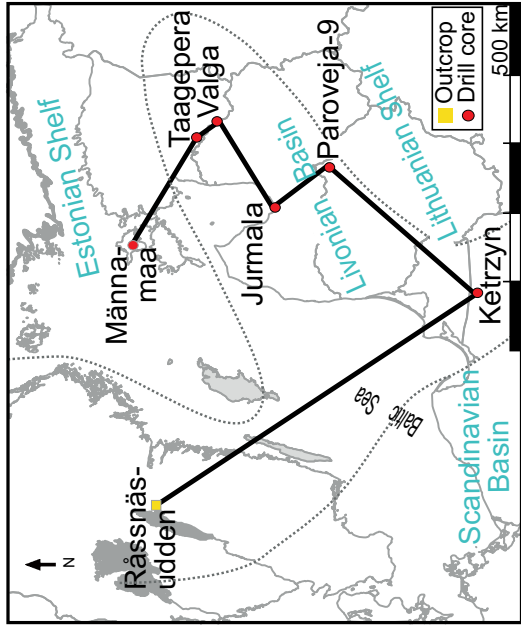


Figure 8.

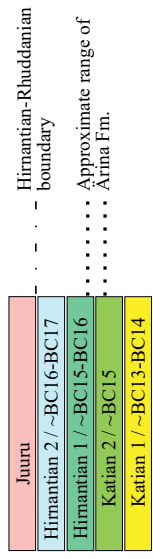
**Figure 8.** A schematic overview of the distribution of the five ostracod associations in different parts of the BPB from the late Katian up to the earliest Silurian (A). The sections used are marked on the map (C). Colours mark the distribution intervals of different associations and approximately correspond to the Baltic



C

- B**
- 1 *Aechmina groenwalli*
  - 2 *Airina comuta*
  - 3 *Baltonotella* sp.
  - 4 *Circulinella gailitae*
  - 5 *Dageoceryella sulcata*
  - 6 *Dateiella rotundata*
  - 7 *Drepanella pauxilla*
  - 8 *Easchmidtiella orbicularis*
  - 9 *Gryphiswaldensis plavinenensis*
  - 10 *Harpobolitia harparum*
  - 11 *Kinnekullea reducta*
  - 12 *Longiscula porrecta*
  - 13 *Longiscula smithii*
  - 14 *Medianella aequa*
  - 15 *Medianella bidenensis*
  - 16 *Microcheilina globulosa*
  - 17 *Microcheilina lubrica*
  - 18 *Microcheilina mobile*
  - 19 *Microcheilina rozdestvenskaja*
  - 20 *Microcheilina* sp.
  - 21 *Pseudoancora confragosa*
  - 22 *Pseudulrichia disputabile*
  - 23 *Pultvillites laevis*
  - 24 *Rectella carinaspinata*
  - 25 *Rectella composita*
  - 26 *Rectella explanata*
  - 27 *Rectella ronboformis*
  - 28 *Rectella* sp.
  - 29 *Rectella sturiensis*
- 30 *Scamispithia rectangularis*
- 31 *Sigmobolbina camarota*
- 32 *Spingerites spinger*
- 33 *Steusloffina cuneata*
- 34 *Cryptophyllus gutta*
- 35 *Cryptophyllus pitus* sp. n.
- 36 *Ardenita kriukensis*
- Spinachitina taugourdeai*

X No ostracods



Hirnantian-Rhuddanian boundary

Approximate range of Arina Fm.

The  $\delta^{13}\text{C}$  levels rise fast up to 5–6‰ (e.g. in the Ruhnu (500) and Jurmala R-1 drill cores) in the lower half of the Kuldiga Fm. (Ainsaar *et al.*, 2010). Although BC16 is missing in many northern Estonian sections due to the sedimentary hiatus, it is still observable in some Estonian Shelf sections where the containing strata have been preserved, e.g. in the Puhmu-567 (N Estonia) and Männamaa F-367 (NW Estonian) cores (Paper III).

Carbon Isotopic Zones (B). The distribution of the most common or characteristic species is marked with schematic drawings, explanations to the numbers are given in Figure 8B. The yellow bar (in the Männamaa F-367, Taagepera and Valga-10 columns) marks the FAD and LAD of *Spinachitina taugourdeaui*, blue bar (Taagepera, Valga-10) marks the appearance of the first typical elements of the *H. harparum* association. Sections are not drawn to scale. “Juuru” marks the appearance of the survival fauna. “Sil.” next to the topmost association at the Rässnäsudden section marks the real lower Silurian recovery fauna.

The Juuru cluster comprises samples from the Laeva-18, Aidu-427, Viljandi-91 and Rässnäsudden sections (Fig. 6E; Paper III). The taxonomic composition of the ostracod association gathered from the samples of the Juuru cluster differs conspicuously from those of the other four aforementioned associations. The association is very poor: basically all of the specimens are metacopes belonging mostly to the genera *Microcheilinella* and *Longiscula*. This association is tied to the intervals of low but still gradually dropping carbon stable isotopic values corresponding to BC17 and above (Fig. 2).

## Hirnantian in North Estonia

The cluster analysis conducted for this study makes a very clear separation between the Hirnantian ostracod samples in N Estonia and S Estonia (Fig. 2 in Paper III). Samples from N Estonia, comprising the very shallow-water Estonian Shelf during the Late Ordovician (Fig. 6C), agglomerate into a distinct cluster Hirnantian-1 representing the endemic metacope-dominated N Estonian ostracod association, also called the *Medianella aequa* association (Meidla, 1996b). This association has only very few common species with the Hirnantian-2 cluster but has similarity with the rich warm-water Katian-1 cluster, aside from being heavily impoverished (Paper III).

## Hirnantian in South Estonia

South Estonia was a marginal area of the Livonian Basin during the latest Ordovician. Samples of Hirnantian age from S Estonian sections form the cluster Hirnantian-2 representing the distinct binodicope-dominated Hirnantian cold-water ostracod association (Meidla, 1996b, 2007). Species characteristic of the specific Hirnantian ostracod association have been described from the Taagepera,

Abja-92, Valga-10 and Otepää-2 drill cores in S Estonia (Fig. 6D; Meidla, 1996b). The N Estonian endemic association associated with the cluster Hirnantian-1 is absent here, except for a few specimens in the basal part of the Hirnantian succession (Fig. 6C).

## Hirnantian in Latvia

During the latest Ordovician, most of the Latvian area comprised a part of the Livonian Basin (Fig. 1). The presence and distribution of the typical Hirnantian *H. harparum* ostracod association in this area has been confirmed in several papers (e.g. Ulst *et al.*, 1982; Brenchley *et al.*, 2003; Meidla *et al.*, 2011; Paper III, IV). Samples from the Hirnantian strata in Latvia contain a relatively abundant *H. harparum* ostracod association and fall into the cluster Hirnantian-2. All four typical dominant species of this association (*sensu* Meidla, 2007), *Harpabollia harparum*, *Circulinella gailitae* Meidla, 1996b, *Aechmina groenwalli* Troedsson, 1918 and *Rectella sturiensis* Gailite, 1975, are present in the Hirnantian rock material from the Riekstini drill core (W Latvia). One of the most complete late Ordovician sections in Baltoscandia is the Jurmala R-1 drill core in Central Latvia (Paper IV) which has yielded a little less diverse *H. harparum* association than in other parts in the Livonian Basin (e.g. Kętrzyn IG 1 drill core in N Poland). Still, a conspicuous change in the composition of ostracod associations in transition from the Katian to the Hirnantian is definitely present here too. This core section yielded also few specimens of *Circulinella gailitae*, *Pseudoancora confragosa* (Gailite 1970) and *Scanipisthia rectangularis* (Troedsson 1918) in the Saldus Fm. The *H. harparum* association disappears at the top of this formation that is marked as a disconformity (depth 730.9 m).

## Hirnantian in Lithuania

Only two drill cores, Sutkai 89 and Sutkai 101 in SW Lithuania, contain the strata that are attributed to the upper part of the Vaineikiai Fm., correlated to the Kuldiga and Saldus formations in Latvia and S Estonia (Sidaravičiene, 1996). Still, no faunal proof for the Hirnantian age of these strata has been found in this material as the recorded taxa are typical of the cluster Katian-2 and have little or no affinity to either the Hirnantian-1 or Hirnantian-2 cluster. The collected ostracod specimens represent either typical pre-Hirnantian species or widespread long-ranging meta-cope species (Sidaravičiene, 1996). However, the ostracod species characteristic of the Hirnantian-2 cluster have been found in W and NW Lithuania. The association collected from the Paroveja-9 drill core (NW Lithuania; Paper III) has the taxonomic composition typical of the Hirnantian containing species such as *C. gailitae*, *A. groenwalli* and *R. sturiensis* although the nominate species of the association is missing.

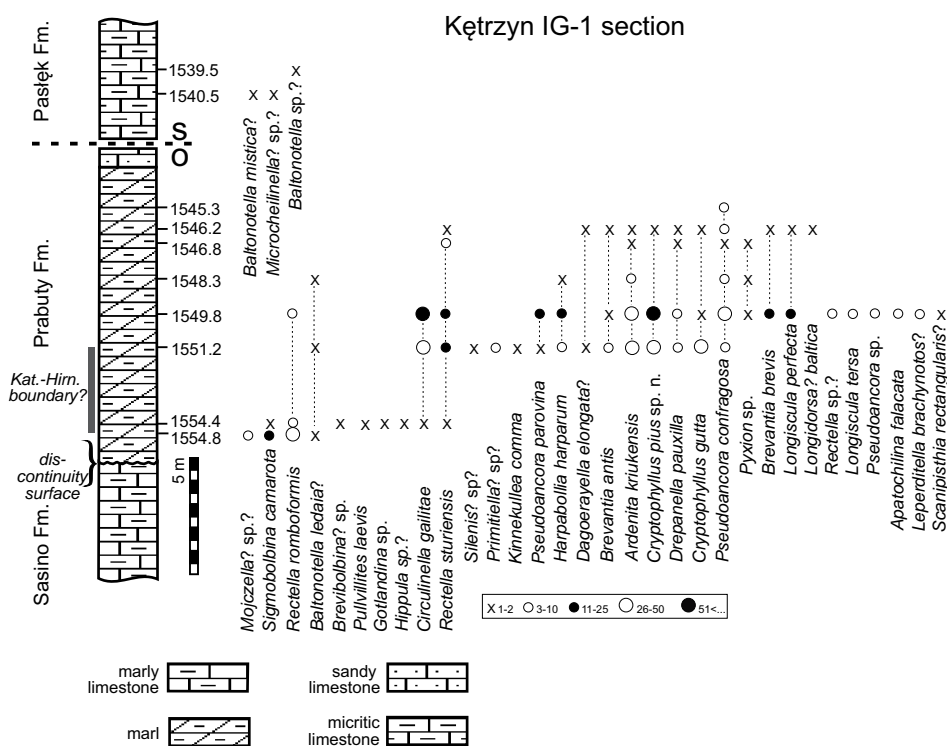


Unfortunately, no carbon stable isotopic analyses have been conducted on Lithuanian Late Ordovician material, so it is currently only tentatively possible to juxtapose ostracod data with the isotopic curve. Considering that the Hirnantian-2 association appears close to or at the peak of the carbon isotopic excursion in the sections where both the isotopic and ostracod data are available, we can suggest that the isotopic zone BC16 and possibly a part of BC17 are present in W and NW Lithuania but most likely missing in E and SE Lithuania (Fig. 2).

## Hirnantian in North and North-East Poland

Currently no  $\delta^{13}\text{C}$  data are available from N and NE Poland, so the relative timing of carbon isotopic fluctuations and the appearance of the *H. harparum* association in this region could not be demonstrated. No  $\delta^{13}\text{C}$  data are available also for the N Polish Kętrzyn IG 1 drill core but the ostracod data from this drill core show that some of the Hirnantian-2 ostracod association species (*Circulinella gailitae*, *Rectella sturiensis*) appear at a depth of 1554.4 m and the core species of the Hirnantian-2 association (*H. harparum*, *Drepanella pauxilla* Gailite, 1970, *Pseudoancora parovina* (Sidaravičiene, 1975) nearly 3 m-s higher. Knowing that the Hirnantian-2 association appears on the rising limb of the  $\delta^{13}\text{C}$  curve and ranges up to the O–S boundary in the Jurmala R-1 drill core, we can assume an approximate position of BC16 and BC17 in the Kętrzyn IG 1 drill core as indicated in Figure 8. The Katian–Hirnantian boundary was up to now only tentatively drawn in N Poland due to the lack of zonal graptolites,  $\delta^{13}\text{C}$  data and insufficient chitinozoan data. The level of the appearance of the species of the Hirnantian-2 association (Fig. 9) also allows us to draw the Katian–Hirnantian boundary in the interval of 1551.2–1554.8 m in this drill core (Paper II). By and large, the warm-water pre-Hirnantian and specific cold-water Hirnantian ostracod associations do not occur together in the BPB. A clear turnover of ostracod associations that is recorded in every other part of the studied area does not seem to be that conspicuous in NE Poland. Although the ostracod association of Hirnantian age resembles that of other sections within the Livonian Basin (S Estonia, Latvia and W Lithuania), it is aberrantly more diverse. This material contains some metacope species (*Dagoerayella elongata* (Meidla, 1983), *Brevantia brevis* Meidla, 1996b, *Pullvillites laevis* Abushik et Sarv, 1983) untypical of the *H. harparum* association in other parts of the basin, and two species of the ostracod genus *Cryptophyllus* Levinson, 1951 which otherwise is typical of shallow warm-water environments in the BPB. One of these species, *C. pius* Truuver et Meidla 2015, is strongly dominating this assemblage, and the other, *C. gutta* Schallreuter, 1968, is among the most abundant species as well (Paper II).

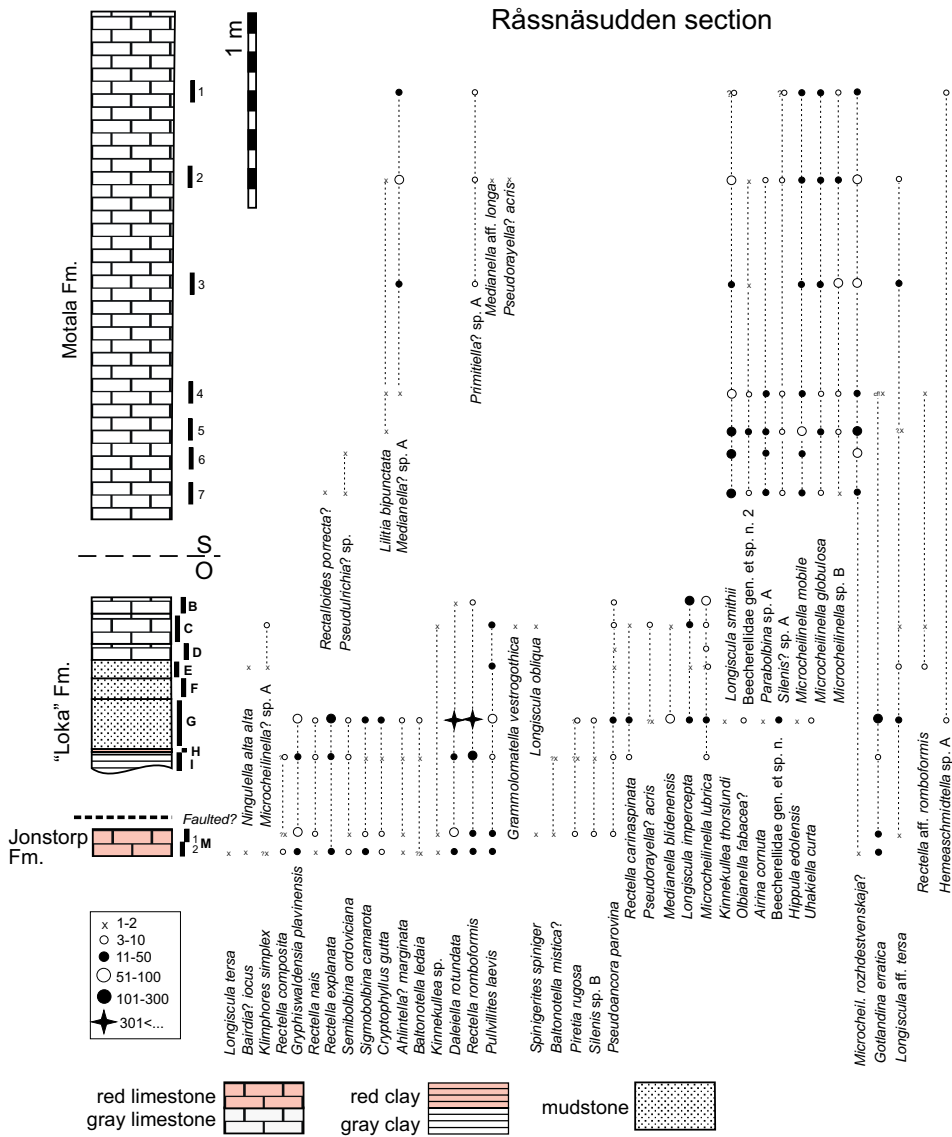
Few metacope and binodicope ostracods have been found in the Hirnantian strata of eastern Poland (Stejn, 1989; Meidla, *et al.*, 2013). This scarce association contains no key elements of the *H. harparum* association. The few taxa recorded here (*Pyxion* sp., *Rectella* sp.) are common in N Estonian ostracod association of the Ärina Fm. and may refer to the Hirnantian-1 association.



**Figure 9.** Chart of ostracod distribution in the Kętrzyn IG 1 drill core (N Poland). Modified from Figure 4 in Paper II.

## Hirnantian in Sweden

In S Sweden the *H. harparum* association and the  $\delta^{13}\text{C}$  positive excursion have been described in the Borensult area (Meidla, 2007; Bergström *et al.*, 2012; Paper I). The two lowermost samples collected from the Jonstorp Fm. of the nearby Råsnäsudden section contain clearly pre-Hirnantian species (e.g. *Sigmobolbina camarota* Jaanusson, 1966, *Daleiella rotundata* Meidla, 1996b, *Rectella explanata* Meidla, 1996b). The overlying “Loka” Fm. was assigned to the Hirnantian Stage by Bergström and Bergström (1996) on the basis of macrofossil data. The current study revealed no ostracod species characteristic of the *H. harparum* association in other locations in the BPB which would confirm that notion (Fig. 10; Paper I). The  $\delta^{13}\text{C}$  analysis conducted on this material does not show any conspicuous positive shift similar to the HICE either (Paper I).



**Figure 10.** Chart of ostracod distribution in the Råsnäsudden section (S Sweden). Modified from Figure 4 in Paper I.

## DISCUSSION

Sztejn (1989) points out a clear interconnection between the ostracod associations and the sedimentary environments in the BPB. The considerable environmental changes related to the Hirnantian glaciation brought along substantial changes in the ostracod communities all over the BPB. Kaljo *et al.* (2008) argue that the diversity of many faunal groups in the BPB (e.g. brachiopods, conodonts, acritarchs, chitinozoans) started dropping already in the latest Katian and suggest that the first pulse of the end-Ordovician extinction was not a very sudden event. The same was observed in the latest Katian ostracod communities as well. In all studied sections, the uppermost Katian samples are rich and abundant but get considerably poorer or are devoid of ostracods towards the Katian–Hirnantian boundary (Meidla, 1996b; Paper I, II). The statistical analyses of this study support this judgement. The diversity indices in most of the studied sections start dropping already in the uppermost Katian (Fig. 8 in Paper III) indicating that the previously rich and abundant pre-Hirnantian ostracod association starts to decline already below the Katian–Hirnantian boundary and the beginning of the carbon stable isotope excursion.

The sedimentary environment of the Lithuanian Shelf (SE and S Lithuanian area) was very similar to that of the Estonian Shelf in the Late Ordovician, lying in the equivalent position in the basinwide facies zonation. The strong affinity between the ostracod associations of the N Estonian Shelf and the Lithuanian Shelf was expected, but could not be properly demonstrated up to now. This may likely result from the collection bias in the Lithuanian material. Podocopes, heavily dominating in this assemblage within the Estonian Shelf, were likely undersampled or omitted from the Lithuanian studies (as stated by Sidaravičienė, 1992, p. 8).

The sections of the Livonian Basin (*sensu* Harris *et al.*, 2014) represent the deeper part of the BPB and contain species of the so-called *Harpabollia harparum* ostracod association characteristic of the Hirnantian of Baltoscandia. The new, distinct association does not appear at the lower boundary of the Hirnantian Stage, but somewhat above it (Fig. 2) and always above the LAD of *Spinachitina taugourdeaui*, in the *Spinachitina scabra* Zone, as has been observed in every section where both of the groups are present (Fig. 6; Paper IV). Setting the ostracod data against the  $\delta^{13}\text{C}$  curve shows that the *H. harparum* association species does not appear concurrently with the beginning of the stable carbon positive excursion at the base of the Baltic Carbon Isotopic Zone BC16 but on the rising limb or at the peak of it (Fig. 2). Meidla (1996b, 2007) has shown that the *H. harparum* association co-occurs with some of the typical *Hirnantia* fauna species *sensu stricto* and thus can be considered as *Hirnantia* fauna *sensu lato*. The *H. harparum* association co-occurs with *Eostropheodonta hirnantensis* in the Prabuty Fm. of the Kętrzyn IG 1 drill core in NE Poland (Rubel in Modliński *et al.*, 2002; Paper II), confirming again that this association can be considered an indicator of Hirnantian age as suggested by Meidla (1996a, 2007).

Most of the sections within the Livonian Basin contain either one or more sedimentational gaps in the Kuldiga and Saldus formations (e.g. Taagepera, Riekstini, Paroveja-9 drill cores). Ostracod associations in these formations are considerably poorer than the pre-Hirnantian associations, especially in the Saldus Fm. Although the highly stressful environmental conditions probably had a direct effect on the abundance of ostracods, the sedimentary environments must also be taken into consideration here. The Saldus Fm. was deposited in a high-energy environment and is often represented by oolitic limestones that are barren of ostracods because the shells were most likely “washed out” as too light sedimentary particles. Microlaminated limestones that were formed in extremely shallow-water conditions may contain occasional specimens but domeritic layers are barren again because of preservational reasons (dolomitizations has destroyed the shells). The most complete section in this area is the Jurmala R-1 section in Latvia (Fig. 2; Paper IV) which displays a unique continuous carbonate succession throughout the uppermost Katian and Hirnantian into the Rhuddanian (Paper IV), with a sharp diversity decline and rise in dominance, followed by a complete turnover (Paper IV).

Sidaravičiene (1996) suggests that the Vaineikiai Fm. (considered a counterpart of the Estonian Kuldiga Fm. by Paškevičius, 1973, 1997) is present in the Butkunai borehole (NE Lithuania) although she recorded only the pre-Hirnantian taxa. As the *Harpabollia harparum* association is missing in the North Estonian sections, it is possible that the Vaineikiai Fm. in this section is coeval with the Ārina Fm. in N Estonia (Fig. 1 in Paper III).

The *H. harparum* association is not of completely uniform distribution and composition in the latest Ordovician BPB but varies both in abundance and species composition in different parts of the BPB. South Estonia represents the northernmost distribution area of the *H. harparum* ostracod association inhabiting the deeper-water Livonian Basin. The taxonomic composition of both the pre-Hirnantian and Hirnantian ostracod associations here is similar to the rest of the Livonian Basin, although the ranges of the typical species of the cold-water Hirnantian association are shorter than in the sections of the deeper part of the BPB (Meidla, 1996b; Meidla *et al.*, 2020). The sharp turnover of ostracod associations which has been described in the other studied sections does not seem to have happened in the Kętrzyn IG 1 drill core in NE Poland, but instead some of the typical Katian ostracod species occur alongside the *H. harparum* association species (Paper II).

In Sweden, Bergström and Bergström (1996) described the Loka Fm. in the Råsnäsudden outcrop, just about 7 km east of the Borenshult locality (Fig. 1 in Paper I), and dated it as being of Hirnantian age, based on occasional finds of “Silurian-type” taxa (*Walliserodus curvatus* (Branson et Branson, 1947), *Ozarkodina?* sp.) together with some typical Hirnantian taxa. Sixteen years later, Bergström *et al.* (2012) studied the uppermost Ordovician strata in the nearby Borenshult drill core and concluded that the lower part of the Loka Fm. in this section is coeval with the Kuldiga Fm. in Estonia and the upper part of Loka Fm. is at least partly coeval with the Saldus Fm. This agrees with the revelation of Meidla (2007) that a specimen of *N. persculptus* and ostracods belonging to the

*H. harparum* association appeared together on the same rockslab from the Borenshult locality, showing that the *H. harparum* association ranges into the *persculptus* Zone. The Råssnäsudden outcrop was studied for ostracods by Truuver *et al.* (2012) in order to confirm the Hirnantian age of the Loka Fm. in this section. A faunal turnover and appearance of the abundant *H. harparum* association were expected in the strata overlying the Jonstorp Fm., but this was not the case. The ostracod association with dominating *Gryphiswaldensia plavinensis* (Gailite, 1975), *Sigmobolbina camarota*, *Pullvillites laevis* and *Daleiella rotundata* strongly resembles that of the Jonstorp Fm. and is very similar to the ostracod associations attributed to the cluster Katian-2. The vast majority of the species range from the Jonstorp Fm. into the overlying strata designated as the “Loka” Fm. (Paper I). The  $\delta^{13}\text{C}$  analysis conducted on the Råssnäsudden material did not show any significant positive shift at the lower boundary of the “Loka” Fm. either, which is considered one of the markers of the beginning of the Hirnantian Stage globally. The slightly elevated (up to 1.39‰)  $\delta^{13}\text{C}$  values could correspond to BC14 and the so-called Paroveja isotopic excursion. The absence of elements of the distinct cold-water ostracod association typical of the Hirnantian in the BPB and also parts of the Gondwana palaeocontinent (South America (Reily *et al.*, 2018), Bohemia (Schallreuter and Krüta 1990), the Carnic Alps (Schallreuter, 1990), Prague Basin (Lajblová and Kraft, 2018)), along with the absence of a positive  $\delta^{13}\text{C}$  excursion, suggest that the strata attributed to the Loka Fm. in the Råssnäsudden section by Bergström and Bergström (1996) represent the pre-Hirnantian and the Hirnantian Stage is missing in the Råssnäsudden outcrop section (Paper I).

The *H. harparum* association is well represented in most sections in the middle part of the Livonian Basin (e.g. Riekstini and Jurmala R-1 drill cores in West Latvia, Paroveja-9 drill core in Lithuania and Kętrzyn IG 1 drill core in NE Poland). All the typical species are represented in the Riekstini drill core and the association ranges fairly evenly through the Kuldiga Fm. In the Jurmala R-1 drill core, the nominate species is missing and the key elements of the *Hirnantia* association have somewhat surprisingly short ranges (Paper IV). The association as a whole is also less diverse compared to some other sections within the Livonian Basin, but this is the first section where the *H. harparum* association is recorded ranging through the Saldus Fm. up to the regional disconformity. The ostracod association is more abundant in the Kuldiga Fm.; the diversity indices drop and dominance grows towards the Kuldiga–Saldus formation boundary. Few species (*Scanipisthia rectangularis* (Troedsson, 1918), *Pseudoancora confragosa*, *Circulinella gailitae*) are present in the lower part of the Saldus Fm. but *S. rectangularis* ranges up to the upper boundary of the formation. This proves that the *H. harparum* association is not only confined to the Kuldiga Fm. and lower half of the Saldus Fm., but ranges up to the regional disconformity and the appearance level of the post-glacial survival association (see below).

In the Kętrzyn IG 1 drill core (NE Poland) the key elements of the *H. harparum* association (*H. harparum*, *Drepanella pauxilla* Gailite, 1970, *Pseudoancora parovina* (Sidaravičiene, 1975), *Circulinella gailitae*, *Rectella sturiensis*) occur

together with some typical pre-Hirnantian ostracods in the Hirnantian. The species mixture suggests that the N Polish area in the deeper part of the Livonian Basin seems to have acted as a kind of temporary refuge at the beginning of the crisis (Paper II). *Cryptophyllus pius* Truuver *et* Meidla (2015) is by far the most dominant species of the Hirnantian ostracod association in the Kętrzyn IG 1 section. The genus *Cryptophyllus* is typical of the pre-Hirnantian associations, but the species is unknown in every other section in the BPB. This kind of species mixture gives this association a transitional appearance between the *Medianella aequa* and *Harpabollia harparum* associations, something that has not been described anywhere else in the eastern Baltic area. The ostracod data together with the record of *Eostropheodonta hirnantensis* (McCoy) (Rubel in Modliński *et al.*, 2002) confirms the Hirnantian age of the Prabuty Fm. as suggested in previous papers (e.g. Modliński and Podhalańska, 2010), but lifts the stage boundary in the Kętrzyn IG 1 drill core a bit higher than suggested by Modliński *et al.* (2002), into the interval of 1551.2–1554.8 m (Paper II).

The poor post-glacial ostracod association, in the present study called “the ‘Silurian’ association”, has been described in several sections of the BPB: in the Varbola and Õhne formations in the Laeva-18, Aidu-427, Viljandi-91 sections in Central Estonia (Meidla, 1996b), in the Stačiūnai Fm. of the Jurmala R-1 section in mid-Latvia, in the Paslek Fm. in the Kętrzyn IG 1 section in N Poland, in the Motala Fm. of the Råsnäsudden section in southern Sweden, and in several sections of Latvia (Gailīte *et al.* 1968) and Lithuania (Pranskevičius, 1972).

The newly appearing association is poor compared to the ostracod associations in the underlying Ārina and Saldus formations, consisting mostly of specimens of the podocope genera *Longiscula* and *Microcheilinella*. Both genera are well known in the Upper Ordovician, although the appearing species are new. The most common and usually dominant species in the post-glacial association is *Longiscula smithii* (Jones, 1887) which is usually accompanied by several species of *Microcheilinella* (e.g. *Microcheilinella rozhdestvenskaja* Neckaja, 1966, *M. mobile* Gailīte, 1967, *M. globulosa* Pranskevičius, 1971). *Bipunctoprimitia bipunctata* (Gailīte, 1991), *Rectella procera* Pranskevičius, 1971 and *Longiscula immensa* Pranskevičius, 1972 are among less abundant post-glacial species in the Central Latvian Jurmala R-1 drill core, along with the species of *Longiscula* and *Microcheilinella* (Paper IV). This association is characterized by very high dominance values, which may refer to slow recovery after the end-Ordovician glaciation-related extinction event, and could be characterized as a survival fauna. In N Poland (Kętrzyn IG 1 section), only questionable specimens of the genus *Baltonotella* were found in the Pasłek Fm. (Fig. 9; Paper II). This part of the section looks not very representative for discussing the composition of the early survival fauna, although the scarcity of ostracods could also be tentatively interpreted as indicative of a very slow beginning of the recovery.

The age of the appearance of this assemblage is likely the latest Ordovician, as quite a few recent studies (e.g. Meidla *et al.*, 2011, 2014, Gorjan *et al.*, 2012, Ainsaar *et al.* 2015) have suggested, on the basis of  $\delta^{13}\text{C}$  values that are declining above the “traditional” O-S boundary, that the Ordovician-Silurian boundary is

located higher in the BPB. Due to the almost complete absence of graptolites in the latest Katian and earliest post-Hirnantian strata within the BPB, it is very hard to correlate this part of the succession with the global scale. Juxtaposing the  $\delta^{13}\text{C}$  curve of the Jurmala R-1 section with the  $\delta^{13}\text{C}$  curve in the Monitor Range, Nevada, USA (Finney *et al.*, 1999; LaPorte *et al.*, 2009) shows that the curves have a very similar shape. The correlation of graptolite data and  $\delta^{13}\text{C}$  data in the Monitor Range section suggests that a substantial part of the Stačiunai Fm. may belong to the *persculptus* Zone (Papers III, IV). The co-occurrence of a specimen of *N. persculptus* on the same piece of rock with specimens of some core species of the *H. harparum* association confirms that the *H. harparum* association ranges into the *N. persculptus* Graptolite Zone in the BPB (Meidla, 2007; Papers III, IV). Taken together, these data suggest that the post-glacial association appearing after the demise of the *H. harparum* association in the BPB represents the terminal Ordovician (or terminal Ordovician–Rhuddanian) survival fauna.

The ostracod association of the Motala Fm. in the Råsnäsudden section (S Sweden) has the same dominant as the survival fauna documented in Estonia, Latvia and Lithuania but differs in its higher diversity and abundance. The most abundant species is again *Longiscula smithii* but the co-occurring species (e.g. *Microcheilinella globulosa*, *Microcheilinella* sp. B, *M. mobile*, *M. rozhdestvenskaja*) are much more abundant and accompanied by a diverse association of less abundant species (Paper I). These species are formerly known only from the strata traditionally considered as basal Silurian (references to rare *M. rozhdestvenskaja* and *L. smithii* in the post-glacial terminal Ordovician according to Pranskevičius (1972) were not confirmed by later studies by Sidaravičiene (1992, 1996). The  $\delta^{13}\text{C}$  values in the strata containing this association at Råsnäsudden stay constantly around 0–0,3‰ through the studied interval (Fig. 7 in Paper I). Considering the findings of the conodonts *Icriodella discreta* Pollock, Rexroad *et* Nicoll, 1970 in the lower Aeronian of Britain and in the upper Rhuddanian and lower Aeronian of the Oslo region, Bergström and Bergström (1996) state that the Motala Fm. at Råsnäsudden is somewhat younger. The relatively high diversity of the association also suggests that this association does not reflect the beginning of the recovery process but is younger. Taking the integrated conodont, ostracod and stable isotope evidence into account, it is safe to claim that this association can be interpreted as the Silurian recovery fauna.

## Conclusions

1. Although the end-Ordovician mass extinction is attributed to the beginning of the Hirnantian in many older papers, the declining ostracod diversity towards the Hirnantian suggests that the deterioration commenced already in the late Katian. The trend of gradual decrease in ostracod diversity towards the Katian–Hirnantian boundary before the carbon stable isotopic excursion in the studied sections supports that idea. The major rearrangements in the Hirnantian



- ostracod succession of the BPB are marked by the appearance of the *H. harparum* ostracod association and the so-called “Silurian fauna” in the lower and upper parts of the stage, respectively.
2. Two distinct Hirnantian ostracod associations can be distinguished in BPB. The endemic metacope-dominated *Medianella aequa* association is present only in the Ärina Fm. of N Estonian Shelf. The distinct Hirnantian *Harpa-bollia harparum* ostracod association appears in the Hirnantian strata of the Livonian Basin but is missing in the studied sections of the Estonian and Lithuanian shelves. The association does not appear at the lower boundary of the Hirnantian Stage but somewhat above it. Comparison with ostracod, chitinozoan and  $\delta^{13}\text{C}$  data shows that this association always appears above the LAD of *Spinachitina taugourdeui* and on the rising limb or at the peak of the  $\delta^{13}\text{C}$  positive excursion, not at the beginning of it. In the Jurmala R-1 drill core, the association was documented ranging through the Kuldiga and Saldus formations up to the regional disconformity, disappearing immediately before the appearance of the post-glacial ostracod association.
  3. The *H. harparum* association has been considered a part of the cosmopolitan *Hirnantia fauna sensu lato*. This view gains further support from the co-occurrence of the *H. harparum* association with *Eostropheodonta hirnantensis* (McCoy) in Poland and from the increasing number of occurrences of this association outside the BPB.
  4. The abundance and stratigraphic range of the *H. harparum* association in the BPB is variable. The rich and abundant *H. harparum* association described in the Borensult locality (S Sweden) was not found in the basal strata of the nearby Råsnäsudden outcrop assigned to the Loka Fm. by Bergström and Bergström (1996). The clearly pre-Hirnantian nature of the ostracod association described in samples of both the Jonstorp and Loka formations, and low  $\delta^{13}\text{C}$  values allow suggesting that the Loka Fm. *sensu* Bergström and Bergström (1996) is of pre-Hirnantian age. The slight rise in  $\delta^{13}\text{C}$  values in the lower part of the “Loka” Fm. at Råsnäsudden may represent the Paroveja excursion corresponding to the Baltic Carbon Isotopic Zone BC14.
  5. The co-occurrence of the typical pre-Hirnantian and Hirnantian ostracod species in the lower Prabuty Fm. of the Kętrzyn IG 1 drill core (NE Poland) created a unique species mixture which suggests that deeper parts of the basin might have acted as a temporary refuge for more resilient pre-Hirnantian species at least for some time after the beginning of glaciation.
  6. The appearance of the typical elements of the *H. harparum* association in the interval of 1551.2–1554.8 m in the Kętrzyn IG 1 drill core allowed us to justify the position of the lower boundary of the Hirnantian Stage in the area and suggest it to be positioned in the interval of 1551.2–1554.8 m in that section.
  7. The lower part of the Juuru RS (the Hirnantian–Rhuddanian transition interval) is characterized by an impoverished ostracod assemblage dominated by *Longiscula smithii* and accompanied by the species of *Microcheilinella* and *Rectella*. This association replaces the *H. harparum* association on the background of gradual decline in the  $\delta^{13}\text{C}$  values. The late Hirnantian appearance

of this very low-diversity assemblage allows us to consider it a post-glacial survival fauna.

The ostracod assemblage described from the Motala Fm. of the Råsnäsudden outcrop has the same key species as the post-glacial survival fauna but is much more abundant and diverse. Micropalaeontological and chemostratigraphic data suggest that it is considerably younger and could thus be characterized as a recovery fauna.

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## SUMMARY IN ESTONIAN

### Ordoviitsiumi ja Siluri piirikihtide ostrakoodid

Hilis-Ordoviitsiumis, Hirnanti eal aset leidnud Hirnanti jäätumise ajal katsid lõunapoolkeral asuvat Gondwana hiidmandrit ulatuslikud jääkilbid ja maailmameere veetase langes ligikaudu 100 m. Hirnanti jääajaga langes kokku esimene viiest suurimast väljasuremisest Fanerozoikumis, nn. Hirnanti (või Ordoviitsiumi ajastu lõpu) väljasuremissündmus. Nende sündmuste uurimisega on Eestis tegeldud mitu viimast aastakümnet. On uuritud Ülem-Ordoviitsiumi ostrakoodikoosluste koosseisu ja dünaamikat (e.g. Meidla, 1996b, 2007; Meidla, jt. 2013; Perrier jt. 2012; artiklid I–IV) ning  $\delta^{13}\text{C}$  (süsiniku stabiilsete isotoopide  $^{13}\text{C}/^{12}\text{C}$  suhte) väärtuste dünaamikat (e.g. Ainsaar jt. 2010, 2015; Bauert jt., 2014) Eestis ja lähieümbuses. Siiski on mõnede Baltoskandia piirkondade (Leedu, Lõuna-Rootsi, Põhja-Poola) ostrakoodikooslusi siiani ebapiisavalt uuritud, samuti on tänapäevaste uurimismeetoditega ning uusi andmeid lisades võimalik varem publitseeritud andmestikku oluliselt täpsustada. Käesolev doktoritöö käsitleb taksonoomilisi muutusi Baltoskandia paleobasseini (BPB) ostrakoodikooslustes Hirnanti jääajal ning sellele vahetult eelneval ja järgneval perioodil. Töö eesmärgiks oli analüüsida BPB ostrakoodikoosluste taksonoomilist koosseisu ja dünaamikat Katy ea lõpust kuni Siluri alguseni ning nende tulemuste alusel kontrollida Hirnanti väljasuremissündmuse varasema alguse hüpoteesi, täiendada ning täpsustada Hirnanti lademe stratigraafiat Leedus, Lõuna-Rootsis ja Põhja-Poolas, analüüsida ostrakoodikoosluste muutuste ja  $\delta^{13}\text{C}$  väärtuste muutuste vahelisi seoseid ning Ordoviitsiumi–Siluri piiri asendi muutmise vajadust Baltoskandias.

Ostrakoodid ehk karpvähilised on väikesed (<2 mm) lüliljalsed, kes ilmusid Vara-Ordoviitsiumis (Tinn ja Meidla, 2004; Meidla jt. 2013, Rodriguez-Lazaro ja Ruiz-Muñoz, 2012). Tõenäoliselt olid varased ostrakoodid elukeskkonna suhtes generalistid (Williams jt. 2008), kuid juba varaseks Kesk-Ordoviitsiumiks arenes neil välja endemism (Meidla jt. 2013). Pikka aega olid ostrakoodid vaid mereasukad ning esimesed maismaalisi veekogusid asustavad liigid ilmusid alles Karboni ajastul (Smith jt. 2015). Tänapäeval leidub ostrakoode kõikvõimalikes veelistes keskkondades alates meresügavustest kuni väikeste tiikideni.

Käesolevas töös kasutatud ostrakoodimaterjal pärineb Eesti, Läti, Leedu, Lõuna-Rootsi ja Kirde-Poola Poola 16 puuraugust ja 7 paljandist. Varem publitseeritud ostrakoodiandmestikku on täiendatud uute andmetega Lõuna-Rootsist, Põhja-Poolast ja Lääne-Leedust ning see andis võimaluse töö geograafilist haaret varasemate uuringutega võrreldes laiendada.

Lõuna-Rootsis oli *Harpabollia harparum*'i ostrakoodikooslus varem kirjeldatud Borenshulti leiukohast, kuid kuna see ostrakoodikollektsioon koguti lahtisest materjalist, ei olnud võimalik andmeid kasutada statistilise analüüsi eesmärgil ning see ei sobinud korreleerimiseks teiste läbilõigete ning süsiniku stabiilsete isotoopide andmestikuga. Sellega seoses valiti uurimiseks Rässnäsuddeni läbilõige, et saada andmeid *H. harparum*'i ostrakoodikoosluse iseloomustamiseks Lõuna-Rootsis Östergötlandi piirkonnas. Samal põhjusel valiti uurimise objektiks

Kętrzyn IG 1 läbilõige Põhja-Poolast, saamaks andmeid piirkonna ostrakoodikoosluste liigilise koosseisu täpsustamiseks ning Hirnanti lademe alumise piiri usaldusväärsemaks määramiseks. Paroveja-9 läbilõige kaasati töösse selleks, et täiendada ja täpsustada ostrakoodikoosluste taksonoomilist koosseisu ja levikuandmestikku Lääne-Leedus. Uutest ja Eesti ning Läti alade varempubliceeritud andmetest koostati kogu BPB ala hõlmav detailne ostrakoodide andmematriks.

Töös kasutatud kitiinikute ja graptoliitide leiuandmestik pärineb varem avaldatud teadustöödest.

Stratigraafilise korrelatsiooni hõlbustamiseks on töös kasutatud süsiniku stabiilsete isotoopide suhte ( $\delta^{13}\text{C}$ ) muutuse kõverate interpretatsioonil põhinevaid isotooptsoone (Ainsaar jt., 2010). Stabiilse süsiniku isotoopandmestik koguti peamiselt avaldatud töödest, kuid Rässnäsudden'i läbilõike isotoopandmestik koguti ja analüüsi käesoleva töö raames. Kuna on teada, et liustike teke mõjutab kaudselt ka süsinikuringlust ning on empiirilisel täheldatud head korrelatsiooni kogukivimi süsiniku ja hapniku isotoopsuhte kõverate vahel, on isotooptsoonid hea abimaterjal ostrakoodikoosluste leviku analüüsimiseks vajaliku stratigraafilise tausta loomisel kihtides, kus muid biostratigraafilisi markereid ei ole alati piisaval hulgal. Ainsaar jt. (2010) on loonud Kesk- ja Ülem-Ordoviitsiumi karbonaatsete kihtide  $\delta^{13}\text{C}$  väärtuste muutusi kirjeldava kemostratigraafilise liigestuse, mis koosneb 17 isotooptsoonist BC1–BC17 (BC = Baltic Carbon). Käesolev töö kajastab sündmusi intervallis, mis vastab isotooptsoonidele BC13–BC17 ja viimasest kõrgemal. Jäätumiseelsed kihid vastavad isotooptsoonidele BC13–BC15, kusjuures tsoonid BC14 ja BC15 puuduvad enamikus Põhja-Eesti läbilõigetes settelünga tõttu (Ainsaar jt., 2010). Isotooptsoon BC16 vastab Hirnanti jäätumise algusele ning sama sündmus on ka Hirnanti lademe alumise piiri täiendav marker. Põhja-Eesti läbilõigetes on sellest isotooptsoonist alles vaid alumine osa, mis viitab settimise lakkamisele Põhja-Eestit Ordoviitsiumi ajastu lõpul katnud rannikumeres Hirnanti ea algupoolel. Paleobasseini sügavamad osa esindavas Liivi basseinis on läbilõigetes enamasti olemas nii jäätumiseelsele perioodile vastavad kihid (isotooptsoonid BC13–BC15) kui ka jäätumisele vastavad kihid (isotooptsoonid BC16 ja BC17; Ainsaar jt. 2010). Isotooptsooni BC17 ülemine piir on paigutatud samale tasemele põiksusega, mis varasemates töödes markerib Ordoviitsiumi–Siluri (O–S) piiri (Ainsaar jt. 2010). Viimase 10 aasta uuringud on näidanud, et  $\delta^{13}\text{C}$  väärtused ei ole traditsioonilisel O-S piiril veel jäätumiseelsele tasemele jõudnud ja isotoopsuhte langus jätkub ka sellest piirist kõrgemal (nt. Ainsaar jt. 2010, 2015; Meidla jt. 2011, 2021; Bauert jt. 2014).

Hilis-Ordoviitsiumi ajastiku soe lähistroopiline BPB oli rikkalike ostrakoodikoosluste arenguks väga soodne keskkond. Katy ea teises pooles asustas paleomere eri piirkondi rikkalik ostrakoodikooslus, kus leidis liike kaheksast erinevast alamseltsist: Palaeocopa, Binodicopa, Podocopa, Eridostraca, Cytherelliformes, Leiocopa, Cypridocopa ja Paraparchitocopa. Selle madalaveelist rannikulähedast osa, Põhja-Eesti šelfimerd asustas Katy eal ostrakoodikooslus, mida iseloomustab tugev podokopiidide ülekaal (Meidla, 1996a). Lähedase koosseisuga kooslus asustas tõenäoliselt ka madalaveelist Leedu šelfimerd. Balti Paleobasseini sügavamad osa, Liivi basseini, asustas liigirikas soojaveelise mudalis-karbonaatse faatsiese kooslus, kus domineerisid paleokopiidid.

Hirnanti jääaeg ja suur väljasuremissündmus mõjutasid ostrakoodikooslusi märkimisväärselt. Põhja-Eestis on säilinud vaid Hirnanti lademe alumised kihid. Siinse šelfimere podokopiidikooslus muutus Hirnanti ea alguseks märgatavalt vaesemaks. Kuna seda kooslust kuskilt mujalt kirjeldatud ei ole, suri see tõenäoliselt jääaja edenedes ning veetaseme langedes välja. Paleomere sügavamas osas, Liivi basseinis, toimus ostrakoodikooslustes silmatorkav muutus. Soojaveeline paleokopiididerikas kooslus kadus ja vabaks jäänud elupaigad asustas uus kooslus, kus domineerisid ebastabiilsete keskkonnatingimustega kohastunud binodikopiidid. Dominantse liigi, *Harpabollia harparum*'i järgi on see kooslus endale ka nime saanud (Meidla, 2007). *H. harparum*'i ostrakoodikoosluse tüüpilisi esindajaid on leitud ka teistelt paleokontinentidelt, täpsemalt mitmest Gondwana hiidmandri piirkondadest (Lõuna-Ameerikast, Praha basseinist ja Karni Alpidest), mis viitab selle koosluse võimalikule kosmopoliitsusele.

Antud töö uuringuala läbilõigetel on peaaegu kõikjal näha soojaveelise koosluse vaesustumist Katy ea teises pooles ning kadumist Hirnanti ea algul. Ainsaks praegu teadaolevaks erandiks on Liivi basseini sügavamas osas Põhja-Poola Kętrzyn IG 1 läbilõikes Hirnanti kihtides kirjeldatud kooslus, kus lisaks *H. harparum*'i ostrakoodikoosluse iseloomulikele liikidele leidub ka mõningaid varasemale kooslusele iseloomulikke liike ning kus domineerib liik, mida kuskil mujal varem kirjeldatud ei ole. Tõenäoliselt sai selline spetsiifiline kooslus tekkida tänu paleokontinenti asukohale ekvaatori lähistel, kus jahenemise mõju ei avaldunud nii selgelt kui kõrgematel laiuskraadidel. Sellegipoolest võimaldas *H. harparumi* ostrakoodikoosluse tüüpiliste liikide ilmumine täpsustada Hirnanti lademe piiri asendit Kirde-Poolas ja paigutada see Kętrzyn IG 1 läbilõikes intervalli 1551.2–1554.8 m.

Jääaja lõppedes toimus Balti paleobasseinis ostrakoodikoosluste vahetus. *H. harparum*'i ostrakoodikoosluse vahetas Juuru ea algul välja väga liigivaene podokopiidide kooslus. Seda kooslust on traditsiooniliselt peetud nn. taastumiskoosluseks (*recovery fauna*). Kuna aga taastumiskoosluse ilmumise hetkel selle koosseisus ühtegi uut, ainult Siluri ajastule iseloomulikku perekonda leitud ei ole ja kooslus on väga liigivaene, on tõenäoliselt pigem tegemist nn. jäänukkooslusega (*survival fauna*). Lõuna-Rootsis asuv Råsnäsuddeni läbilõikes puudub Hirnanti lade ning Katy lademel lasuvad suure tõenäosusega Rhuddani lademe ülemised kihid (Bergström ja Bergström, 1996). Nendest kihtidest kirjeldatud kooslus on oluliselt rikkalikum kui ülejäänud uuringualal kirjeldatud jääajajärgsed kooslused ning seda võis käsitleda taastumiskooslusena.

$\delta^{13}\text{C}$  väärtused ei ole Läänemere regiooni idaosa läbilõigetel vanal, traditsioonilisel O–S piiril jäätumiseelsele tasemele jõudnud ning isotoopsuhte langus jätkub ka sellest piirist kõrgemal. *H. harparum*'i ostrakoodikoosluse kadumise tasemest kõrgemal ilmunud jäänukkooslusega kihid on seega Hilis-Ordoviitsiumi vanusega. O–S piiri asendit Läänemere regioonis ei saa määrata selle ostrakoodikoosluse ning sellega koos ilmuvate teiste fossiilirühmade liikide ilmumise alusel ning see paikneb läbilõikes märgatavalt kõrgemal.

## **PUBLICATIONS**

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