

Changes in the morphology of Late Ordovician ostracods along the shelf-to-basin transect of the Baltic Palaeobasin

Stefi Guitor* and Tõnu Meidla

Department of Geology, Institute of Ecology and Earth Sciences, University of Tartu, Ravila 14a, 50411 Tartu, Estonia

*Corresponding author, stefi.guitor@ut.ee

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Abstract. The present work analyses the numerical distribution data of ostracods in the Late Ordovician (Katian) deposits of Estonia for establishing trends in carapace morphology along a facies profile from a shallow shelf to a deep basin. We present a quantitative analysis of facies-related trends in carapace size, shape and ornamental features. In addition, changes in diversity as well as major changes in the taxonomic composition of the assemblages are addressed, based on the number of individuals. The quantitative analysis of ostracod distribution data reveals distinct trends in the offshore direction: carapaces become larger and shorter, the dominance of smooth valves decreases and the share of ornamented valves increases. Tuberculate valves are most common in open-shelf environments. Species diversity decreases in the offshore direction. The taxonomic composition changes from a clear majority of podocopes to an association of podocopes and palaeocopes, and further to a majority of binodicopes. The fact that these patterns are persistent throughout the Late Ordovician (within three chronostratigraphic units) suggests that they represent environmental control. Some of the results are not in full agreement with previous observations.

Keywords: Ordovician, Katian, Baltic Palaeobasin, Ostracoda, morphology, diversity, facies.

INTRODUCTION

The concept that morphology is an adaptation to the environment has become axiomatic among biologists and palaeontologists, and the ecomorphology of various extant and fossil species has been discussed in a number of publications. However, our knowledge of ecomorphological characteristics of Palaeozoic ostracods is still rather scarce.

Ostracods, by far the most abundant arthropods in the fossil record, are widely used in regional biostratigraphy (Sarv 1959; Sarv and Meidla 1984; Ayress 1993; Meidla 1996; Schudack and Schudack 2009; Sames et al. 2010;) and palaeogeography (Schallreuter et al. 1996; Williams et al. 2001, 2003; Meidla et al. 2013; Perrier and Siveter 2013). It is generally accepted that the early Palaeozoic ostracods were affected by the substrate due to their benthic mode of life, but our knowledge of these relationships, in general, is still relatively scarce. The ecomorphological interpretations of extinct ostracod species are generally based upon finding analogies with recent taxa or comparing the distribution patterns with well-established palaeoenvironmental factors. Sometimes the inter-

pretations are derived from more or less speculative and occasionally even contradictory considerations.

One can only find a handful of publications relating to the ecomorphology of the ostracod carapace: the principal trends in ostracod morphology in relation to the substrate (Remane 1933; Elofson 1941; Benson 1961), the “ecotypes” of Palaeozoic ostracods in relation to depth and hydrodynamical conditions (Becker 1971; Copeland 1982; Becker and Adamczak 1994; Becker 2000) and the taxonomic distribution and main morphology of Palaeozoic ostracods in relation to the sediment type or distance from the shoreline (Warshauer and Berdan 1982; Siveter 1984; Dreesen et al. 1985; Gramm 1985; Brouwers 1988; Vannier et al. 1989; Becker and Bless 1990; Williams and Siveter 1996). Nevertheless, it is still unclear what the depth-related morphological adaptations of Early Palaeozoic ostracods were.

The highly diverse and abundant Estonian Late Ordovician ostracod fauna is one of the most thoroughly studied Palaeozoic faunas, with a research history of approximately 170 years (see Eichwald 1855). This exceptionally well-preserved fauna occurs in a succession of

facies in the Estonian part of the Baltic Palaeobasin, ranging from the shallow carbonate shelf to deeper shelf/basinal conditions (Harris et al. 2004). The possibility of tracing the distribution of a diverse and well-preserved ostracod fauna along a distinct palaeobathymetric gradient promises great potential for revealing trends in ostracod morphological changes along a shelf-to-basin transect. Such trends have never been analysed quantitatively for Ordovician ostracods.

This paper explores the morphological and taxonomic trends in ostracod faunas in relation to facies gradation from the shallow shelf environment to a deeper basin in three stratigraphic intervals in the Middle-Upper Katian of Estonia (Rakvere, Nabala and Vormsi regional stages). The objectives of this research are: 1) to determine whether carapace size, shape and ornamentation were affected by palaeodepth; 2) to analyse principal trends in the taxonomic distribution and diversity of ostracod assemblages along a shelf-to-basin transect. The paper is based upon quantitative data (specimen counts) of Late Ordovician ostracods in Estonia, previously published semi-quantitatively by Meidla (1996). The ostracod classification used in this study is based on Vannier et al. (1989) and Meidla (1996).

GEOLOGICAL SETTING AND STRATIGRAPHY

Estonia is located in the northwestern part of the East European Platform between the Fennoscandian Shield to the north and the Livonian Basin to the south (Fig. 1). During the Late Ordovician, the study area was located in the tropical realm (Cocks and Torsvik 2021) and constituted the northern flank of a shallow cratonic sea with mixed carbonate and fine-grained siliciclastic sediment accumulation (Jaanusson 1973, 1976; Bassett et al. 1989; Nestor and Einasto 1997; Harris et al. 2004).

The general architecture of the Late Ordovician Baltic Basin includes two main structural elements: 1) the Estonian Shelf and 2) the Livonian Basin, corresponding to the North Estonian Confacies Belt and the Central Baltoscandian Confacies Belt in earlier papers (Jaanusson 1976; Fig. 1). The Estonian Shelf is characterised mostly by shallow marine carbonates, while the relatively deeper marine Livonian Basin, often characterised as an intracratonic depression (e.g. Nestor and Einasto 1997), consists predominantly of argillaceous carbonates and mudstones. A transitional zone is distinguished between these two belts (Põlma 1967).

The generalised model of the Upper Ordovician sequences of Estonia includes four facies belts (Nestor 1990a, 1990b; Einasto 1995; Nestor and Einasto 1997; Harris et al. 2004), three of which are represented in the intervals studied herein: 1) mixed facies – micritic lime-

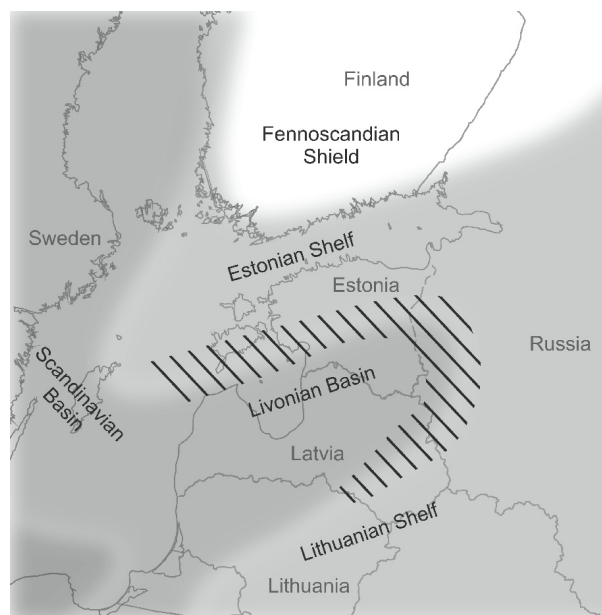


Fig. 1. Late Ordovician facies belts and major tectonic features of the Baltic region (after Jaanusson 1976). The striped area marks a transitional belt between the two principal facies (after Põlma 1967).

stones in mid-shelf settings; 2) mud-supported facies – calcareous mudstones and marls deposited in deep-shelf environments, and 3) black shale facies – graptolitic shales representing basinal conditions (Fig. 2). The facies nearest to the ancient Late Ordovician shoreline are missing due to erosion.

The strata studied here include three stratigraphic intervals: the Rakvere Regional Stage (RS), the lower Nabala RS and the Vormsi RS, representing the Katian Stage, Upper Ordovician (Fig. 3). The arguments for selecting the Rakvere and Vormsi regional stages for this

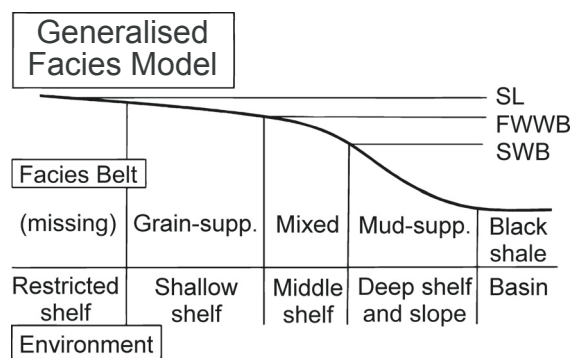


Fig. 2. Facies model of the Upper Ordovician of Estonia (after Harris et al. 2004). *Abbreviations:* SL – sea level, FWWB – fair-weather wave-base, SWB – storm wave-base, supp. – supported.

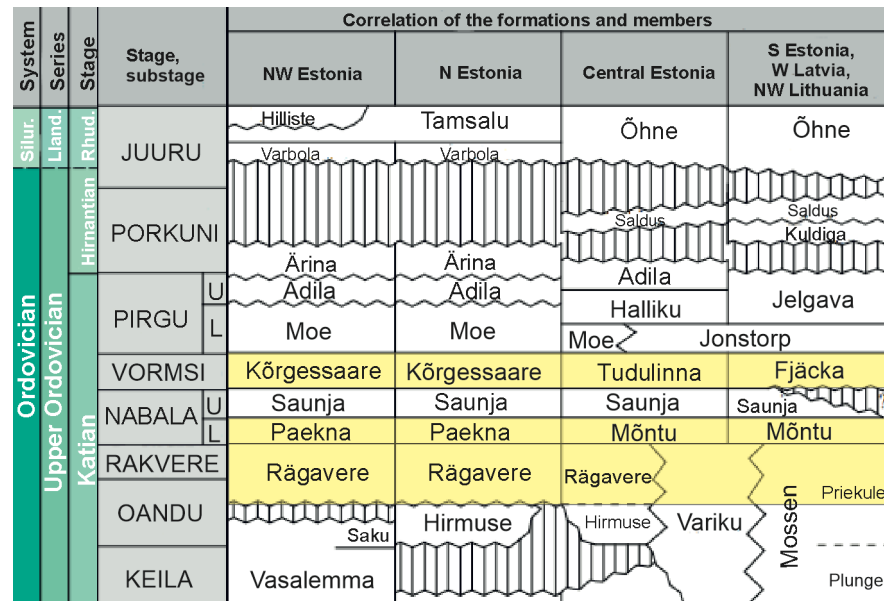


Fig. 3. Stratigraphic correlation of the studied strata (edited from Meidla et al. 2014). Analysed stratigraphic units are highlighted. *Abbreviations:* Silur. – Silurian, Lland. – Llandovery, Rhud. – Rhuddanian, U – Upper, L – Lower, NW – Northwest, N – North, S – South, W – West.

study were the availability of a sufficient number of richly fossiliferous microfaunal samples and a clear facies gradation within the interval. The lower Nabala RS was included due to its intermediate position between the two previous intervals. The range of facies distribution is different for each interval due to environmental differentiation and facies shifts along the depositional transect, eventually due to relative sea-level changes. Stratigraphic correlation within the Baltic area has been well established in the course of a long history of investigation (Bassett et al. 1989; Männil 1990; Männil and Meidla 1994). Although the Baltic region uses regional stages as the main stratigraphic units, correlation with the global series is also well established (Meidla et al. 2014). We adopted a nomenclature of regional stages that conforms to the generally accepted usage (e.g. Meidla 1996; Meidla et al. 2014).

The Rakvere RS is represented by the main part of the Rägavere Formation (Fm) (without the basal strata) in northern Estonia, by the Mossen Fm in southern Estonia and by the Variku Fm in a narrow South Estonian belt, not covered by this study (Fig. 3). The Rägavere Fm consists of pure, partially dolomitised lime mudstones (or occasionally wackestones), which intercalate with more or less argillaceous varieties (Hints and Meidla 1997b; Kröger et al. 2020). The limestones of the Rägavere Fm in northern Estonia are characterised by abundant pyritised burrows, low content of terrigenous material (3–9%) and low content of skeletal sand (less than 15%)

(Kõrvel 1962; Põlma et al. 1988). The limestones become more argillaceous southwards until they are replaced by the carbonate marls of the Mossen Fm in southern Estonia (Hints and Meidla 1997b; Ainsaar and Meidla 2000).

Macrofauna is very scarce in the Rakvere RS with rare bryozoans, brachiopods and trilobites. However, the microfauna of ostracods, chitinozoans and calcareous algae is abundant and diverse (Hints and Meidla 1997b; Nõlvak and Meidla 1990). The taxonomic composition of ostracod assemblages changes remarkably in the Rakvere RS (Meidla 1996). A high amount of calcareous green algae among the skeletal fragments (up to 50%) indicates a shallow-water environment within the euphotic zone (Granier 2012; Kröger et al. 2020).

The Nabala RS is composed of the overlying Saunja Fm and the underlying Paekna and Mõntu formations (Fig. 3). The Saunja Fm was not included in this study due to an incomplete facies transect (the unit thins out in central Estonia) and uncertainty of correlation in more offshore areas, as well as scarcity and very uneven distribution of ostracods (Meidla 1996). The Paekna Fm in northern Estonia and the Mõntu Fm in southern Estonia were used for the analysis.

The Paekna Fm comprises pure micritic limestones intercalated with skeletal nodular argillaceous wackestones. In central Estonia, the Paekna Fm is replaced by the glauconite-containing argillaceous limestones (wackestones) of the Mõntu Fm (Hints and Meidla 1997c; Kröger

et al. 2020). The rocks of the Nabala RS are relatively rich in phosphorus (average P_2O_5 content 0.3%) compared to other Katian rocks of the Estonian Shelf (average P_2O_5 content between 0.05% and 0.1%) (Kiipli et al. 2010). Macrofossils are rare in the Paekna Fm, and mostly brachiopods have been reported. A change in the taxonomic composition of the scarce trilobite and bryozoan fauna is recorded at the boundary of the Rakvere and Nabala regional stages. Microfossils include ostracods, calcareous algae and chitinozoans (Hints and Meidla 1997a; Kaljo et al. 2017). The reorganization of ostracod assemblages, which started already in the Rakvere RS, continued during the Nabala Age (Männil 1966; Meidla 1996). Chitinozoans exhibit a short-lived diversity peak against the generally falling Katian trend (Hints et al. 2011; Kaljo et al. 2011). This, along with an elevated concentration of phosphorus and the presence of glauconite in the Mõntu Fm, could imply a regional upwelling event (Kiipli et al. 2010; Hints et al. 2011).

The Vormsi RS comprises the Kõrgessaare, Tudulinna and Fjäckä formations (Fig. 3). The bioclastic micritic wackestones of the Kõrgessaare Fm grade into argillaceous glauconite-containing limestones and marls of the Tudulinna Fm in central Estonia. The limestones and marls are replaced by clays and graptolitiferous black shales of the Fjäckä Fm in southern Estonia (Männil and Meidla 1994; Hints and Meidla 1997c).

The Kõrgessaare Fm contains a diverse shelly fauna of corals, bryozoans, brachiopods, molluscs and trilobites. Southwards, in the Tudulinna Fm, the diversity and abundance are lower and the fauna is mostly composed of brachiopods. The fauna of the Fjäckä Fm is monotonous and scarce, consisting mainly of a few brachiopods, although the microfauna is common (Hints and Meidla 1997c). The change in the percentage of calcareous algae among the skeletal fragments drops from 50% in the Kõrgessaare Fm to 5% in the Fjäckä Fm (Põlma 1982), suggesting a distinct palaeobathymetric change.

MATERIAL AND METHODS

This paper is based on the large collection of Late Ordovician ostracods taxonomically described and biostratigraphically analysed by Meidla (1996). However, the quantitative data (specimen counts) of this collection have not been previously published. The drill core sampling was carried out at an interval of 1–1.5 m, with each sample ca 300–700 g. The number of samples per section varies due to differences in the thickness of the strata. The samples were disintegrated by means of repeated heating and cooling in sodium hyposulphite. Very clay-rich samples were subsequently processed with hydrogen peroxide to accelerate the washing process. The palae-

ontological collection is deposited at the Department of Geology, Tallinn University of Technology.

For the purpose of this study, the samples were summarised per stratigraphic interval in each core section. Data were gathered for 129 species and 10 603 specimens. The morphological analysis of ostracod carapaces is based on previously published data (species descriptions, drawings, scanning electron microscope micrographs) and the palaeontological collection of Late Ordovician ostracods in Estonia (Meidla 1996). The analysis is based on the results of morphological and taxonomic analyses are presented as a relative abundance of a trait or a taxon within a section interval.

The R package ‘ggtern’ was used for creating a ternary graph (Hamilton and Ferry 2018) and the palaeontological statistics software PAST (Hammer et al. 2001) was used for the analysis of diversity indices. Carapace/valve dimensions were given as a weighted arithmetic mean per section interval (specimen counts as weights).

Ostracods were analysed in 14 drill core sections within three stratigraphic intervals, designated as the Rakvere, lower Nabala and Vormsi regional stages (Katian Stage, Upper Ordovician; Figs 4–6). Altogether 35 section intervals were analysed. The studied cores are aligned along the shelf-to-basin transect (with some lateral variance) across the Estonian Shelf and into the Livonian Basin (Fig. 1). Depending on the stratigraphic interval, the transect spans across one to three facies belts: mixed, mud-supported and black shale facies. The core sections containing the black shale facies are under-represented due to the depth and limited distribution of these layers. The boundaries of the facies belts are interpreted to coincide with the identified lateral boundaries of the

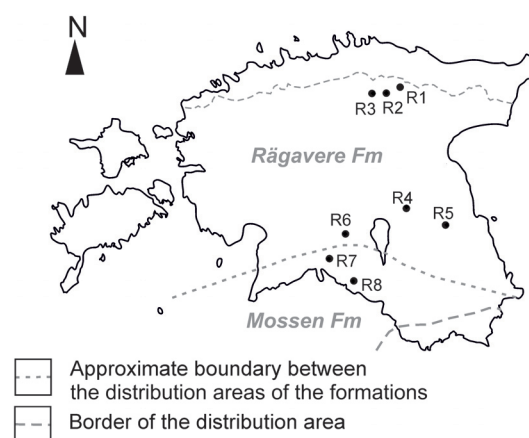


Fig. 4. Distribution of the Rakvere RS and the location of the studied sections. The distribution of the Mossen Fm has been drawn based on the latest observations (Meidla et al. 2017). R1 – Vinni, R2 – Laiamäe, R3 – Moe, R4 – Laeva, R5 – Kaagvere, R6 – Viljandi, R7 – Abja, R8 – Taagepera.

distribution areas of the formations (in reality, both are more or less transitional).

The range of facies in the **Rakvere RS** spans from mixed facies in the Rägavere Fm to mud-supported facies in the Mossen Fm (Meidla 1996; Ainsaar and Meidla 2000). The Rakvere RS is distinguished in 8 drill core sections (Rägavere Fm in 6 and Mossen Fm in 2 core sections). The shelf-to-basin transect of the analysed section intervals is as follows: Vinni (T-112), Laiamäe-259, Moe (H-50), Laeva-18, Kaagvere-1, Viljandi-91, Abja-92 and Taagepera (Fig. 4). Puhmu-567 and Otepää-2 core sections, which include strata from all the three studied regional stages, are excluded from the Rakvere RS analysis due to anomalous ostracod associations and/or uncertain stratigraphic correlation (Meidla 1996).

Differences in basin depth between the northern and southern peripheries of the study area were subtle and less defined during the Nabala Age compared to the Rakvere and Vormsi ages. The shelf-to-basin zonation in the **lower Nabala RS** is limited to mixed facies, although the deposits become more argillaceous offshore in the Mõntu Fm (Meidla 1996). The Nabala RS is distinguished in 13 drill core sections (Paekna Fm in 5 and Mõntu Fm in 9 core sections). The shelf-to-basin sequence of the analysed section intervals is as follows: Vinni (T-112), Laiamäe-259, Moe (H-50), Puhmu-567, Vodja H-191, Ruskavere-451, Aidu-427, Laeva-18, Kaagvere-1, Viljandi-91, Otepää-2, Abja-92 and Taagepera (Fig. 5).

The facies belts in the **Vormsi RS** cover the mixed facies of the Kõrgessaare Fm, the mud-supported facies of the Tudulinna Fm and the black shale facies of the Fjäckä Fm (Meidla 1996). The Vormsi RS is distinguished in 14 drill core sections (Kõrgessaare Fm in 4, Tudulinna

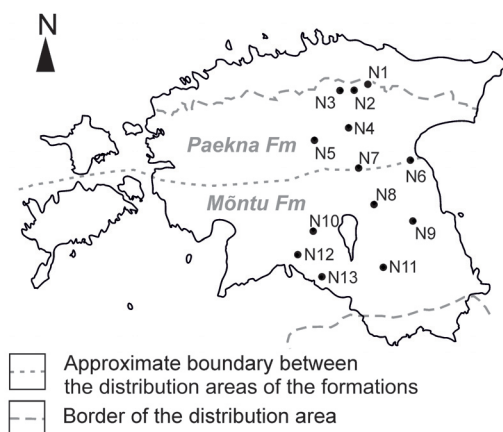


Fig. 5. Distribution of the lower Nabala RS and the location of the studied sections. N1 – Vinni, N2 – Laiamäe, N3 – Moe, N4 – Puhmu, N5 – Vodja, N6 – Ruskavere, N7 – Aidu, N8 – Laeva, N9 – Kaagvere, N10 – Viljandi, N11 – Otepää, N12 – Abja, N13 – Taagepera.

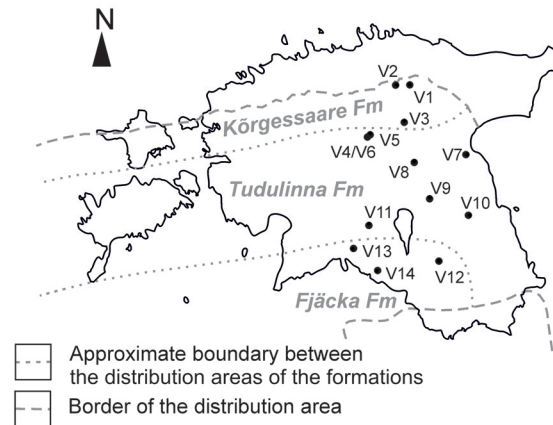


Fig. 6. Distribution of the Vormsi RS and the location of the studied sections. V1 – Laiamäe, V2 – Moe, V3 – Puhmu, V4 – Vodja-190, V5 – Vodja-191, V6 – Vodja-190, V7 – Ruskavere, V8 – Aidu, V9 – Laeva, V10 – Kaagvere, V11 – Viljandi, V12 – Otepää, V13 – Abja, V14 – Taagepera.

Fm in 7 and Fjäckä Fm in 3 core sections). The shelf-to-basin transect of the analysed section intervals is as follows: Laiamäe-259, Moe (H-50), Puhmu-567, Vodja-190 (Kõrgessaare Fm), Vodja-191, Vodja-190 (Tudulinna Fm), Ruskavere-451, Aidu-427, Laeva-18, Kaagvere-1, Viljandi-91, Otepää-2, Abja-92 and Taagepera (Fig. 6).

The lower part of the Vormsi RS in the Vodja-190 drill core consists of argillaceous limestones of the Tudulinna Fm with the *Uhakiella curta* ostracod association, while the upper part consists of slightly argillaceous limestones (wackestones) containing the *Steusloffina cuneata*–*Medianella blidenensis* ostracod association, characteristic of the Kõrgessaare Fm (Meidla 1996). Meidla (1996) distinguished the whole section as the Tudulinna Fm, but as several authors have indicated a sequential occurrence of these formations in northern Central Estonia (e.g. Rõdmusoks 1983; K. Suuroja in personal communication), in the current paper we attribute the upper part of the core section to the Kõrgessaare Fm.

DISTRIBUTION OF TAXONOMIC GROUPS

The studied material consists mostly of podocopes, palaeocopes and binodicopes, with some rare leiocopids and eridostracans. The podocope ostracods were almost exclusively bairdiocypridoids, while the palaeocopes were mostly hollinoids. The change in biofacies did not always coincide with the interpreted facies boundaries (formation boundaries). This could be expected, considering the rather gradual change in facies succession.

Figures 7–8 and Tables 1–2 show the taxonomic distribution of ostracods in the analysed section intervals and also in the analysed facies (formations). Additionally, the palaeocope, binodicope and podocope specimen counts per section interval were plotted on a ternary graph (Fig. 9).

All the sections of mixed facies had a high podocope component (at least 57%), except for the most offshore section of the Rägavere Fm (R6 in Fig.7), where the percentage of podocopes was significantly lower (23%). The occurrence of palaeocopes was less frequent and binodicoopes were almost entirely missing in the mixed facies.

The mud-supported facies contained predominantly palaeocopes, which co-occurred with podocopes in the Vormsi and lower Nabala regional stages, and binodicoopes in the Rakvere RS. The mud-supported facies of the lower Nabala RS was characterised by an oscillation in the percentage of podocopes and palaeocopes and a scarcity of binodicoopes. The mud-supported facies of the Rakvere RS was characterised by a high prevalence of binodicoopes (average relative abundance 43%), whereas in the mud-supported facies of the Vormsi RS the relative abundance of binodicoopes was high only in the basinmost section (51%; V11 in Fig.7). The percentage of podocopes in the

mud-supported facies of the Vormsi and Rakvere regional stages was lower compared to the mixed facies and it decreased further in the most offshore sections (V11 and R8 in Fig. 7)

All the sections of black shale facies had a high relative abundance of binodicoopes (at least 62%).

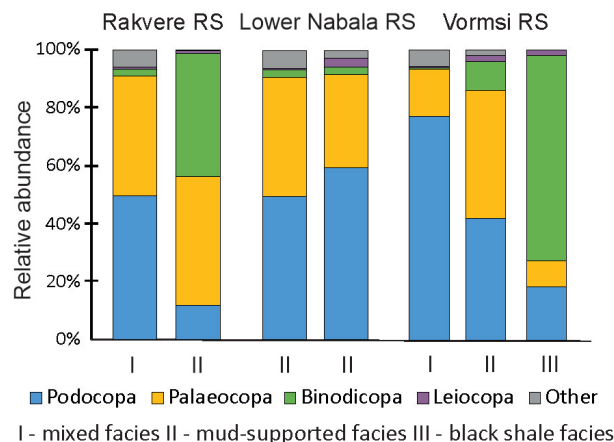


Fig. 8. Taxonomic distribution of ostracods in the analysed formations of the Rakvere, lower Nabala and Vormsi regional stages.

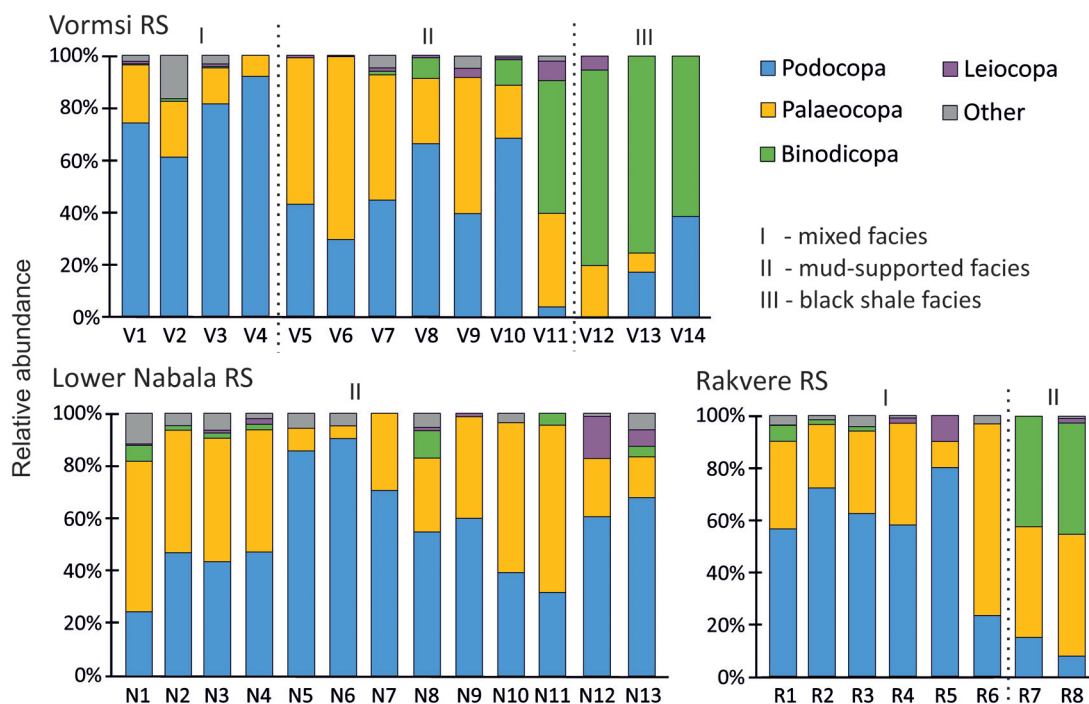


Fig. 7. Taxonomic distribution of ostracods in the analysed section intervals. Rakvere RS: R1 – Vinni, R2 – Laiamäe, R3 – Moe, R4 – Laeva, R5 – Kaagvere, R6 – Viljandi, R7 – Abja, R8 – Taagepera; Lower Nabala RS: N1 – Vinni, N2 – Laiamäe, N3 – Moe, N4 – Puhmu, N5 – Vodja, N6 – Ruskavere, N7 – Aidu, N8 – Laeva, N9 – Kaagvere, N10 – Viljandi, N11 – Otepää, N12 – Abja, N13 – Taagepera; Vormsi RS: V1 – Laiamäe, V2 – Moe, V3 – Puhmu, V4 – Vodja-190, V5 – Vodja-191, V6 – Vodja-190, V7 – Ruskavere, V8 – Aidu, V9 – Laeva, V10 – Kaagvere, V11 – Viljandi, V12 – Otepää, V13 – Abja, V14 – Taagepera.

Table 1. Taxonomic distribution of ostracods (specimen counts and relative abundance in sections and intervals)

Section interval	Formation and facies	Podocopa	Palaeocopa	Binodicopa	Leiocopa	Other
Vormsi RS						
Laiamäe	Kõrgessaare (mixed facies)	329 (74.1%)	99 (22.3%)	2 (0.5%)	4 (0.9%)	10 (2.3%)
Moe		114 (61.0%)	40 (21.4%)	2 (1.1%)	–	31 (16.6%)
Puhmu		512 (81.4%)	87 (13.8%)	3 (0.5%)	6 (1.0%)	21 (3.3%)
Vodja-190		57 (91.9%)	5 (8.1%)	–	–	–
Vodja-191	Tudulinna (mud-supported facies)	48 (42.9%)	63 (56.3%)	–	1 (0.9%)	–
Vodja-190		183 (29.3%)	439 (70.2%)	1 (0.2%)	2 (0.3%)	–
Ruskavere		1287 (44.5%)	1390 (48.0%)	41 (1.4%)	38 (1.3%)	139 (4.8%)
Aidu		74 (66.1%)	28 (25.0%)	9 (8.0%)	1 (0.9%)	–
Laeva		34 (39.5%)	45 (52.3%)	–	3 (3.5%)	4 (4.7%)
Kaagvere		98 (68.5%)	29 (20.3%)	14 (9.8%)	1 (0.7%)	1 (0.7%)
Viljandi		2 (3.8%)	19 (35.8%)	27 (50.9%)	4 (7.5%)	1 (1.9%)
Otepää	Fjäckä (black shale facies)	–	11 (19.6%)	42 (75.0%)	3 (5.4%)	–
Abja		7 (17.1%)	3 (7.3%)	31 (75.6%)	–	–
Taagepera		5 (38.5%)	–	8 (61.5%)	–	–
Lower Nabala RS						
Vinni	Paekna (mud-supported facies)	284 (24.5%)	663 (57.2%)	71 (6.1%)	6 (0.5%)	136 (11.7%)
Laiamäe		130 (46.9%)	129 (46.6%)	5 (1.8%)	0 (0.0%)	13 (4.7%)
Moe		87 (43.5%)	94 (47.0%)	4 (2.0%)	2 (1.0%)	13 (6.5%)
Puhmu		69 (47.3%)	68 (46.6%)	3 (2.1%)	3 (2.1%)	3 (2.1%)
Vodja		30 (85.7%)	3 (8.6%)	–	0 (0.0%)	2 (5.7%)
Ruskavere	Mõntu (mud-supported facies)	19 (90.5%)	1 (4.8%)	–	–	1 (4.8%)
Aidu		12 (70.6%)	5 (29.4%)	–	–	–
Laeva		142 (54.8%)	73 (28.2%)	27 (10.4%)	3 (1.2%)	14 (5.4%)
Kaagvere		138 (60.0%)	89 (38.7%)	–	3 (1.3%)	–
Viljandi		11 (39.3%)	16 (57.1%)	–	–	1 (3.6%)
Otepää		7 (31.8%)	14 (63.6%)	1 (4.5%)	–	–
Abja		49 (60.5%)	18 (22.2%)	–	13 (16.0%)	1 (1.2%)
Taagepera		290 (67.9%)	66 (15.5%)	17 (4.0%)	27 (6.3%)	27 (6.3%)
Rakvere RS						
Vinni	Rägavere (mixed facies)	874 (56.6%)	519 (33.6%)	94 (6.1%)	1 (0.1%)	57 (3.7%)
Laiamäe		124 (72.1%)	42 (24.4%)	3 (1.7%)	–	3 (1.7%)
Moe		73 (62.4%)	37 (31.6%)	2 (1.7%)	–	5 (4.3%)
Laeva		58 (58.0%)	39 (39.0%)	–	2 (2.0%)	1 (1.0%)
Kaagvere		16 (80.0%)	2 (10.0%)	–	2 (10.0%)	–
Viljandi		7 (23.3%)	22 (73.3%)	–	–	1 (3.3%)
Abja	Mossen (mud-supported facies)	5 (15.2%)	14 (42.4%)	14 (42.4%)	–	–
Taagepera		18 (8.0%)	105 (46.7%)	96 (42.7%)	4 (1.8%)	2 (0.9%)

DIVERSITY

Some analysed sections contained samples with few individuals and/or a high relative abundance of the most common taxa. For this reason, the Shannon index was chosen instead of the commonly used Simpson index for describing changes in ostracod diversity along the shelf-to-basin transect. The values of both diversity indices are influenced by these factors, but less so for the Shannon index than for the Simpson index. The samples with few individuals caused a considerable amount of scatter or

noise, which is why a linear trendline was also calculated.

Each studied interval showed a trend of basinward decline in species diversity (Fig. 10). This trend was most prominent in the Vormsi RS, where facies differentiation was highest.

Interestingly, the lower Nabala RS (all mud-supported facies) seemed to exhibit a more evident trend than the Rakvere RS, although the facies differentiation was higher in the latter. The changes in diversity in the lower Nabala RS did not coincide with any higher-level taxonomic changes.

Table 2. Average relative abundance of principal ostracod groups in the studied formations; I – mixed facies, II – mud-supported facies, III – black shale facies

Formation and facies	Podocopa	Palaeocopa	Binodicopa	Leiocopa	Other
Vormsi RS					
Kõrgessaare (I)	77.1%	16.4%	0.5%	0.5%	5.5%
Tudulinna (II)	42.1%	44.0%	10.0%	2.2%	1.7%
Fjäcka (III)	18.5%	9.0%	70.7%	1.8%	–
Lower Nabala RS					
Paekna (II)	49.6%	41.2%	2.4%	0.7%	6.1%
Mõntu (II)	59.4%	32.4%	2.4%	3.1%	2.7%
Rakvere RS					
Rägavere (I)	49.6%	41.2%	2.4%	0.7%	6.1%
Mossen (II)	11.6%	44.5%	42.5%	0.9%	0.4%

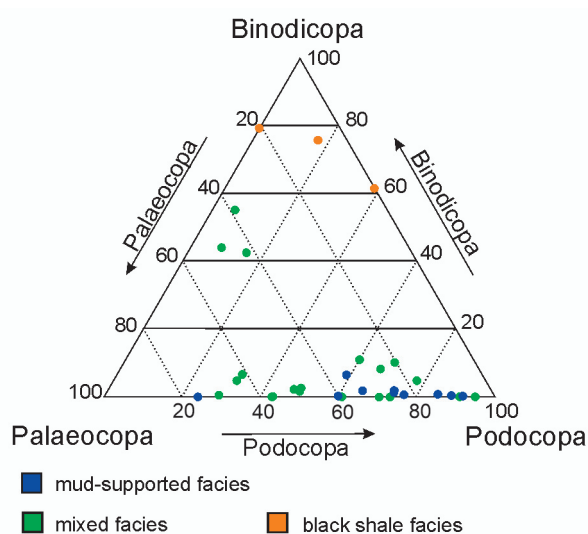


Fig. 9. Taxonomic distribution of ostracods in the analysed section intervals.

DIMENSIONS

It is common practice to use carapace length (L) and height (H) as measures to describe ostracod size and shape. Carapace length (L) is a good indicator of carapace size and the ratio between carapace length and height (L/H) describes an ostracod’s overall shape – shorter shells would have lower L/H values, while elongated shells would have higher L/H values.

The weighted average carapace lengths of adults in the studied collection were between 0.84 and 1.59 mm and the weighted average L/H ratios were between 1.48 and 1.88 (Fig. 11).

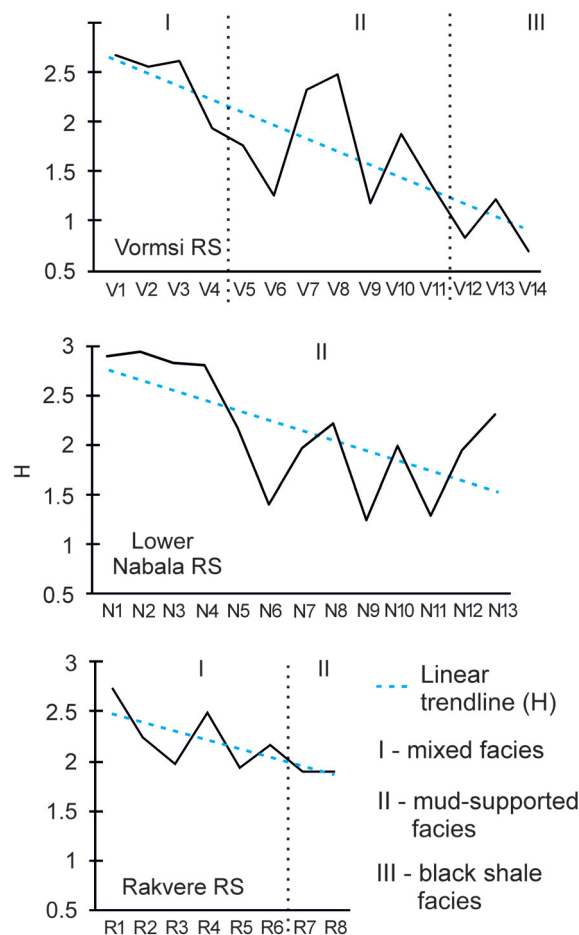


Fig. 10. Shannon index values showing the general trends of species diversity. H – Shannon index; I – mixed facies, II – mud-supported facies, III – black shale facies. Numbered section intervals are listed in the caption of Fig. 7.

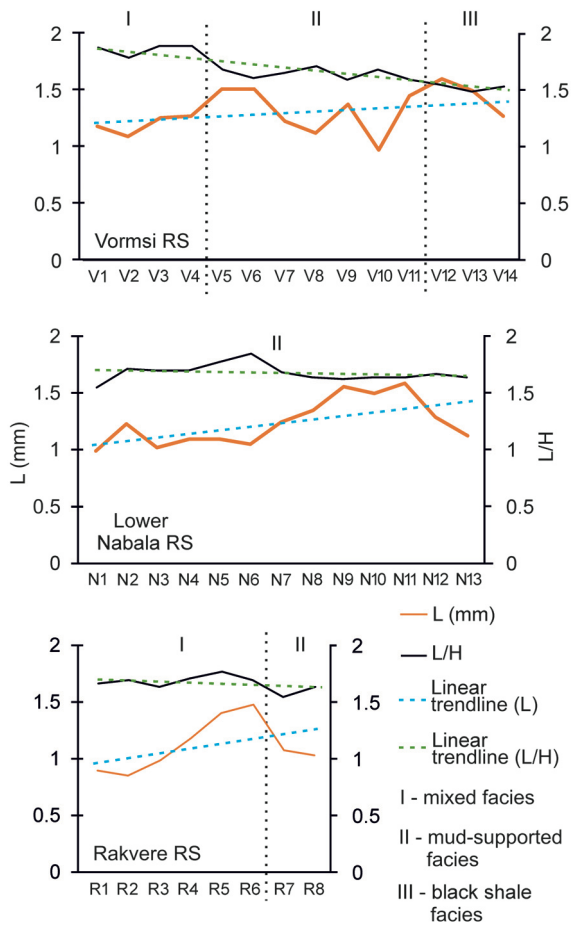


Fig. 11. Weighted arithmetic mean carapace size and shape in the analysed section intervals (specimen counts as weights). L – carapace length (mm), H – carapace height (mm); I – mixed facies, II – mud-supported facies, III – black shale facies. Numbered section intervals are listed in the caption of Fig. 7.

Our analysis indicates that carapaces became shorter and, as a general rule, also larger in the offshore direction. This phenomenon was seen in all the studied stratigraphic intervals, but the most dramatic change occurred in the Vormsi RS, where the facies differentiation was highest.

The mixed facies with a high podocope component (Fig. 8) was characterised by small elongated carapaces in the shoremost sections and large elongated carapaces in the most offshore sections. This change in carapace size was gradual and independent of any changes in the higher-level taxonomic composition of the assemblages.

In the mud-supported facies, ostracod shells became shorter and gradually shortened further in the offshore direction. The average carapace size was more variable compared to the L/H ratio, but as a general rule, increased in the offshore direction. Neither of these trends could be

explained by higher-level taxonomic changes. Ostracods with relatively smaller carapaces were found in the middle sections of the mud-supported facies of the Vormsi RS and in both sections of the mud-supported facies of the Rakvere RS. The decrease in carapace size in the Vormsi RS coincided with an increase in the abundance of palaeocopes.

The black shale facies was characterised by even shorter carapaces while the average size reached a maximum. The basinward increase in size and decrease in the L/H ratio from the mud-supported facies to the black shale facies coincided with the increasing abundance of binodicopes (Fig. 7).

ORNAMENTATION

Changes in carapace ornamentation along the shelf-to-basin transect were analysed for all ostracods and separately solely for palaeocopes and binodicopes (Fig. 12, Tables 3–4).

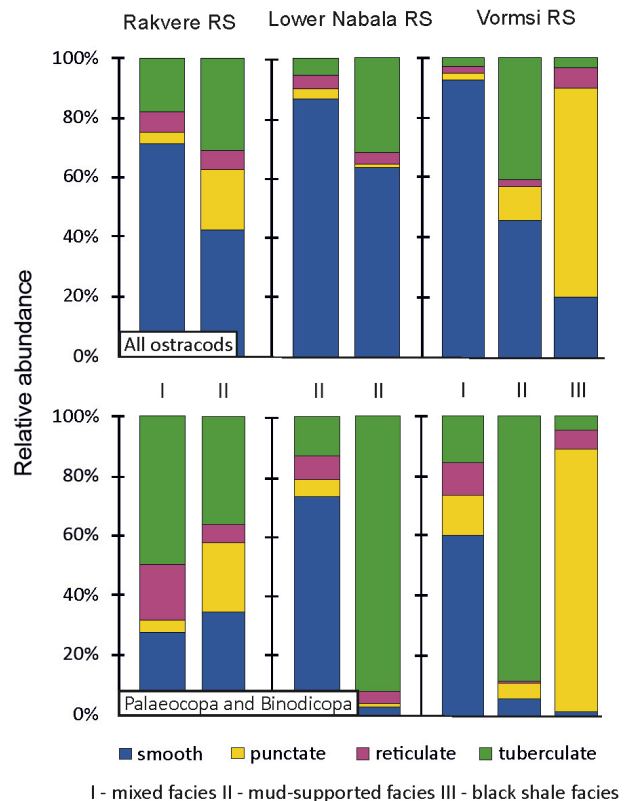


Fig. 12. Valve ornamentation (average relative abundances) in the formations of the analysed regional stages. Upper graph – valve ornamentation of all ostracods; lower graph – valve ornamentation of palaeocopes and binodicopes; I – mixed facies, II – mud-supported facies, III – black shale facies.

Table 3. Distribution of valve ornamentation (specimen counts and relative abundance in sections and intervals)

Section interval	Formation and facies	Valve ornamentation			
		smooth	punctate	reticulate	tuberculate
Vormsi RS					
Laiamäe	Kõrgessaare (mixed facies)	391 (88.1%)	15 (3.4%)	28 (6.3%)	10 (2.3%)
Moe		183 (97.9%)	1 (0.5%)	–	3 (1.6%)
Puhmu		555 (88.2%)	33 (5.2%)	6 (1.0%)	35 (5.6%)
Vodja-190		59 (95.2%)	1 (1.6%)	–	2 (3.2%)
Vodja-191	Tudulinna (mud-supported facies)	193 (30.9%)	2 (0.3%)	1 (0.2%)	429 (68.6%)
Vodja-190		51 (45.5%)	2 (1.8%)	–	59 (52.7%)
Ruskavere		1472 (50.8%)	46 (1.6%)	51 (1.8%)	1326 (45.8%)
Aidu		83 (74.1%)	4 (3.6%)	1 (0.9%)	24 (21.4%)
Laeva		38 (44.2%)	3 (3.5%)	–	45 (52.3%)
Kaagvere		99 (69.2%)	14 (9.8%)	1 (0.7%)	29 (20.3%)
Viljandi		3 (5.7%)	31 (58.5%)	5 (9.4%)	14 (26.4%)
Otepää	Fjäckä (black shale facies)	–	43 (76.8%)	11 (19.6%)	2 (3.6%)
Abja		9 (22.0%)	29 (70.7%)	–	3 (7.3%)
Taagepera		5 (38.5%)	8 (61.5%)	–	–
Lower Nabala RS					
Vinni	Paekna (mud-supported facies)	962 (82.9%)	61 (5.3%)	108 (9.3%)	29 (2.5%)
Laiamäe		237 (85.6%)	14 (5.1%)	12 (4.3%)	14 (5.1%)
Moe		188 (94.0%)	4 (2.0%)	4 (2.0%)	4 (2.0%)
Puhmu		111 (76.0%)	5 (3.4%)	12 (8.2%)	18 (12.3%)
Vodja		33 (94.3%)	–	–	2 (5.7%)
Ruskavere	Mõntu (mud-supported facies)	20 (95.2%)	–	–	1 (4.8%)
Aidu		12 (70.6%)	–	–	5 (29.4%)
Laeva		157 (60.6%)	2 (0.8%)	31 (12.0%)	69 (26.6%)
Kaagvere		138 (60.0%)	–	4 (1.7%)	88 (38.3%)
Viljandi		12 (42.9%)	–	–	16 (57.1%)
Otepää		8 (36.4%)	–	–	14 (63.6%)
Abja		50 (61.7%)	1 (1.2%)	13 (16.0%)	17 (21.0%)
Taagepera		327 (76.6%)	25 (5.9%)	9 (2.1%)	66 (15.5%)
Rakvere RS					
Vinni	Rägavere (mixed facies)	1314 (85.0%)	50 (3.2%)	95 (6.1%)	86 (5.6%)
Laiamäe		158 (91.9%)	2 (1.2%)	7 (4.1%)	5 (2.9%)
Moe		95 (81.2%)	–	21 (17.9%)	1 (0.9%)
Laeva		62 (62.0%)	4 (4.0%)	–	34 (34.0%)
Kaagvere		16 (80.0%)	2 (10.0%)	–	2 (10.0%)
Viljandi		8 (26.7%)	1 (3.3%)	4 (13.3%)	17 (56.7%)
Abja	Mossen (mud-supported facies)	19 (57.6%)	7 (21.2%)	1 (3.0%)	6 (18.2%)
Taagepera		60 (26.7%)	45 (20.0%)	20 (8.9%)	100 (44.4%)

Table 4. Distribution of valve ornamentation in formations (average relative abundance); I – mixed facies, II – mud-supported facies, III – black shale facies

Formation and facies	Valve ornamentation							
	All ostracods				Palaeocopa and Binodicopa			
	smooth	punctate	reticulate	tuberculate	smooth	punctate	reticulate	tuberculate
Vormsi RS								
Kõrgessaare (I)	92.3%	2.7%	1.8%	3.2%	54.9%	15.8%	8.6%	20.7%
Tudulinna (II)	45.8%	11.3%	1.8%	41.1%	10.7%	9.4%	0.4%	79.4%
Fjäckä (III)	20.1%	69.7%	6.5%	3.6%	2.0%	88.2%	5.7%	4.2%
Lower Nabala RS								
Paekna (II)	86.6%	3.1%	4.8%	5.5%	66.5%	4.6%	6.8%	22.1%
Mõntu (II)	63.0%	1.0%	4.0%	32.0%	2.6%	1.8%	3.7%	91.9%
Rakvere RS								
Rägavere (I)	71.1%	3.6%	6.9%	18.3%	30.7%	3.7%	17.0%	48.7%
Mossen (II)	42.1%	20.6%	6.0%	31.3%	35.0%	23.2%	6.3%	35.6%

Ostracods in the mixed facies were predominantly smooth-shelled (average relative abundance at least 55%), except for palaeocopes and binodicopes in the mixed facies of the Rakvere RS, which had mostly tuberculate ornamentation (49% on average).

The mud-supported facies was characterised by an increase in the percentage of ornamented ostracods, with the exception of the Rakvere RS, where the relative abundance of smooth-shelled palaeocopes and binodicopes did not change much compared to the mixed facies, and the change was considerably smaller than the change in higher-level taxonomic ratios (Fig. 8). Ostracods in the mud-supported facies had generally smooth or tuberculate carapaces, but in the Rakvere RS punctate specimens were also quite common (21% on average).

Within the mud-supported facies of the lower Nabala RS, palaeocope and binodicope carapace ornamentation changed dramatically. The more nearshore Paekna Fm

included mostly smooth-shelled specimens (67% on average), while the basinward Mõntu Fm included mostly tuberculate palaeocopes and binodicopes (92% on average).

Ostracods in the black shale facies had mostly punctate carapaces, comprising an average of 70% of the specimens. The average relative abundance of smooth-shelled specimens fell to only 20%. The sample size in the sections of the black shale facies was very small due to the limited distribution of these deposits, low core yield from deep boreholes (Fig. 6) and overall low faunal density. Therefore, this observation should be interpreted with caution.

PREVIOUS STUDIES

Several publications related to the subject of this study are reviewed and summarised herein (Tables 5–7). The

Table 5. Previous studies of the systematic composition of ostracods in relation to ecological parameters

Publication	Palaeocopa	Binodicopa	Podocopa
Becker 1971, 2000; Becker and Adamczak 1994;	nearshore, high-energy environment	N/A	low-energy environment
Vannier et al. 1989	carbonate-dominated environment	unstable environment, fine-grained detrital sediments	N/A
Gramm 1985	N/A	N/A	benthic nearshore environment
Copeland 1982	shallow shelf	N/A	deeper littoral
Current results	mud-supported facies	black shale facies	mixed and mud-supported facies

N/A – not applicable

Table 6. Previous studies of ostracod diversity in relation to ecological parameters

Publication	Low diversity	High diversity
Becker 1971, 2000; Becker and Adamczak 1994	low-energy environment	nearshore high-energy environment
Warshauer and Berdan 1982	carbonate substrate, high-energy environment	muddy substrate, low-energy environment
Siveter 1984	nearshore high-energy and deeper marine environment	mid-shelf to upper shelf slope
Williams and Siveter 1996	nearshore (depth 5 m or less)	offshore low-energy environment (depth approx. 80 m)
Tinn and Meidla 2001	offshore low-energy environment	nearshore high-energy environment (regressive event)
Bretsky and Lorenz 1970	unstable environments	stable environments
Brouwers 1988	upper bathyal	middle sublittoral
Van Harten 1986	nearshore	base of the photic zone or further offshore
Current results	fine-grained clastic substrate	carbonate substrate

Table 7. Previous studies of ostracod carapace morphology in relation to ecological parameters

Publication	Smaller carapace	Larger carapace	Elongated carapace	Shorter carapace	Ornamented carapace	Smooth carapace
Remane 1933; Elofson 1941	sand dwellers (endopsammon)	soft sediment	soft mud burrowers (endopelos)	N/A	higher sand content; unstable environment, epifauna	soft sediment; stable environment
Benson 1959, 1961, 1981	infauna in coarse sediment	N/A	soft sediment; infauna	coarse sediment	coarse sediment; more calcareous sediment; epifauna	soft sediment (fine-grained mud); infauna
Becker 1971, 2000; Becker and Adamczak 1994	N/A	N/A	N/A	N/A	high-energy nearshore environment	low-energy environment
Copeland 1982	shallow subtidal	deep subtidal	N/A	N/A	intertidal	littoral and deep sublittoral
Brouwers 1988	outer sublittoral to upper bathyal	inner sublittoral	middle sublittoral	outer sublittoral to upper bathyal	inner to middle sublittoral	middle sublittoral and upper bathyal
Current results	mixed facies	black shale facies	mixed facies	black shale facies	black shale facies	mixed facies

publications include studies of both fossil and recent ostracods as well as a general palaeoecological model for estimating diversity in marine environments.

Remane (1933) and Elofson (1941) studied recent ostracods and observed the highest number of smooth-shelled species in the deep muddy facies (depth ca 400 m according to Elofson 1941), with a decreasing abundance towards more unstable nearshore environments and higher sand content of the substratum. The shortest (with the lowest L/H ratio) and smallest forms were the sand dwellers, while the soft mud burrowers (endopelos) had the longest and thinnest carapaces. The average carapace was smaller in the coarse-grained sediment and larger in soft-bottom facies (measured by carapace length L).

Brouwers' (1988) analysis of subarctic Holocene ostracod assemblages revealed that large carapaces were prevalent in the inner sublittoral zone, elongated forms were typical of the middle sublittoral zone and the smallest and shortest carapaces were common in the outer littoral to upper bathyal zones. Elaborately ornamented carapaces were typical of the inner to middle sublittoral zones, while smooth carapaces were more common in the middle sublittoral to the upper bathyal zones. Besides the small and smooth-shelled species, the upper bathyal zone also included ostracods with large and ornamented carapaces. Both species diversity and abundance attained their maximum values in the middle sublittoral zone, from where they decreased in both the offshore and nearshore directions. The upper bathyal zone was characterised by the lowest diversity and abundance indices. Benson's (Benson 1959, 1961, 1981) studies of both recent and fossil ostracods give a similar result. He concluded that the smooth-shelled forms were predominant in fine-grained muds and the rougher, more ornate ostracods occurred mostly in coarser or more calcareous sediments. The carapaces of most epifaunal ostracods were strongly ornamented and durable, while the carapaces of infaunal ostracods were smooth and elliptical. He noted that the epifaunal species inhabiting coarse sediments tended to have reticular or spinous ornamentation, probably for strengthening the shell and protecting the animal from mechanical damage. The few infaunal species inhabiting coarse sediments tended to have small, short and usually robust carapaces. He also noted that species inhabiting deeper environments had mostly spinous carapaces, presumably due to higher predatory stress. Species with smooth carapaces usually inhabited environments with lower predatory and mechanical stress.

Becker (1971, 2000; Becker and Adamczak 1994) developed a palaeoecological model in which the distribution of Palaeozoic ostracods was controlled by hydrodynamical conditions. He distinguished between a diverse Eifelian ecotype, characteristic of high-energy environments, and the rather monotonous Thuringian ecotype,

characteristic of low-energy environments. The diverse Eifelian ecotype, restricted to nearshore areas, is characterised by heavily lobed and ornamented ostracods. Smooth-shelled, often spinous species – mostly podocopes – are typical of the Thuringian ecotype. The spines typical of the Thuringian forms are rather long and sporadic, and were interpreted by Becker as having the purpose of keeping the animal from sinking into the soft substrate. Becker's observations on diversity are similar to those of Tinn and Meidla (2001), who reported that a regressive marine event with an occurrence of high-energy sediments coincided with a rise in ostracod diversity. Becker and Adamczak (1994) conducted a study on Middle to Late Ordovician open-shelf ostracods, where the geological setting was analogous to the study herein. They reported the majority of the ostracods being small-sized, thin-shelled and mostly reticulate or spinous, and concluded that the fauna was characteristic of a low-energy environment (Thuringian ecotype).

Copeland (1982) analysed the morphology and taxonomy of Upper Ordovician ostracods in relation to bathymetry from soft-bottom shallow subtidal to deep subtidal shelf environments of Laurentia. The part of the succession interpreted as the shallowest marine contained an equal amount of small and large species. The abundance of small species increased with palaeodepth, while the abundance of large species decreased accordingly. In the shallowest and deepest marine parts, the species with smooth carapaces were slightly more common than the species with ornamented carapaces, while the latter was clearly dominant in the middle of the studied transect. All of the species in the shallowest sections were palaeocopes or binodicopes, whose abundance decreased with depth. The abundance of podocopes coincidentally increased until the ratio of palaeocopes and binodicopes to podocopes was the same in the deepest subtidal section.

Warshauer and Berdan (1982) conducted a quantitative analysis of Middle to Late Ordovician ostracods, where they distinguished two types of assemblages that differed in the preferred substrate and hydrodynamical conditions. Moderate to high-energy environments with a carbonate substrate were characterised by low to moderate diversity, and low-energy environments with a muddy substrate were characterised by high to moderate ostracod species diversity. Their findings conform to the general palaeoecological model of Bretsky and Lorenz (1970), where labile (and/or homogeneous) environments were characterised by lower diversity, and stable (and/or heterogeneous) environments accommodated high-diversity communities. Nearshore areas were interpreted to be labile environments and more offshore areas were generally considered as stable environments. Van Harten (1986) reported the highest diversity in recent ostracode assemblages at the base of the photic zone, from where it

decreases in both the nearshore and offshore directions. He noted that, due to post-mortem transport, the diversity maximum in most ostracod taphocoenoses occurs on the outer shelf or even beyond the shelf edge.

Vannier et al. (1989) divided the Ordovician ostracod fauna into two distinct groups: palaeocope or binodicope dominated associations. According to their results, palaeocopes were more abundant in carbonate-dominated environments and binodicopes preferred environments with unstable hydrodynamical conditions or environments with fine-grained clastic sediments. The ratio of palaeocope to binodicope genera was above 1 and below 1, respectively.

Gramm (1985) noted that the body and carapace plans of podocopes were perfectly adapted to the benthic nearshore environment.

According to Siveter (1984), the highest diversity among palaeocope-dominated ostracod faunas in the Silurian occurred in the mid-shelf to upper shelf slope, and both deeper marine and more nearshore high-energy environments were characterised by reduced diversity.

Williams and Siveter (1996) analysed Late Ordovician open-shelf ostracod associations and found that the subtidally deposited sediments (depth up to 80 m according to Longman 1982) were inhabited by palaeocopes and leiocopes, although some eridostracan, binodicope and podocope taxa were also present. Overall diversity was high with an increase towards offshore environments.

DISCUSSION

The aims of this study were to determine whether carapace ornamentation and dimensions were affected by palaeodepth and to describe taxonomic distribution and diversity of ostracod assemblages along a shelf-to-basin transect. Our results show systematic changes in all the characteristics in question (Fig. 13).

The general trend for taxonomic distribution was that the mixed facies was dominated by podocopes, the mud-supported facies mostly by palaeocopes, and the black shale facies by binodicopes. The mud-supported facies of the Rakvere RS and the basinmost section of the mud-supported facies of the Vormsi RS clustered between the sections of black shale facies and sections of shallower environments, suggesting their transitional nature. In the Rakvere RS both a decrease in podocopes and an increase in binodicopes occurred in a shallower facies, compared to the Vormsi RS. Such effects could be produced by selective transport of skeletal material either basinward during the Vormsi Age or shoreward during the Rakvere Age. However, a more likely explanation for this pattern is the well-known transgressive event during the Rakvere Age (Dronov et al. 2011), which entailed a shelfward

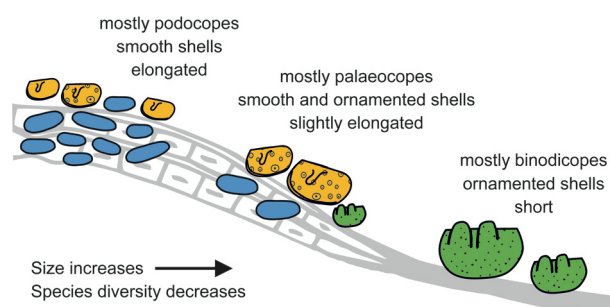


Fig. 13. General changes in ostracod assemblages along the facies gradient (see Fig. 2). Ostracods generally had smooth shells in the mixed facies (this can be seen in all major taxonomic groups – podocopes, palaeocopes and binodicopes), smooth and tuberculate shells in the mud-supported facies and (according to the preliminary data) punctate shells in the black shale facies.

migration of the fauna. The effects could be further amplified by a general faunal rearrangement during the Rakvere Age, as documented in an earlier publication (Meidla 1996). The lack of a clear trend in the distribution of palaeocopes and podocopes in the lower Nabala RS could be expected as the facies gradient was rather weak. The absence of binodicopes in these sections indirectly supports the assumption that they inhabited the deepest parts of the carbonate shelf.

According to Becker (1971, 2000; Becker and Adamczak 1994), Devonian nearshore high-energy environments were dominated by palaeocopes (Eiffelian ecotype) and a low-energy environment by podocopes (Thuringian ecotype). He also described a mixed ecotype of both Eiffelian and Thuringian ostracods. When trying to apply the same criteria, the ostracod association of the Estonian Shelf seems to belong to the mixed ecotype, but the higher prevalence of podocopes in the shoremost mixed facies and the abundance of binodicopes in the back shale facies do not seem to fully agree with the pattern described by Becker (1971, 2000; Becker and Adamczak 1994).

Our results are mostly in agreement with the observations of Vannier et al. (1989), who noted the high abundance of palaeocope species on Ordovician carbonate platforms but did not refer to the abundance of podocopes. Their statement that binodicope-dominated associations are characteristic of either fine-grained clastic sediments or environments with unstable hydrodynamical conditions is in agreement with our results documenting the maximum abundance of binodicopes in offshore clay-rich deposits (Fig. 7).

Our results are also in agreement with Gramm (1985), who stated that podocopes inhabited the (benthic) nearshore environment. Copeland (1982) stated that palaeocopes inhabited shallow shelf areas and podocopes were

confined to deeper littoral settings. Both of his conclusions are in good agreement with our results, considering that the Late Ordovician sedimentary deposits of the shallowest shelf zone have been eroded on the Estonian Shelf.

Species diversity decreased in the offshore direction in all the analysed stratigraphic intervals. This result is in accordance with Siveter (1984), Williams and Siveter (1996) and Brouwers (1988), who stated that the highest diversity occurred in the mid-shelf to upper shelf slope (or middle sublittoral) and decreased basinward (as well as shoreward). According to Van Harten (1986), diversity among fossil ostracods increased from the shoreline towards the base of the photic zone and decreased subsequently in the offshore direction. In the case of post-mortem transport, the highest diversity should generally occur on the outer shelf or even further offshore. In our study, species diversity peaked in the mixed facies, which indicates that the down-slope transport of ostracod carapaces must have been minimal. In the Vormsi RS, the percentage of calcareous algae among skeletal fragments drops from 50% in the mixed facies to 5% in the black shale facies (Põlma 1982). This suggests that the base of the photic zone in the Vormsi RS was located somewhere in the mud-supported facies, not in the mixed facies, where diversity was highest. Overall, our results are mostly in agreement with the findings of Van Harten (1986). The results of Becker (1971, 2000; Becker and Adamczak 1994), Tinn and Meidla (2001), Warshauer and Berdan (1982) and Bretsky and Lorenz (1970) are not fully applicable to the current study, considering the erosion of nearshore high-energy sedimentary deposits on the Estonian Shelf.

Our results show a clear trend of carapace shortening in the offshore direction. The results on carapace size were more ambiguous, but as a general rule, it seemed to increase in the offshore direction. Higher-level taxonomic changes do not seem to be the driving reason for changes in carapace size, as the increase in palaeocopes coincided with decreasing size in the Vormsi RS and increasing size in the Rakvere RS. Additionally, the emergence of binodicoles in the basinward sections coincided with larger carapace size in the Vormsi RS and smaller carapace size in the Rakvere RS. The binodicole-rich mud-supported facies of the Rakvere RS was represented by only two sections, therefore further investigation is needed in this regard.

Our results are in agreement with the findings of Remane (1933), Elofson (1941) and Copeland (1982), where the average carapace size increased with decreasing grain size or in the offshore direction. Our results are not in agreement with the findings of Brouwers (1988), who reported that carapace size decreases with depth up to the upper bathyal zone, where both small and large species are present. He stated that elongated carapaces are

prevalent in the middle sublittoral, while short carapaces are the most common in the outer sublittoral to upper bathyal zones, and this conforms to our findings. According to Remane (1933), Elofson (1941), Benson (1959, 1961, 1981) and Brouwers (1988), the ostracods with elongated carapaces generally have an endopelic mode of life (soft mud burrowers), and our results show the same tendency since the facies characterised by high prevalence of podocopes (Fig. 8, Table 2) – the assumed infaunal taxa – is also characterised by a higher average carapace L/H ratio.

Our study found that the abundance of ornamented valves increased in the offshore direction, with the exception of palaeocopes and binodicole shells in the Rakvere RS.

Such a discrepancy could possibly be related to the small particle size in the cryptocrystalline micritic lime muds of the Rägavere Fm, which could make the substrate properties more similar to those of the clay-rich sediments of the Mossen Fm. This would be in agreement with the claim that carapace ornamentation is greatly affected by the particle size of the substrate. Additionally, our study found that the mud-supported facies was characterised by smooth and tuberculate carapaces and the black shale facies by punctate carapaces. The relatively high percentage of punctate shells in the mud-supported facies of the Rakvere RS suggests its transitional position between the shallower mud-supported facies and black shale facies. The higher-level taxonomic distribution indicated the same. The relative abundance of smooth-shelled specimens in the mud-supported facies of the lower Nabala RS was considerably higher compared to the Rakvere and Vormsi regional stages. In addition to that, the ratio of palaeocope and binodicole ornamentation types underwent a dramatic change in the lower Nabala RS. The lower Nabala RS, although with minimal facies gradation and no apparent change in higher-level taxonomic distribution, exhibited distinct trends in the offshore direction: diversity declined significantly and the ornamentation of palaeocopes and binodicoles changed from smooth to tuberculate. A change of this magnitude is surprising, considering that 1) both formations are part of the mud-supported facies; 2) the change was much more significant for palaeocopids compared to the change for all ostracods. This peculiarity, together with an elevated concentration of phosphorus and the presence of glauconite in the Mõntu Fm, could potentially be related to an environmental disturbance, the suggested Nabala upwelling event (Kiipli et al. 2010; Hints et al. 2011).

According to the studies of Remane (1933), Elofson (1941) and Benson (1959, 1961, 1981), infaunal species inhabiting soft sediment tend to have smooth carapaces, while epifaunal species or species living in a more calcareous environment tend to have ornamented carapaces. Our results support these hypotheses since the mixed

facies was characterised by smooth-shelled podocopes presumably having an infaunal mode of life (Gramm 1985), whereas the black shale facies was characterised by (mostly) rough-shelled binodicopes, who were most likely benthic crawlers or bottom-swimmers (Schallreuter and Siveter 1985; Vannier et al. 1989). The reason for a higher relative abundance of smooth-shelled palaeocopes in the mixed facies remains unexplained, as their body plan did not support an infaunal way of life. According to Becker (1971, 2000; Becker and Adamczak 1994) and Copeland (1982), ostracods living in a nearshore high-energy or intertidal environment had mostly ornamented carapaces, and ostracods in a low-energy or littoral to deep sub-littoral environments had mostly smooth carapaces. Our results are generally in agreement with these hypotheses if we consider the lack of nearshore high-energy sediments in the studied core sections. However, our data on the prevalence of ornamented ostracods in the deepest facies do not conform to the findings of Becker and Copeland. According to Brouwers (1988), the inner and outer sublittoral zones are characterised by ornamented carapaces and the middle sublittoral and upper bathyal zones are characterised by both ornamented and smooth carapaces. Our results would generally be in agreement with these findings if we assume that our transect begins in the middle sublittoral (ornamented and smooth carapaces) and ends in the outer sublittoral (mostly ornamented carapaces).

CONCLUSIONS

The basic assumption among ostracod researchers is that the morphology of the carapace is adaptively responsive, and assuming that most Early Palaeozoic ostracods had a benthic mode of life, at least some of their morphological features should have been an adaptation to the properties of the surrounding sediment. The change in carapace morphology in relation to various environmental factors has been discussed by previous authors, but the conclusions were not always consistent with the previous results.

1. Comparing ostracod carapaces along the facies profile, we found that the mixed facies of the carbonate shelf is characterised by a clear majority of podocopes, the mud-supported facies by podocopes together with palaeocopes, and the black shale facies by mostly binodicopes.
2. The diversity of ostracod communities decreases basinward from the mixed facies to the black shale facies. Interestingly, the decline in diversity is more prominent in the lower Nabala RS than in the Rakvere RS, although the facies differentiation is higher in the latter.
3. The average carapace tends to be shorter, and the size tends to decrease with increasing marine depth, although some smaller-scale fluctuations occur within the studied transect. The podocope-rich mixed facies

is characterised by a more elongated carapace shape. The reason behind the basinward trend for enlargement of carapaces needs further investigation.

4. The abundance of smooth-shelled ostracods decreases basinward while the number of ornamented ostracods increases simultaneously. The same trend characterises both the entire ostracod fauna and also palaeocopes and binodicopes specifically, suggesting that this feature was environmentally controlled. The mixed facies includes primarily smooth-shelled ostracods and most of the ostracods in the mud-supported facies have tuberculate carapaces. Ostracods in the black shale facies seem to have mostly punctate valves, but the material was too limited to make any definitive judgments.
5. The difference in the ratios of ornamentation types between the mixed facies and the mud-supported facies in the Rakvere RS is considerably smaller than the difference in higher-level taxonomic ratios. This could possibly be the result of the similarly small particle size of the primary sediment of both the very fine-grained micritic lime mudstones of the Rägavere Fm and the clay-rich marls of the Mossen Fm.
6. Taxonomic distribution together with the distribution of valve ornamentation in the mud-supported facies of the Rakvere RS (Mossen Fm) indicate that it contained a transitional ostracod assemblage between the shallower mud-supported facies and the black shale facies.

The described trends of morphological features along the shelf-to-basin transect apply to the Katian faunas of the Baltic Palaeobasin, but do not completely agree with the trends documented in younger strata. Further research is required to gain a better understanding of the distribution patterns of the Early Palaeozoic ostracod faunas and to understand whether they truly differ from the patterns of younger periods.

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Supplementary online data

Specimen counts along with morphological and taxonomic data are available at <https://doi.org/10.23679/514>

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Muutused Hilis-Ordoviitsiumi ostrakoodide morfoloogias Balti paleobasseini fatsiaalsel gradiendil

Stefi Guitor ja Tõnu Meidla

Publikatsioon põhineb ulatuslikul Eesti Hilis-Ordoviitsiumi ostrakoodide kvantitatiivsel levikuandmestikul. Analüüsitakse trende ostrakoodide taksonoomias ja liigilises mitmekesisuses ning koja morfoloogias Balti paleobasseini karbonaatselt šelfialt basseini sügavamasse ossa ulatuval profiilil. Töö põhineb 14 puursüdamikü andmetel kolmest stratigraafilisest üksusest: Rakvere, Nabala ning Vormsi lademetest. Kokku analüüsitakse ostrakoode 35 puursüdamiku intervallis. Valitud puursüdamikest moodustub põhja-lõunasuunaline läbilõige (mõningase ida-läänesuunalise variatsiooniga) Eesti karbonaatselt šelfilt Balti sünekliisi settevööndisse. Olenevalt stratigraafilisest tasemest ulatub läbilõige maksimaalselt läbi kolme fatsiaalse vööndi: karbonaatne faatsies, savikas faatsies ning musta kilda faatsies. Fatsiaalsete vööndite ja kihistute lateraalne levik loetakse käesolevas töös kokkulangevaks. Kvantitatiivsest analüüsist selgub, et teralis-mudalise põhimassiga faatsiesest musta kilda faatsieseni muutuvad ostrakoodide kujud suuremaks ja ümaramaks, siledakojaliste ostrakoodide osakaal väheneb ning ornamenteeritud ostrakoodide osakaal suureneb. Teralis-mudalise põhimassiga faatsieses on enimlevinud siledakojalised ostrakoodid ning savikas faatsieses on sagedaseimad noduleeritud ornamentatsiooniga ostrakoodid. Teralis-mudalise põhimassiga faatsiesele on iseloomulik podokopiidide ülekaal, savikale faatsiesele aga podokopiidide ja paleokopiinide kooslus ning ostrakoodid musta kilda faatsieses on valdavalt binodikopiinid. Ostrakoodide liigiline mitmekesisus langeb basseini sügavama osa suunas.