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Arenig (Middle Ordovician) ostracods from Baltoscandia: Fauna, assemblages and biofacies

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Abstract

The Arenig ostracod fauna of Baltoscandia is the oldest known and amongst the most thoroughly studied ostracod faunas in the world. The fauna is dominated by eridostracans and palaeocopes, and comprises altogether about fifty species from seven suborders. The ten most abundant ostracod species make up 90% of the total Arenig fauna. Overall ostracod diversity estimates in the Arenig of the Baltoscandian Palaeobasin are low, but show gradual increase in diversity at younger horizons. Low diversity may be due to unfavourable climate conditions in the Baltoscandian Palaeocontinent during the earlier Arenig and may also be due to the early stage of evolution of ostracod faunas (i.e. pre their main diversification during the Llanvirn). Thirteen facies related Arenig ostracod assemblages are distinguished in the Baltoscandian Palaeobasin. In early- and mid-Volkhov time, the assemblages show almost basinwide distribution suggesting many ostracod species were environmental generalists. Major distinctions between different ostracod biofacies zones can be seen from the late Volkhov onwards, when the differentiation of ostracod biofacies in the Palaeobasin marks the onset of major depth differences. Ostracod assemblage-based reconstruction of sea-level changes in the studied area agrees well with the sequence stratigraphic interpretation of the succession and with a sea level curve determined on the basis of sedimentological data.

Keywords: Ordovician; Arenig; Baltoscandia; Ostracods; Palaeoecology; Biofacies

1. Introduction

Ostracods are an important component of fossil assemblages in the Arenig of Baltoscandia, being also one of the oldest thoroughly studied ostracod faunas in the world. The extensive data of the Arenig ostracods of Baltoscandia covers their taxonomy and stratigraphy at different outcrops and sections (Öpik, 1935, 1939; Hessland, 1949; Henningsmoen, 1953a,b, 1954; Sarv, 1959, 1960, 1963; Schallreuter, 1983, 1988, 1989, 1993, Gailīte, 1982a; Sidaravičienė, 1992; Vannier et al., 1989; Põldvere et al., 1998; Melnikova, 1999). The major objective of the present paper is to give a comprehensive taxonomic overview of the early ostracod fauna and its diversity through the Arenig of Baltoscandia.

Fossil ostracods, like modern species, were probably highly sensitive to environmental conditions and are thus increasingly used for palaeoecologic studies all over the world (Boomer et al., 2003). Systematic sampling for ostracods in different parts of the Baltoscandian area during recent years has lead to several papers dealing with ostracod facies analysis (Meidla et al., 1998; Tinn and Meidla, 1999, 2001). However, these papers have

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analysed ostracod faunas of single localities only, with some references to adjacent regions. The second objective of this paper is to define ostracod assemblages by statistical methods and to demonstrate palaeoecological relationships between Arenig ostracod taxa. Numerous studies have shown that the distribution of benthic ostracod assemblages can be controlled by several environmental and sedimentological parameters, like water depth, substrate, salinity, temperature, etc. (Siveter, 1984). Detailed data on temporal and geographical distribution of ostracod assemblages are used for defining ostracod biofacies in the Arenig Baltoscandian Palaeobasin by presence–absence data and cluster analysis.

2. Geological setting

Palaeomagnetic data and palaeontological evidence (Scotese and McKerrow, 1990; Torsvik et al., 1991; Torsvik, 1998; Cocks and Torsvik, 2005) suggest that the Baltica palaeocontinent occupied temperate southern palaeolatitudes (about 45–60°) during the Early Ordovician. The Early and Middle Ordovician sediments of Baltoscandia were deposited in a sediment-starved epicontinental sea with extremely flat sea bottom topography, on a gently tilted ramp (Nestor and Einasto, 1997). Low-rate deposition of carbonates replaced the siliciclastic-dominated sedimentation of the Baltoscandian epicontinental sea during latest Early Ordovician time. The Middle Ordovician skeletal debris-rich carbonates with numerous discontinuity surfaces are lacking in evidence for tropical conditions (e.g. pelletal and oolitic deposits, coral–stromatoporoid reefs etc.) and have been interpreted as cool-water sediments (Jaanusson, 1973; Lindström, 1984; Nestor and Einasto, 1997).

The Ordovician strata of the Palaeobasin developed in an array of distinct facies belts, characterized by specific sedimentological and palaeontological features (Männil, 1966; Jaanusson, 1973, 1976, 1982) and maintaining a fairly constant relative position within the depositional area through time. Jaanusson (1976) termed this type of composite facies unit “confacies belt” and suggested that they reflect a broad ecologic zonation, controlled by environmental factors that also influenced depositional conditions (Jaanusson, 1982). The confacies pattern apparently reflects a general depth zonation of the Palaeobasin (Männil and Meidla, 1994). The North Estonian Confacies Belt (Fig. 1) is regarded as the marginal area of the epicontinental sea, where micritic skeletal calcarenites, sometimes containing silt and goethite ooids, abundant glauconite grains and numerous impregnated hardgrounds, indicate a middle to inner ramp zone near the fair-weather wave base (Männil, 1966; Nestor and Einasto, 1997; Meidla et al., 1998).

Opinions vary with respect to the Central Baltoscandian Confacies Belt, but it is generally thought to represent outer ramp or basinal facies near storm wave base. However, the red-coloured or variegated argillaceous limestones and marls of this unit are considered to be of shallow-water origin by Jaanusson (1982) and Nielsen (1995), who attribute the numerous unconformities to either emergence of the basin due to repeated sea level fluctuations or to submarine non-deposition. In contrast, Lindström (1963, 1971, 1979, 1984) has attributed the extremely low sedimentation rate to deep sea conditions,

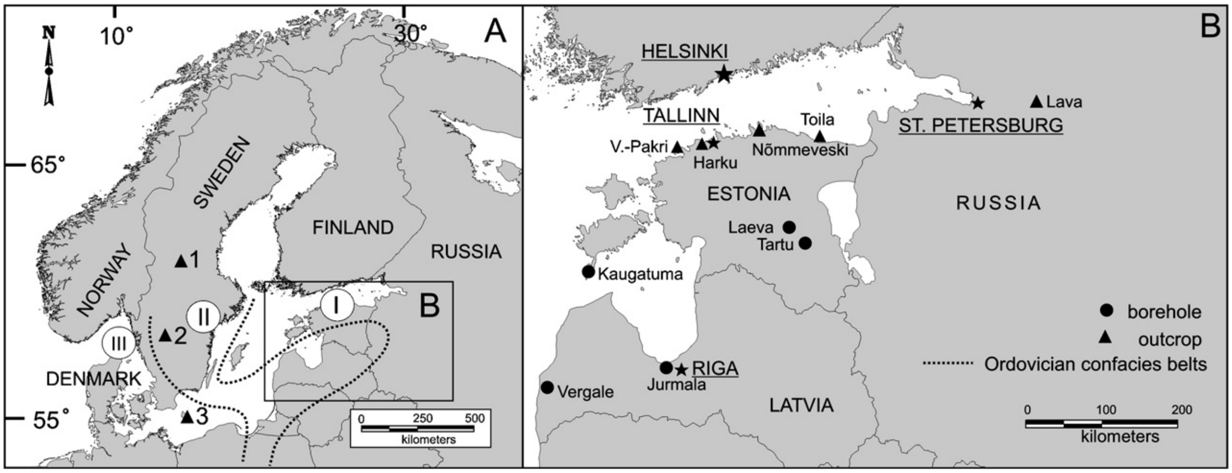


Fig. 1. Schematic map of the study area. Roman numerals mark Ordovician confacies belts (after Jaanusson, 1976): I — North Estonian Confacies Belt; II — Central Baltoscandian Confacies Belt; III — Scanian Confacies Belt. Arabic numerals mark studied sections: 1 — Siljan composite section (Hessland, 1949); 2 — Hällekis; 3 — Skelbro.

where sedimentation was pelagic or neritic and all breaks were submarine. The deposits of the outer ramp were 2 to 10 times as thick as those in the coeval inner ramp (Nestor and Einasto, 1997). A previous ostracod study demonstrated the highest diversity of mid-Arenigian benthic faunal assemblages in Västergötland, Sweden, in sediments which suggest a moderately deep shelf basin, just below the lower boundary of the photic zone (Tinn and Meidla, 2001).

3. Stratigraphy

The stratigraphic framework of the Tremadoc and Arenig sediments of the Baltoscandian Palaeobasin used for the present study is presented in Fig. 2. The oldest ostracod material of Baltoscandia comes from the basal beds of the Bjørkåsholmen Formation (of late Varangu age) in the Oslo Region, Norway (Henningsmoen, 1954; Ebbestad, 1999). In Estonia and Latvia, the corresponding part of the sequence is largely in hiatus. Its only equivalent is the terrigenous Varangu Formation in northern and central Estonia, which does not contain ostracods. Ostracods are also typically absent from the overlying sand- and siltstones of the Leetse Formation, although the calcareous interbeds in the upper part of the Formation require further investigation. The beginning of predominantly carbonate sedimentation in the area during the latest Billingen also marks the beginning of a continuous ostracod faunal record. The reason for absence of ostracods from the earlier sediments is not clear yet, but the generally poor record of carbonate fossils in these layers may be taphonomic (Tinn, 2002).

A remarkable sedimentary structure, pervading the whole area, is the discontinuity surface with "amphora-like borings", known as "*Püstakkiht*" in Estonian (Orviku, 1960). This marks the lower boundary of the Volkhov Stage in the Baltic–Ladoga Klint area. This discontinuity surface can be traced over vast areas in Baltoscandia — from Öland in the west to Russia in the east and from Dalarna (Sweden) in the north to Poland in the south (Ekdale and Bromley, 2001). It occurs in the nearshore areas of the shelf to outer ramp settings.

The Volkhov Stage forms a lithologically distinctive unit in the sections of the Baltic–Ladoga Klint. Biostratigraphically, the Volkhov Stage is defined by the *Megistaspis polyphemus*, *M. simon* and *M. limbata* trilobite biozones (Männil, 1966; Männil and Meidla, 1994), that roughly correspond to the currently used Saka, Vääna and Langevoja substages. Analogously, the Kunda Stage has been subdivided into the *Asaphus expansus*, *A. raniceps* and *Megistaspis gigas*–*M. obtusicauda* trilobite biozones, which are thought to correspond to the Hunderum, Valaste and Aluoja substages. In northern Estonia, the Hunderum Substage and a considerable part of the Langevoja Substage are missing (Fig. 2) (Lamansky, 1905; Orviku, 1960; Männil and Meidla, 1994). In Latvia, the boundary between the Zebre and Kriukai formations was correlated with the lower boundary of the Volkhov Stage (Gailīte, 1982b). A complete overview on stratigraphy of the Volkhov and Kunda stages in Estonia is given by Meidla (1997).

In Västergötland, Sweden, the sequence of the Volkhov and Kunda stages is represented by a macroscopically uniform, red-coloured wackestone–packstone succession, referred to as the Lanna and Holen limestones. This succession is underlain by the Tøyen Shale that in some localities of Sweden is partly equivalent to the lowermost part of the Lanna Limestone (Jaanusson, 1982). A light grey packstone layer at the base of the Holen Limestone, known as Täljsten, forms a marker bed with its thickness varying from several decimetres to two metres in Västergötland. Jaanusson (1982) and Zhang (1998) assigned the Täljsten layer to the lowermost part of the Kunda Stage and this is usually correlated with the Šakyna Formation in the Central East Baltic (Männil and Meidla, 1994). According to Meidla (in Põldvere et al., 1998) the lower boundary of the Täljsten unit lies above this level. Within the North Estonian Confacies Belt, the equivalent of the Täljsten unit passes into the Sillaoru Formation (Dronov et al., 2000).

The dark, thermally altered Komstad Limestone represents the only major limestone bed in the shale-dominated Ordovician succession of Bornholm Island. The rock succession here yields trilobites indicative of the *Megistaspis polyphemus*, *M. simon*, *M. limbata* and *Asaphus expansus* biozones (Poulsen, 1966; Nielsen, 1995) and thus roughly corresponds to the whole Volkhov Stage and the Hunderum Substage of the Kunda Stage. The lower boundary of the Komstad Limestone represents a major unconformity above the Alum Shale Formation (of Varangu, Hunneberg and Billingen age). Another major unconformity is developed over the top of the Komstad Limestone, marking the base of the *Dicellograptus* Shale (and assignable to the middle and upper Kunda) (Nielsen, 1995).

4. Material

The thirteen sections (8 outcrops and 5 core sections) investigated are: Skelbro, Hällekis, Väike-Pakri, Harku, Nõmmeveski, Toila, Saka and Lava outcrops, Jurmala R-1, Tartu-453, Laeva-8, Vergale-50, and Kaugatuma-509 core sections (Figs. 1 and 3). Composite data from outcrops of the Siljan area (Hessland, 1949) were also

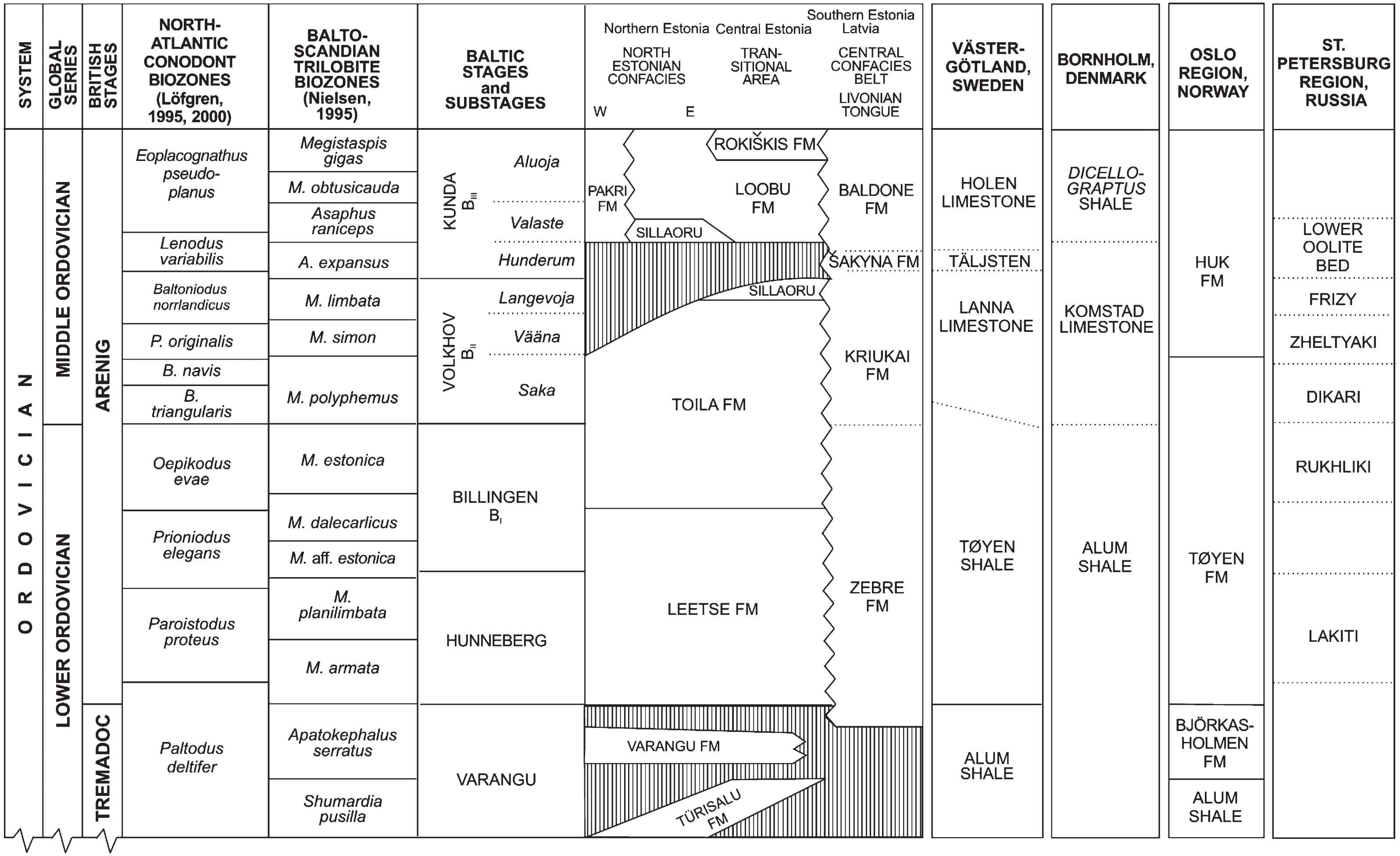


Fig. 2. Stratigraphic framework for the Upper Tremadoc and Arenig strata of the Baltoscandian Palaeobasin, based on the correlation log (Männil and Meidla, 1994) with details and updated information from Meidla (1997) and Heinsalu and Viira (1997) correlations with North-Atlantic conodont biozones (from Löfgren, 1995, 2000) and Baltoscandian trilobite biozones (Nielsen, 1995). Data for Västergötland from Jaanusson (1982) and Dronov et al. (2000), Bornholm from Nielsen (1995); Oslo region from Ebbestad (1999); St. Petersburg region from Tolmacheva (2001).

incorporated in this study. The relevant data and references about the studied sections are presented in Table 1. The lithology and stratigraphy of the studied sections, as well as the sample positions are presented in Figs. 2 and 3.

286 samples were studied in total, the number of samples per rock section varies from 3 in the Skelbro section to 49 in the Lava section. Due to limited thicknesses of fossil-bearing layers, the least sampled (14 samples) is the Billingen Stage. The Volkhov Stage is represented by some 176 samples and the Kunda Stage by 83 samples. The number of specimens per sample varies from one to 1620, the total number of specimens included in the analysis is 39,300.

Most carbonate samples were processed with standard physical disintegration methods, which are comparable to natural weathering. The crushed limestone samples, weighing about 0.5 to 1.5 kg, were disintegrated with sodium hyposulphite. To obtain a satisfactory degree of destruction, heating and cooling cycles were repeated up to 10 times for clay-rich marls, and more than 50 times for hard thermally-altered limestones. The washed and dried material was sieved into four fractions (>2 mm, 0.5–2 mm, 0.25–0.5 mm, <0.25 mm). Ostracods were picked from the two intermediate fractions using a stereoscopic binocular microscope with the magnification at 16–25×. Ostracod material from the clay layers in the Lava and Nõmmeveski sections was obtained by washing through 0.25 mm sieves.

The ostracod material studied is of variable preservation (Table 1). Generally, in the western and southern part of the study area, the calcitic carapaces exhibit good preservation. In several Estonian sections the carbonate fauna of the lower part of the Volkhov Stage has been damaged or destroyed by secondary dolomitization. Occasionally, dolomitization has affected ostracod carapaces also in the Billingen Stage of the Lava section.

Multivariate statistical analyses were performed with statistical software packages STATISTICA 6.1 and PAST, the latter being a special software package designed for palaeontological data analysis (Hammer et al., 2001). The total number of species included in the analysis is 49, representing 36 genera and 7 suborders. The number of species per sample varies from one to 15 in samples with rich and diverse ostracod faunas. For statistical purposes, the data matrix was standardized by converting the counts of specimens in samples to a percentage of the entire sample. Three measures of species diversity were calculated: (1) the Shannon–Wiener index, which measures the amount of uncertainty in the sample (Etter, 1999), (2) the reciprocal diversity index of Simpson, which is a measure of the probability that two organisms picked at random belong to different species (Etter, 1999), and (3) species richness, which is the total number of different species in each sample. The properties of the similarity coefficients have been discussed by several authors (Shi, 1993; Etter, 1999). Etter (1999) has emphasized that the Shannon–Wiener index is the most sensitive to changes in rare

Table 1
Basic data and references for the studied sections

Section	Country	Type	Stratigraphy	No. of samples (B_{I}–B_{III})	Height/depth interval (m)	Preservation of ostracods	References
Hällekis	Sweden	Quarry	B_{II}, B_{III}	16 (0-7-9)	31 m	Good	Tinn and Meidla, 2001
Harku	Estonia	Trench section	B_{I}, B_{II}, B_{III}	32 (1-30-1)	3 m	Good	Meidla et al., 1998; Tinn and Meidla, 2003
Jurmala	Latvia	Drillcore	B_{I},B_{II}, B_{III}	18 (1-14-3)	48.3 m (875.7...924.0)	Good	–
Kaugatuma	Estonia	Drillcore	B_{I}, B_{II}, B_{III}	12 (1-9-2)	3.2 m (462.1...465.8)	Poor...good	–
Laeva-8	Estonia	Drillcore	B_{III}	6 (0-0-6)	1.4 m (298...299.4)	Good	–
Lava	Russia	Natural cliff	B_{I}, B_{II}, B_{III}	49 (7-41-1)	8 m	Good	Tolmacheva and Fedorov, 2001
Nõmmeveski	Estonia	Natural cliff	B_{I}, B_{II}, B_{III}	28 (1-23-3)	3.1 m	Good	–
Saka	Estonia	Trench section	B_{I}, B_{II}, B_{III}	24 (0-23-1)	3 m	Good	Meidla et al., 1998
Siljan	Sweden	Composite	B_{III}	46 (0-0-46)	4 m	Poor....good	Hessland, 1949
Skelbro	Denmark	Quarry	B_{II}, B_{III}	3 (0-2-1)	4 m	Poor	Tinn and Meidla, 1999
Tartu	Estonia	Drillcore	B_{II}, B_{III}	12 (0-5-7)	12.2 m (369.6...381.8)	Poor	Põldvere et al., 1998
Toila	Estonia	Natural cliff	B_{I}, B_{II}	17 (1-16-0)	2.7 m	Good	Dronov et al., 2000
Väike–Pakri	Estonia	Natural cliff	B_{I}, B_{II}, B_{III}	23 (1-21-1)	1.2 m	Good	Dronov et al., 2000
Vergale-50	Estonia	Drillcore	B_{II}, B_{III}	19 (0-9-10)	12 m (952....964.0)	Good	–

B_{I} — Billingen Stage, B_{II} — Volkhov Stage, B_{III} — Kunda Stage.

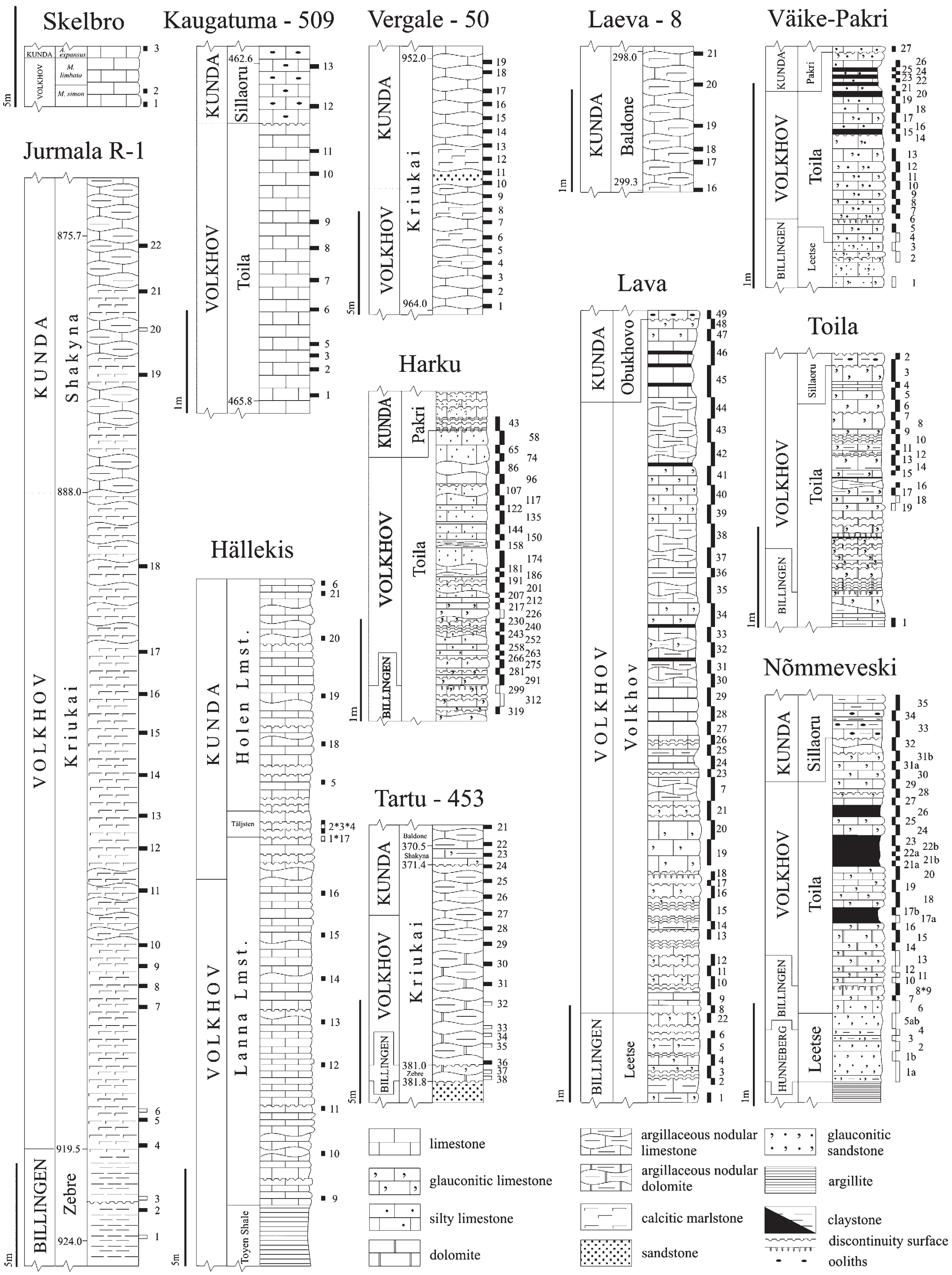


Fig. 3. Stratigraphy and lithology of the studied sections. Rectangles indicate ostracod samples, white rectangles indicate empty samples.

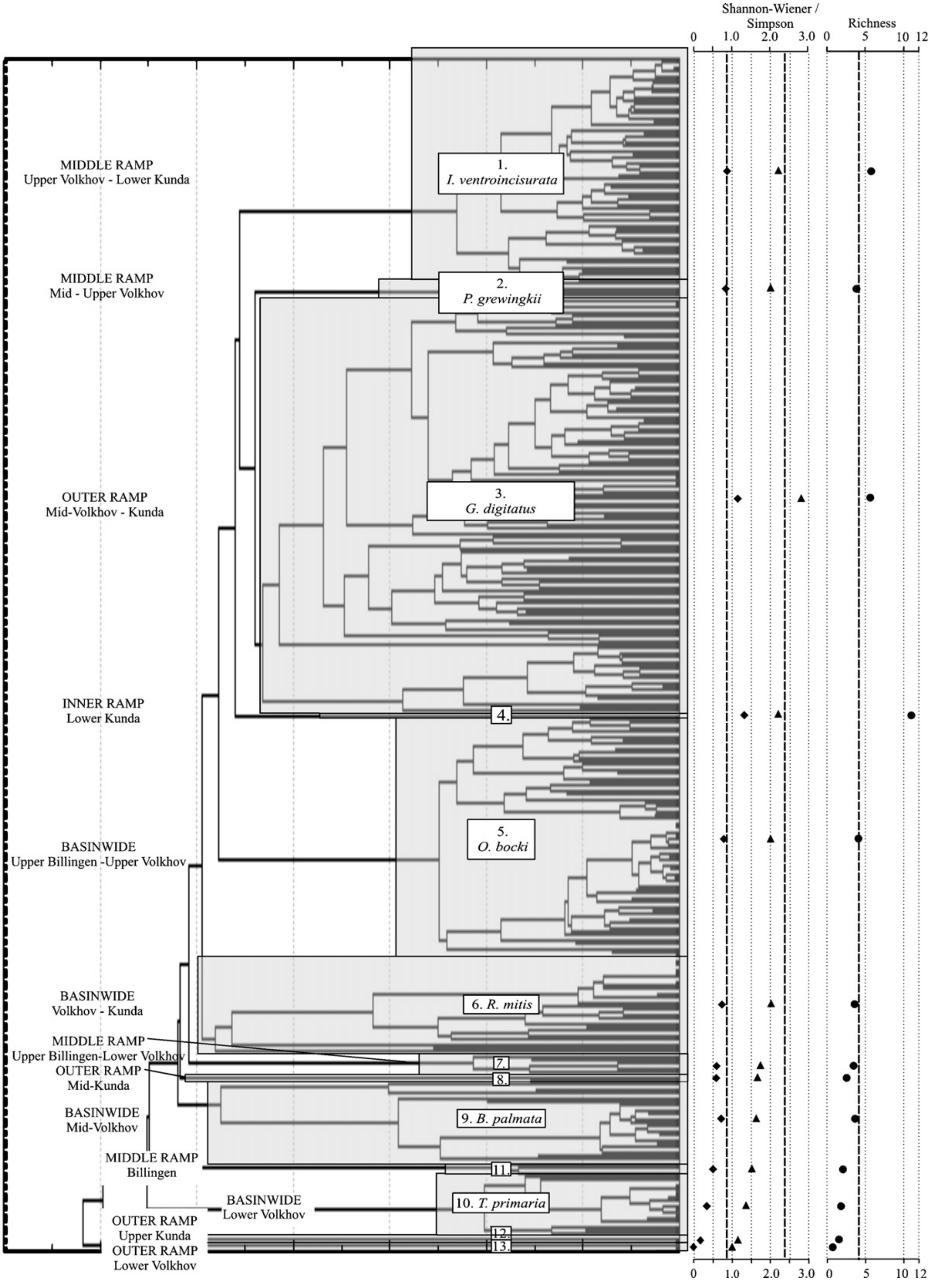


Fig. 4. Tree diagram for 2286 cases, clustered into 13 ostracod assemblages. Unweighted pair-group average, Euclidean distances. 4 — *O. variabilis* assemblage. 7 — *T.*? *viridis* assemblage. 8 — *P. procerus* assemblage. 11 — *U. tolmachovae* assemblage, MIDDLE RAMP, Billingen. 13 — ? *L. spinosa* assemblage, OUTER RAMP, Lower Volkhov. Strong dashed lines indicate Arenig average values for Shannon–Wiener and Simpson's indices and richness.

species, whereas Simpson's index is more sensitive to changes in common species. For comparison, the average of the total count is given for each measure.

The actual number of species recorded in the Arenig of Baltoscandia is larger than used in the present analysis (Meidla et al., 1998; Tinn and Meidla, 2002; Tinn, 2002). Some species were eliminated because of their scant record. However, in some levels/localities the ostracod assemblages were relatively poor but of rather specific composition. To keep these specific localities included in the data matrix, several of such rare taxa ("*Silenis*" sp., *Microcheilinella* sp., *U. tolmachovae*, *H. proximus*, *O. variabilis*) are still included. The problem of selective treatment of outliers – localities with very few taxa or taxa with very few occurrences – has been specifically discussed by Shi (1993).

In order to group species with similar spatial and temporal distribution patterns, cluster analysis using quantitative data was performed. Euclidean distances were clustered with unweighted pair-group average linkage. The analysis resulted in 13 clusters (Fig. 4), treated here as ostracod assemblages. For estimating the species' mutual relationships, Pearson's correlation matrix (Table 2) was computed and Principal Component Analysis was performed.

Ostracod assemblages were defined as consisting of: (1) one dominant species, showing strong prevalence in the assemblage (Fig. 5); (2) additional common species, frequent in the assemblage and closely related in the Pearson's correlation matrix (Table 2); (3) occasional species, with significant positive values in the correlation matrix but present in occasional samples only.

A specific problem concerns *Conchoprimitia socialis*. The species is widespread, occurring through the Arenig all over the study area and has been documented in 83% of the studied samples (Fig. 6A). In comparison with the other Arenig ostracods, the carapace of *C. socialis* is thick and several times larger than that of the other species. This could give *C. socialis* a higher fossilization (preservation) potential than the rest of the studied species with a small and thin carapace, artificially distorting the general picture of ostracod assemblages. Several samples contained specimens of *C. socialis* only, while other ostracod species were either unidentifiable or destroyed by recrystallization. The initial analysis (not presented here) of the dataset showed about half of the studied samples belonging to the *C. socialis* assemblage. It is clear that *C. socialis* was an important component of ostracod assemblages, but its considerably higher preservation potential in comparison with the rest of the ostracod fauna would lead to inadequate results in statistical analysis (some other attempts of analysis resulted in "biofacies" distinguished mainly according to the concentration of *C. socialis*). In order to get a more objective picture, *C. socialis* was omitted from the analytical data matrix, but data about the concentration of this species in samples of a particular biofacies are presented below (compare also Shi, 1993).

Specific problems related to *C. socialis* suggest that the composition of the ostracod assemblages may be, to some extent, influenced by the changing duration of the laboratory treatment (different number of heating cycles due to different rock properties). This could result in a confused picture if the assemblages were distinguished mainly according to different ratios of a small number of dominant species. We still expect the treatment effects to be minor because of the fact that the assemblages are mostly also taxonomically distinct (being characterized by distinct sets of dominant species). However, we have to admit that testing this assumption experimentally would be extremely difficult, because of the similar chemical composition of the fossils and rock matrix, which makes more reliable quantitative methods unusable.

5. Arenig ostracod fauna

The Arenig ostracod fauna (Fig. 6) is dominated by an eridostracan species *Conchoprimitia socialis*, that was present in 83% of studied samples and constitutes about 30% of the total number of specimens. This species is tentatively considered to contain all the variety of Arenigian species of *Conchoprimitia* distinguished in different parts of Baltoscandia by several authors during more than a century (results of a special study are submitted). The majority of other abundant species (Fig. 6) comprise palaeocopes such as: *Ogmoopsis bocki*, *Brezelina palmata*, *Glossomorphites digitatus*, *Rigidella mitis*, and *Protallinnella grewingkii*. The only other non-palaeocope besides *C. socialis* amongst the most abundant species is the eridostracan *Incisua ventroincisurata*, occurring in 32% of samples and constituting about 13% of the studied specimens. Of the 49 studied species, the ten most abundant make up 90% of the total Arenig fauna (Fig. 6B). The other species are either rare, occurring in minor quantities, or restricted to certain stratigraphic levels/biofacies only.

Comparison of ostracod faunas from the Billingen, Volkhov and Kunda stages (Figs. 7–9) shows an uneven picture. The relatively low number of samples from the Billingen Stage (Fig. 9) shows *C. socialis* and *R. mitis* as the most abundant species, present in 91 and 28 samples, respectively. The most abundant species of the Volkhov stage (Fig. 8) are: *C. socialis*, *Ogmoopsis bocki*, *Incisua ventroincisurata*, *Brezelina palmata*, *Rigidella mitis*, *Tallinnellina primaria* and *Protallinnella grewingkii*.

Table 2
Pearson's correlation matrix for 36 species

	C. socialis	*O. bocki*	*I. ventroincisurata*	*B. palmata*	*G. digitatus*	*R. mitis*	*A. simplex*	*P. grewingkii*	*T. primaria*	*A. acuta*	*E.? nonumbonatus*	*U. punctosulcata*	*P. procerus*	*L. curvata*	*O. cornuta*	*E. effusus*	*U. tolmachovae*
C. socialis	1.00																
O. bocki	−0.03	1.00															
I. ventroincisurata	**0.29**	−0.04	1.00														
B. palmata	−0.03	0.02	−0.05	1.00													
G. digitatus	**0.17**	−0.06	0.09	−0.07	1.00												
R. mitis	**0.21**	**0.13**	**0.23**	0.06	0.01	1.00											
A. simplex	0.07	−0.05	0.00	−0.04	0.04	−0.10	1.00										
P. grewingkii	**0.27**	0.24	0.16	0.01	**0.19**	0.23	0.03	1.00									
T. primaria	−0.09	0.02	−0.07	**0.11**	−0.09	−0.01	−0.05	−0.04	1.00								
A. acuta	**0.14**	−0.01	0.04	−0.04	0.05	−0.09	0.03	−0.08	−0.05	1.00							
E.? nonumbonatus	0.05	−0.02	−0.02	−0.01	0.61	−0.01	0.03	−0.02	−0.03	0.06	1.00						
U. punctosulcata	**0.18**	0.00	0.03	0.07	**0.33**	**0.41**	−0.02	**0.12**	0.07	−0.05	**0.21**	1.00					
P. procerus	0.06	−0.02	−0.07	−0.03	0.10	−0.09	0.15	−0.08	−0.04	**0.59**	0.02	−0.08	1.00				
L. curvata	−0.01	−0.03	−0.05	−0.02	0.01	−0.06	**0.34**	−0.06	−0.03	**0.15**	0.10	−0.04	**0.16**	1.00			
O. cornuta	0.02	−0.01	−0.05	−0.02	−0.02	−0.06	0.04	−0.06	−0.03	**0.31**	−0.02	−0.05	**0.41**	0.39	1.00		
E. effusus	−0.04	−0.01	−0.02	−0.01	−0.03	−0.03	**0.12**	−0.03	−0.01	−0.01	−0.01	−0.03	0.03	**0.37**	−0.01	1.00	
U. tolmachovae	0.04	−0.02	−0.03	−0.02	−0.04	−0.04	−0.02	−0.04	−0.02	−0.02	−0.01	−0.03	−0.02	−0.01	−0.01	−0.01	1.00
E. cicatriosa	**0.14**	−0.02	0.00	−0.03	0.04	−0.01	0.05	−0.03	−0.03	**0.51**	0.03	−0.05	**0.51**	0.12	0.27	−0.01	−0.01
H. macroreticulata	0.01	−0.01	−0.02	−0.01	0.05	−0.03	0.01	−0.03	−0.02	**0.26**	0.19	−0.01	0.08	**0.60**	−0.01	0.00	−0.01
L. decumana	0.03	−0.02	−0.04	−0.02	−0.02	−0.06	0.05	−0.06	−0.03	**0.24**	−0.02	−0.04	**0.42**	0.32	0.93	0.06	−0.01
G. grandispinosus	−0.01	−0.02	0.04	−0.01	−0.02	−0.04	**0.14**	−0.02	−0.02	0.01	−0.01	−0.02	0.02	**0.38**	0.00	**0.99**	−0.01
U. irrete	−0.05	**0.28**	0.07	−0.03	0.01	−0.05	−0.02	0.00	−0.05	0.00	−0.03	0.02	−0.06	−0.04	−0.04	−0.02	−0.03
L. ansiensis	0.08	0.03	−0.01	0.07	0.09	**0.36**	−0.02	**0.19**	−0.04	0.01	0.09	**0.33**	0.01	0.07	−0.03	−0.01	−0.02
T. murus	**0.31**	−0.01	0.00	−0.02	0.00	−0.03	−0.01	**0.15**	−0.02	−0.02	−0.01	−0.05	−0.02	−0.02	−0.02	−0.01	−0.01
E. sigma	−0.01	−0.02	−0.03	−0.02	0.10	−0.04	0.00	−0.04	−0.02	**0.13**	0.00	−0.05	**0.20**	0.03	0.01	−0.01	−0.01
O. variabilis	−0.02	−0.01	−0.01	−0.01	−0.03	−0.03	−0.01	−0.03	−0.01	−0.01	0.00	−0.03	−0.01	−0.01	0.02	0.00	−0.01
Baltonotella	0.05	−0.02	−0.04	−0.02	0.00	−0.05	**0.64**	−0.05	−0.03	**0.31**	−0.01	−0.06	**0.57**	0.32	0.28	−0.01	−0.01
H. proximus	0.05	−0.01	−0.02	−0.01	−0.03	−0.03	−0.01	−0.03	−0.01	−0.01	−0.01	−0.03	−0.01	−0.01	−0.01	0.00	**0.72**
E. reticulogranulatus	0.05	−0.01	−0.05	−0.03	0.02	−0.07	**0.33**	−0.05	−0.03	**0.42**	0.00	−0.05	**0.61**	0.14	0.13	−0.01	−0.02
?L. spinosa	−0.05	−0.02	−0.03	−0.01	−0.04	−0.04	−0.02	−0.04	−0.02	−0.02	−0.01	−0.04	−0.02	−0.01	−0.01	−0.01	−0.01
Silenis	−0.03	−0.01	−0.02	−0.01	−0.03	−0.03	−0.01	−0.03	−0.01	−0.01	−0.01	−0.01	−0.01	0.06	−0.01	0.00	−0.01
E. andersoni	0.06	0.00	−0.03	−0.01	0.04	−0.03	0.03	−0.04	−0.02	**0.46**	0.01	−0.04	**0.76**	−0.01	**0.12**	0.00	−0.01
C. levis	−0.01	−0.02	0.03	−0.01	−0.03	−0.04	**0.55**	−0.04	−0.02	−0.01	0.02	−0.04	0.10	**0.24**	−0.01	−0.01	−0.01
Microcheilinella	−0.03	−0.01	−0.02	−0.01	−0.03	−0.03	−0.01	−0.03	−0.01	−0.01	−0.01	−0.01	−0.01	0.06	−0.01	0.00	−0.01

The most abundant species of the Kunda Stage (Fig. 9) are *C. socialis*, *I. ventroincisurata*, *Aulacopsis simplex*, *Glossomorphites digitatus*, *Asteusloffia acuta* and *Pinnatulites procerus*.

A few species have been recorded throughout the studied stratigraphical interval. These long-ranging species are the eridostracans *C. socialis* and *I. ventroincisurata*, the palaeocopes *Ogmoopsis bocki* and *Protallinnella grewingkii*, the kloedenellocope *Unisulcopleura punctosulcata*, and the binodicope *Laterophores ansiensis*.

The composite data of Arenig ostracod assemblages in the Baltoscandian Palaeobasin is presented in Table 3.

6. Arenig ostracod biofacies in the Baltoscandian Palaeobasin

6.1. Distribution of ostracod assemblages in different ramp facies zones

An ostracod biofacies distribution model for the Arenig of the Baltoscandian Palaeobasin is presented in Fig. 11. Three facies zones – inner, middle and outer ramp – are distinguished in the model. In the studied stratigraphical interval, shallow water inner ramp sediments are mostly lacking because of erosion. The only interval showing nearshore sedimentation features is the bioclastic grainstone with quartz sand of the Pakri Formation. It is exposed in the uppermost part of the Väike–Pakri section in northern Estonia and is characterized by the high diversity *Ogmoopsis variabilis* assemblage.

The other northern Estonian sections — Harku, Nõmmeveski, Saka, Toila, and most of the Väike–Pakri and Lava sections, show similar alternations of *Ogmoopsis bocki* and *Brezelina palmata* assemblages in the lower part of the Volkhov Stage and *Incisua ventroincisurata* and *Glossomorphites digitatus* in the upper Volkhov and lower Kunda stages. These assemblages of the middle ramp biofacies occur in packstone–wackestone lithologies representing open marine storm-influenced environments. The Jurmala, Skelbro, Vergale, Laeva, Tartu, Siljan and Hällekis sections preserve outer ramp biofacies. The *Tallinnellina*? *viridis* and *Unisulcopleura tolmachovae* ostracod assemblages have been documented in the Lava section and the *Lavatiella spinosa* assemblage only in the lower Volkhov Stage of the Jurmala section. Most of the

E. cicatriosa	*H. macroreticulata*	*L. decumana*	*G. grandispinosus*	*U. irrete*	*L. ansiensis*	*T. murus*	*E. sigma*	*O. variabilis*	*Baltonotella*	*H. proximus*	*E. reticulogranulatus*	*?L. spinosa*	*Silenis*	*E. andersoni*	*C. levis*	*Microcheilinella*
1.00																
0.12	1.00															
0.21	−0.01	1.00														
−0.01	−0.01	0.06	1.00													
−0.04	−0.02	−0.04	0.03	1.00												
−0.01	**0.14**	−0.03	−0.02	−0.06	1.00											
−0.01	−0.01	−0.01	0.00	−0.03	−0.02	1.00										
0.25	0.04	0.03	−0.01	−0.03	−0.02	−0.01	1.00									
−0.01	0.00	−0.01	0.04	**0.22**	−0.01	−0.01	−0.01	1.00								
0.55	−0.01	**0.23**	0.00	−0.02	−0.02	−0.01	0.05	0.04	1.00							
−0.01	0.00	−0.01	−0.01	−0.02	−0.01	−0.01	−0.01	0.00	−0.01	1.00						
0.38	0.02	**0.11**	−0.01	−0.04	−0.03	−0.02	**0.52**	−0.01	**0.58**	−0.01	1.00					
−0.01	−0.01	−0.01	−0.01	−0.02	−0.02	−0.01	−0.01	−0.01	−0.01	−0.01	−0.01	1.00				
−0.01	0.00	−0.01	−0.01	−0.02	−0.01	−0.01	−0.01	0.00	−0.01	0.00	−0.01	−0.01	1.00			
0.49	0.00	0.09	−0.01	−0.02	−0.02	−0.01	0.03	0.00	**0.46**	0.00	**0.63**	−0.01	0.00	1.00		
0.02	−0.01	−0.01	0.00	−0.02	−0.02	−0.01	0.03	−0.01	**0.54**	−0.01	**0.26**	−0.01	−0.01	−0.01	1.00	
−0.01	0.00	−0.01	−0.01	−0.02	−0.01	−0.01	−0.01	0.00	−0.01	0.00	−0.01	−0.01	1.00	0.00		−0.01

lower and middle parts of the Volkhov Stage show alternations of the *R. mitis*, *T. primaria*, *B. palmata* and *O. bocki* assemblages representing middle ramp biofacies. The upper Volkhov and Kunda Stages are dominated by the *Glossomorphites digitatus* assemblage. These assemblages are also related to wackestones and packstones.

6.2. Temporal distribution of ostracod biofacies

Data about the Billingen Stage ostracod assemblages comes mostly from the Lava section. The lower Billingen Stage is dominated by the low diversity *Unisulcopleura tolmachovae* assemblage, whereas the middle and upper part of the Billingen Stage show alternations of the *Ogmoopsis bocki* and *Tallinnellina*? *viridis* assemblages. In the Billingen Stage of the Toila section the *Rigidella mitis* assemblage representing the middle ramp biofacies was documented (Fig. 10). An outer ramp ostracod biofacies is unknown from the Billingen Stage.

Low diversity assemblages dominate also in the lower part of the Volkhov Stage. In the outer ramp zone, the low diversity *Lavatiella spinosa* assemblage occurs (Fig. 10). The middle part of the Volkhov Stage shows basin wide distribution of the low diversity *Rigidella mitis*, *Tallinnellina primaria*, *Ogmoopsis bocki* and *Brezelina palmata* assemblages (Fig. 11).

The first high diversity assemblages appear in the Baltoscandian Palaeobasin during late Volkhovian time, when the *Glossomorphites digitatus* assemblage was documented in the outer ramp, and the *Incisua ventroincisurata* assemblage in the inner ramp facies (Fig. 11). Basically, the same situation can be seen in the Kunda Stage, with high diversity *G. digitatus* assemblages in the outer ramp, *I. ventroincisurata* in the middle ramp, and *O. variabilis* in the inner ramp facies zone.

6.3. Spatial and temporal ostracod biofacies dynamics during the Arenigian

The general stratigraphic framework of the Arenig strata in the Baltoscandian area (Fig. 2) is used as a background for analysing the spatial/temporal distribution of ostracod biofacies (Fig. 11). In the studied area, conodont data is present for the Lava (Tolmacheva and Fedorov, 2001), Tartu (Põldvere et al., 1998; Stouge, 1998) and Mäekalda sections (12 km NE from the Harku section;

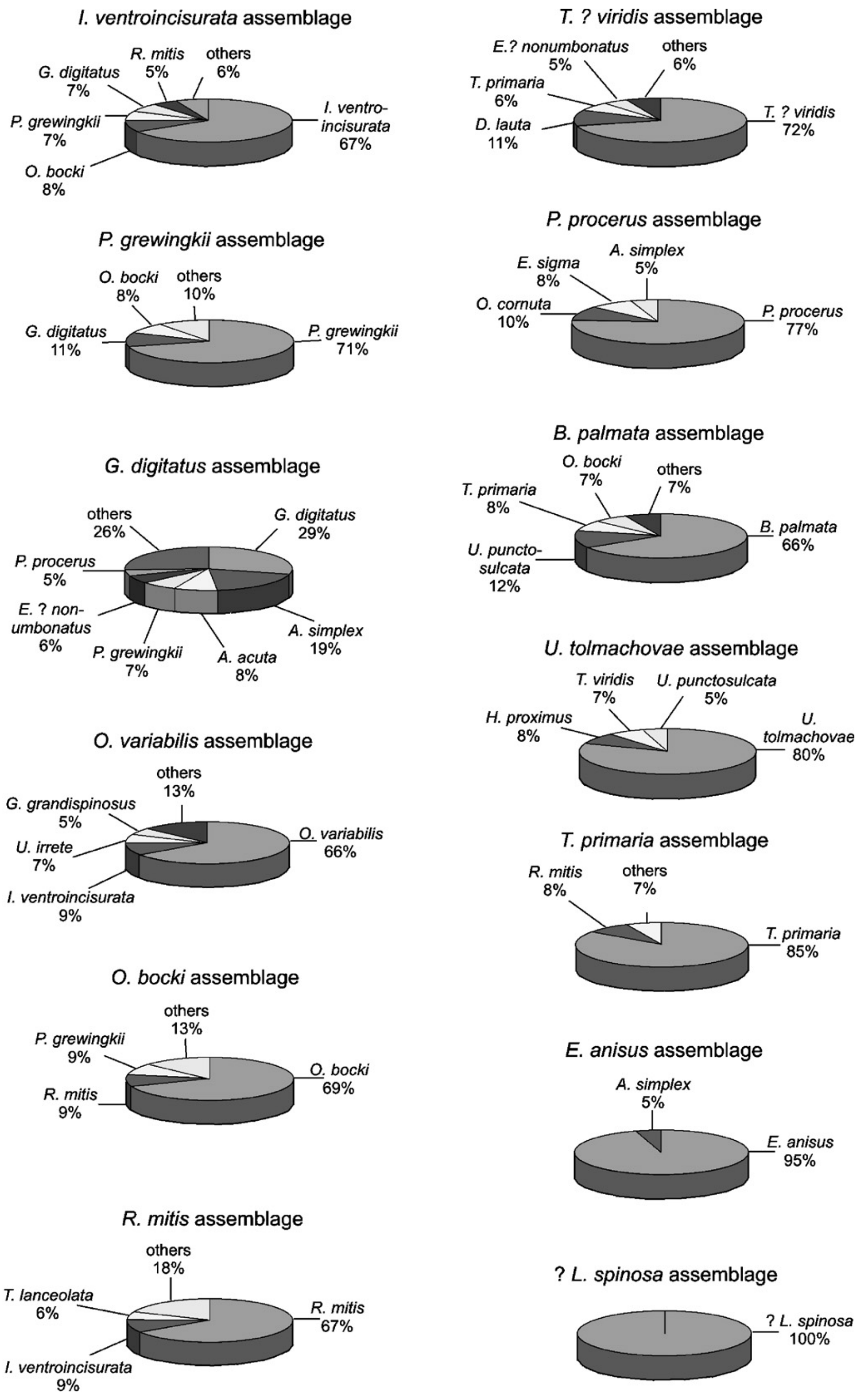
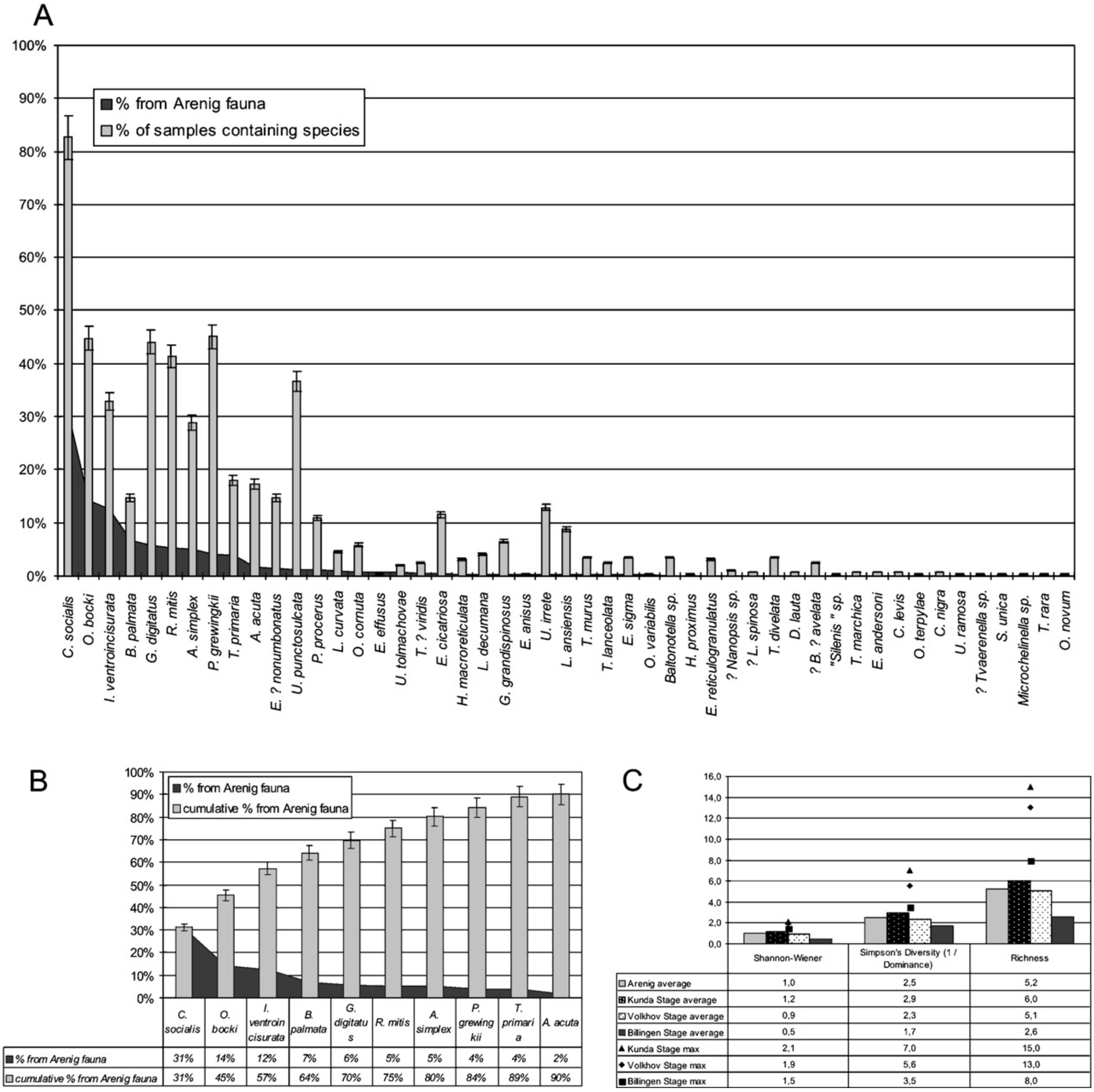


Fig. 5. Species composition of the studied ostracod assemblages.

Viira et al., 2001). Trilobite data is available for the Skelbro section (Nielsen, 1995). More detailed analysis is based on 29 laterally traceable "quarrymen's beds" (Dronov et al., 2000). Individual beds in the Upper-Billingen–Volkhov stratigraphic interval differ in rock type, colour, specific hardground surface morphologies and trace fossils, glauconite grains, etc., and can be traced over a distance of 250 km, from the easternmost sections of the Baltic–Ladoga Klint up to the central-northern Estonia (Dronov et al., 2000). These beds were identified as tempestites and thus can be used as a framework for detailed event-stratigraphic correlation.

The distribution of ostracod biofacies in Harku, Saka, Toila and Lava sections against combined conodont and event-stratigraphical correlation of the Saka, Toila and Lava sections is presented in Fig. 12. The comparison of bed-by-bed lithostratigraphical correlation of the Saka, Toila and Harku sections (Dronov et al., 2000) with the



	C. socialis	O. bocki	I. ventroin cisurata	B. palmata	G. digitatu s	R. mitis	A. simplex	P. grewing kii	T. primari a	A. acuta
■ % from Arenig fauna	31%	14%	12%	7%	6%	5%	5%	4%	4%	2%
□ cumulative % from Arenig fauna	31%	45%	57%	64%	70%	75%	80%	84%	89%	90%

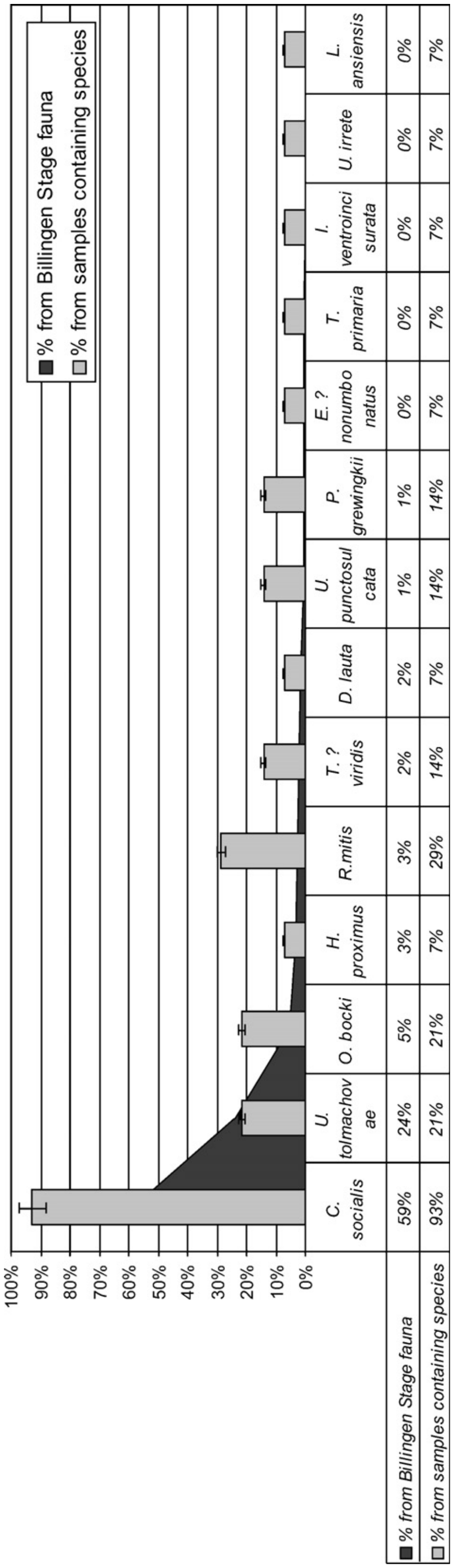
	Shannon-Wiener	Simpson's Diversity (1 / Dominance)	Richness
□ Arenig average	1,0	2,5	5,2
⊞ Kunda Stage average	1,2	2,9	6,0
□ Volkhov Stage average	0,9	2,3	5,1
■ Billingen Stage average	0,5	1,7	2,6
▲ Kunda Stage max	2,1	7,0	15,0
◆ Volkhov Stage max	1,9	5,6	13,0
■ Billingen Stage max	1,5	3,5	8,0

Fig. 6. Arenig ostracod fauna of Baltoscandia. A — relative abundance of Arenig ostracod species; B — cumulative percentages of the ten most abundant ostracod species; C — diversity measures for total Arenig, Billingen, Volkhov and Kunda Stage ostracod assemblages. Bars indicate ±5% error.

distribution of ostracod assemblages in the same sections reveals a spatial biofacies shift. The appearance of the mid-Volkhov *B. palmata* assemblage in the Saka and Toila sections is related to the same event-stratigraphic level. However, in the Lava section this assemblage appears deeper in the section and the particular event horizon marks the appearance of the *R. mitis* assemblage. This discrepancy is proved also by conodont data. The appearance of the *B. palmata* assemblage in the Lava section coincides with the lower boundary of the *Microzarcodina parva* conodont Biozone but in the Harku section the *B. palmata* assemblage appears above the lower boundary of the *M. parva* conodont Biozone.

In the Saka and Toila sections, the *R. mitis* assemblage lies above the *B. palmata* assemblage and contemporaneous appearance of this assemblage in regard to event-stratigraphic framework is confirmed in both sections (Fig. 12). The same stratigraphic level in the Lava section marks the appearance of a new, *G. digitatus* assemblage which in the Toila section appeared considerably later.

Considering the boundaries of conodont biozones and event-stratigraphic markers as time boundaries, the earlier appearance of certain ostracod biofacies in the Lava section can be inferred. According to the Arenig lithofacies zonation of the Baltoscandian Palaeobasin (Dronov et al., 2000), the Harku, Saka and Toila sections lie in the middle ramp closer to the shore than the Lava section (Fig. 1) and this interpretation is also supported by the data on ostracod population age structure (Tinn and Meidla, 2003). It follows, therefore, that the *B. palmata*, *R. mitis* and *G. digitatus* assemblages shifted landward in the course of a transgression in mid-Volkhov time.



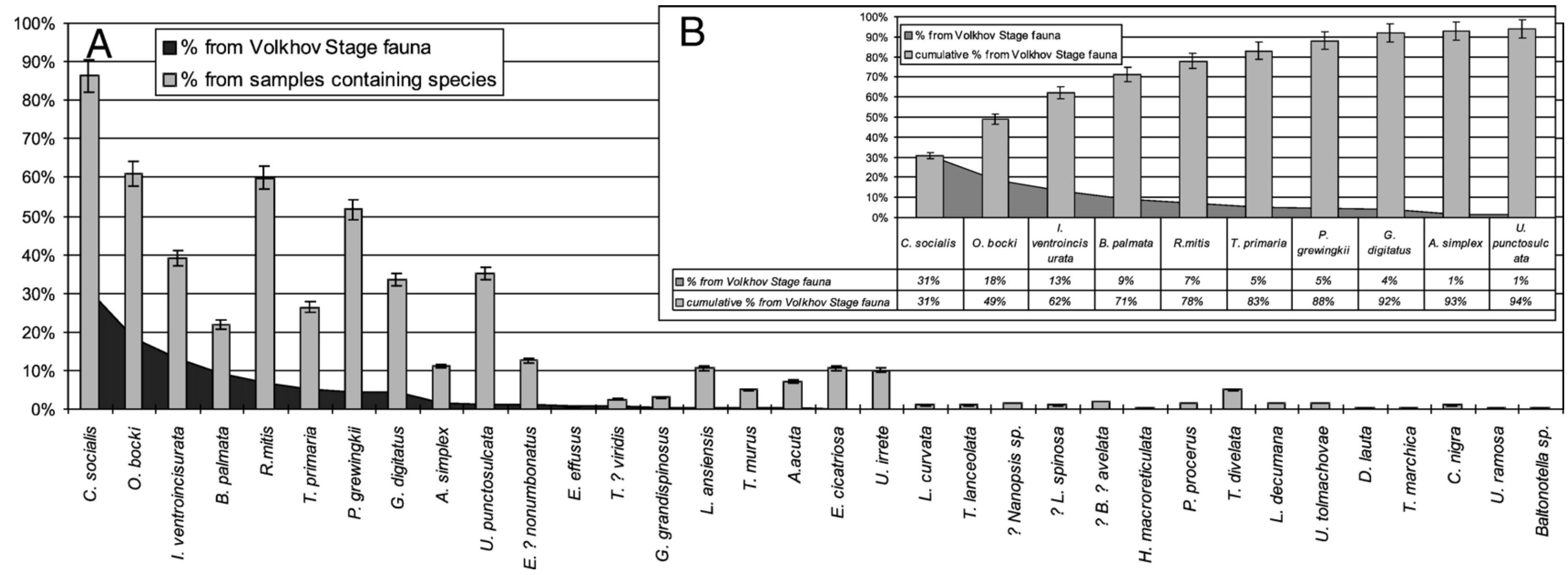
	C. socialis	U. tolmachovae	O. bocki	H. proximus	R.mitis	T. ? viridis	D. lauta	U. punctosulcata	P. grewingkii	E. ? nonumbonatus	T. primaria	I. ventroincisurata	U. irrete	L. ansiensis
■ % from Billingen Stage fauna	59%	24%	5%	3%	3%	2%	2%	1%	1%	0%	0%	0%	0%	0%
□ % from samples containing species	93%	21%	21%	7%	29%	14%	7%	14%	14%	7%	7%	7%	7%	7%

Fig. 7. Relative abundance of Billingen Stage ostracods. Bars indicate ±5% error.

7. Discussion

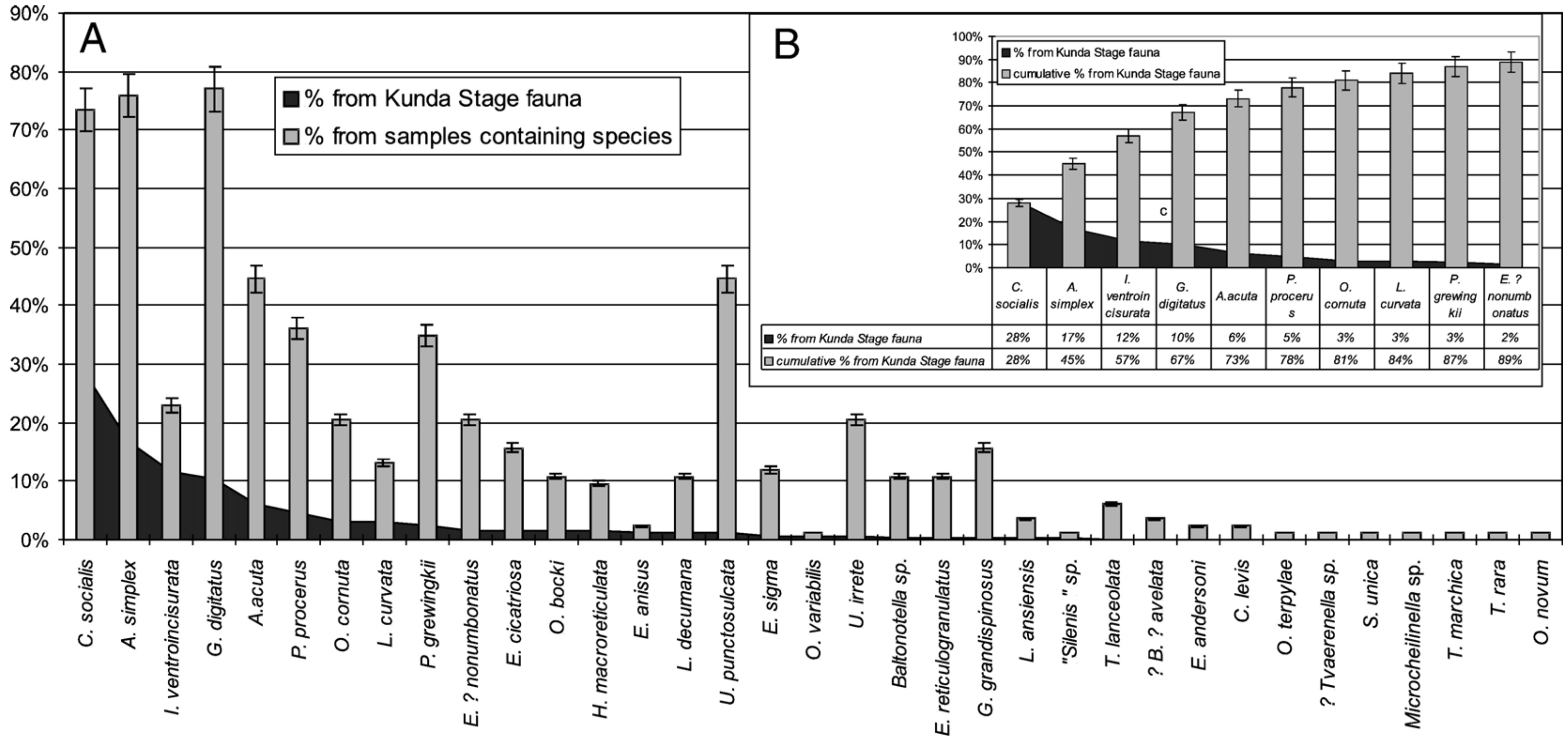
7.1. Ostracod diversity changes

Calculated average and maximum values of ostracod diversity for the Billingen, Volkhov and Kunda stages are presented in Fig. 6C and for the studied ostracod assemblages in Fig. 4. The diversity measures range from the least possible (1 for Simpson's index and richness, 0 for Shannon–Wiener index) to the maximum Shannon–Wiener value 2.1, Simpson's diversity 7.0 and richness 15. All calculated diversity measures (Fig. 6C) show a gradual increase through younger horizons, the lowest being in the Billingen Stage with mean species richness of 2.6, and the highest in the Kunda Stage with richness up to 6.0. This reflects a continuous, progressive diversification in the studied interval. Unfortunately, we lack a similar



	C. socialis	O. bocki	I. ventroincisurata	B. palmata	R.mitis	T. primaria	P. grewingkii	G. digitatus	A. simplex	U. punctosulcata
■ % from Volkhov Stage fauna	31%	18%	13%	9%	7%	5%	5%	4%	1%	1%
▨ cumulative % from Volkhov Stage fauna	31%	49%	62%	71%	78%	83%	88%	92%	93%	94%

Fig. 8. Volkhov Stage ostracods. A — relative abundance of Volkhov Stage ostracod species; B — cumulative percentages of ten most abundant Volkhov Stage ostracod species. Bars indicate ±5% error.



	C. socialis	A. simplex	I. ventroincisurata	G. digitatus	A.acuta	P. procerus	O. cornuta	L. curvata	P. grewingkii	E. ? nonumbonatus
■ % from Kunda Stage fauna	28%	17%	12%	10%	6%	5%	3%	3%	3%	2%
▨ cumulative % from Kunda Stage fauna	28%	45%	57%	67%	73%	78%	81%	84%	87%	89%

Fig. 9. Kunda Stage ostracods. A — relative abundance of Kunda Stage ostracod species; B — cumulative percentages of ten most abundant Kunda Stage ostracod species. Bars indicate ±5% error.

Table 3
Ostracod assemblages of the Arenig Baltoscandian Palaeobasin

Assemblage name	Common species	Occasional species	Diversity measures			Distribution
			Shannon–Wiener	Simpson	Richness	
Incisua ventroincisurata	*G. digitatus*, *O. bocki*, *P. grewingkii*	*R. mitis*, *T. primaria*, *A. acuta*, *T. lanceolata*, *T. murus*, *B. palmata*, *U. punctosulcata*, *U. irrete*, *E. nonumbonatus*	0.9	2.2	5.2	Volkhov Stage in northern Estonia and Lava sections; lower part of the Kunda Stage in the Siljan area
Protallinnella grewingkii	*G. digitatus*, *O. bocki*	*B. palmata*, *R. mitis*, *T. primaria*, *L. ansiensis*	0.8	2.0	3.8	North Estonia and transitional area of the Volkhov age
Glossomorphites digitatus	*A. simplex*, *A. acuta*, *P. grewingkii*, *E. nonumbonatus*	*P. procerus*, *O. cornuta*	1.1	2.9	5.3	Volkhov and Kunda stages
Ogmoopsis variabilis	*I. ventroincisurata*	*U. irrete*, *G. grandispinosus*, *O. terpylae*, *T. marchica*, *T. rara*, *O. novum*	1.3	2.2	11	Kunda Stage of the Väike–Pakri section
Ogmoopsis bocki	*Rigidella mitis*, *Protallinnella grewingkii*	*T. primaria*, *U. irrete*, *B. palmata*, *I. ventroincisurata*, *E. cicatriosa*, *U. punctosulcata*	0.8	2.0	4.1	Volkhov stage of the North Estonian sections
Rigidella mitis	*I. ventroincisurata*	*P. grewingkii*, *O. bocki*, *U. punctosulcata*, *L. ansiensis*, *T. lanceolata*	0.7	2.0	3.3	Lower part of the Volkhov Stage in North Estonia and in the Volkhov and Kunda stages in the Hällekis section
Tallinnellina? *viridis*	*D. lauta*, *T. primaria*, *E. nonumbonatus*	*U. punctosulcata*, *U. tolmachovae*	0.6	1.7	3.2	Billingen and Volkhov stage of the Lava section
Pinnatulites procerus	*O. cornuta*, *E. sigma*	*A. simplex*	0.8	1.9	3.0	Kunda age of the Tartu and Siljan sections
Brezelina palmata	*U. punctosulcata*, *T. primaria*, *R. mitis*>	*O. bocki*, *P. grewingkii*	0.7	1.6	4.3	Volkhov age and from the Siljan composite section of the Kunda age
Unisulcopleura tolmachovae	*H. proximus*, *T.*? *viridis*	*U. punctosulcata*	0.7	1.7	3.5	Billingen age of the Lava section
Tallinnellina primaria	*R. mitis*	*T.? viridis*, *U. punctosulcata*	0.4	1.4	2.4	Lower part of the Volkhov Stage in northern Estonian sections, as well as in the Jurmala, Tartu and Lava
Euprimites anisus	*A. simplex*	–	0.2	1.1	2.0	Upper part of the Kunda Stage in the Hällekis section
?*Lavatiella spinosa*	–	–	0	1	1	Base of the Volkhov Stage at the Jurmala section

detailed ostracod diversity analysis for the Arenig in other palaeobasins, but Late Ordovician ostracods of the Baltoscandian Palaeobasin show continuation of the same trend. Ostracod samples with 15 to 20 species are common in the Caradoc, but at certain levels the number of species can reach up to 25 or even 30 (Meidla, 1996). In this context, the ostracod fauna of the Arenig Palaeobaltic Basin may be characterized as a low-diversity fauna.

From the Tremadoc of Baltoscandia, only one ostracod species – *Nanopsis nanella* (Moberg and Segerberg, 1906) – has been documented (Henningsmoen, 1954). Similarly, the Billingen and early Volkhov stages yield low-diversity *U. tolmachovae* and ?*L. spinosa* assemblages. Higher ostracod diversity assemblages were recorded in late Volkhov and early Kunda sediments. While the Arenig sediments have yielded about 50 species from the whole palaeobasin, the number of species and subspecies documented from the Upper Ordovician of Estonia, reaches nearly 360 (Meidla, 1996).

The palaeogeographical reconstructions (Torsvik et al., 1996) show the Baltoscandian Palaeocontinent lying at higher southern palaeolatitudes during the Cambrian and Early Ordovician. According to the carbonate sedimentation type (Jaanusson, 1973; Lindström, 1984; Nestor

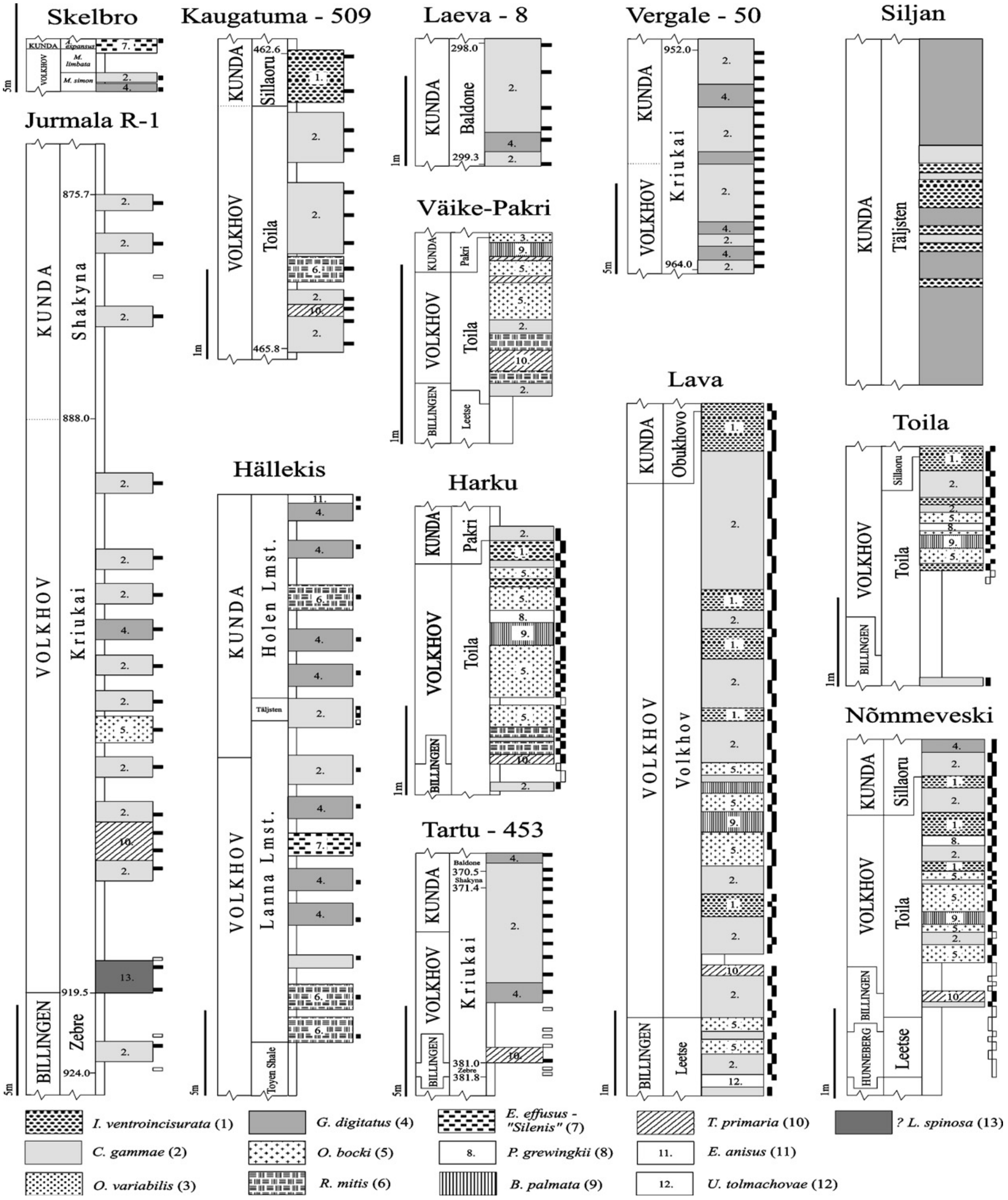


Fig. 10. Position of ostracod assemblages in the studied sections.

and Eeinasto, 1997), the investigated faunal assemblages from the Arenig of Baltoscandia represent faunas of a cool-water sediment-starved shelf basin. Nearly all authors emphasize the particular importance of the rapid northward drift of Baltica (Vannier et al., 1989; Torsvik et al., 1996) which turned the climate in the Baltoscandian

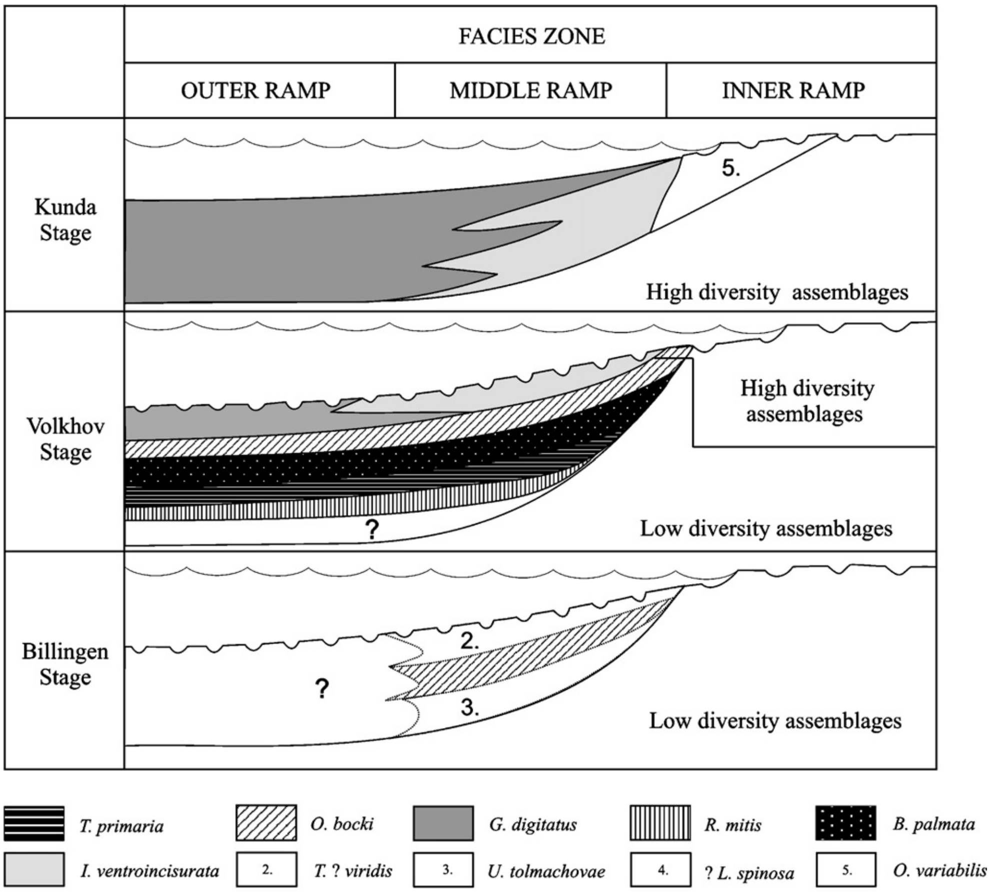


Fig. 11. Distribution of ostracod assemblages in the inner, middle and outer ramp facies zones of the Arenig Baltoscandian Palaeocontinent.

area gradually warmer and led to the appearance of bahamitic sediments (Jaanusson, 1973), first tabulates (Mõtus, 1997), rugosan corals (Kaljo, 1997) and stromatoporoids (Nestor, 1997) during the early Upper Ordovician. Gradual increase of diversity in various shelly fossil groups like that of trilobites (Adrain et al., 2004) can be ascribed to this amelioration of climate.

In recent environments, ostracod diversity changes have a rough correlation with broad temperature zonation, although this general pattern is modified by several other factors. Progressive diversification of ostracods throughout the Tremadoc and Arenig of Baltoscandia (see above) could have evolutionary reasons, but further diversity increase towards the Upper Ordovician (data from Meidla, 1996 discussed above) is obvious and could tentatively be ascribed to the same reason. As the palaeocontinent moved towards the Equator, climatic conditions were gradually improving perhaps resulting in the highly diverse and abundant Late Ordovician ostracod fauna that appeared in the Caradoc (Meidla, 1996). At the same time, the diversity was increasing remarkably fast during the Early to early Middle Ordovician, from one ostracod species in the Tremadoc up to 50 species recorded in the Arenig (Tinn, 2002; Tinn and Meidla, 2004). It is obvious that the Tremadoc and Arenig were periods of rapid evolution of the early ostracod fauna, an early evolutionary stage of ostracods, and the aforementioned growing diversity trend was not simply due to the improvement of the climate related to the northward drift of the Baltica continent.

Presumably ostracod faunas from once isolated continents, like Laurentia, could also migrate to Baltica. Contraction of the Tornquist Sea and the Iapetus Ocean during the Middle to Late Ordovician improved the links between the isolated terranes (Schallreuter and Siveter, 1985; Williams et al., 2003). Ostracod faunal links between the plates were firmly established in the latest Middle Ordovician and increasingly so in the Late Ordovician. As a result from all these processes, the diversity of ostracods in the latest pre-Hirnantian was remarkably

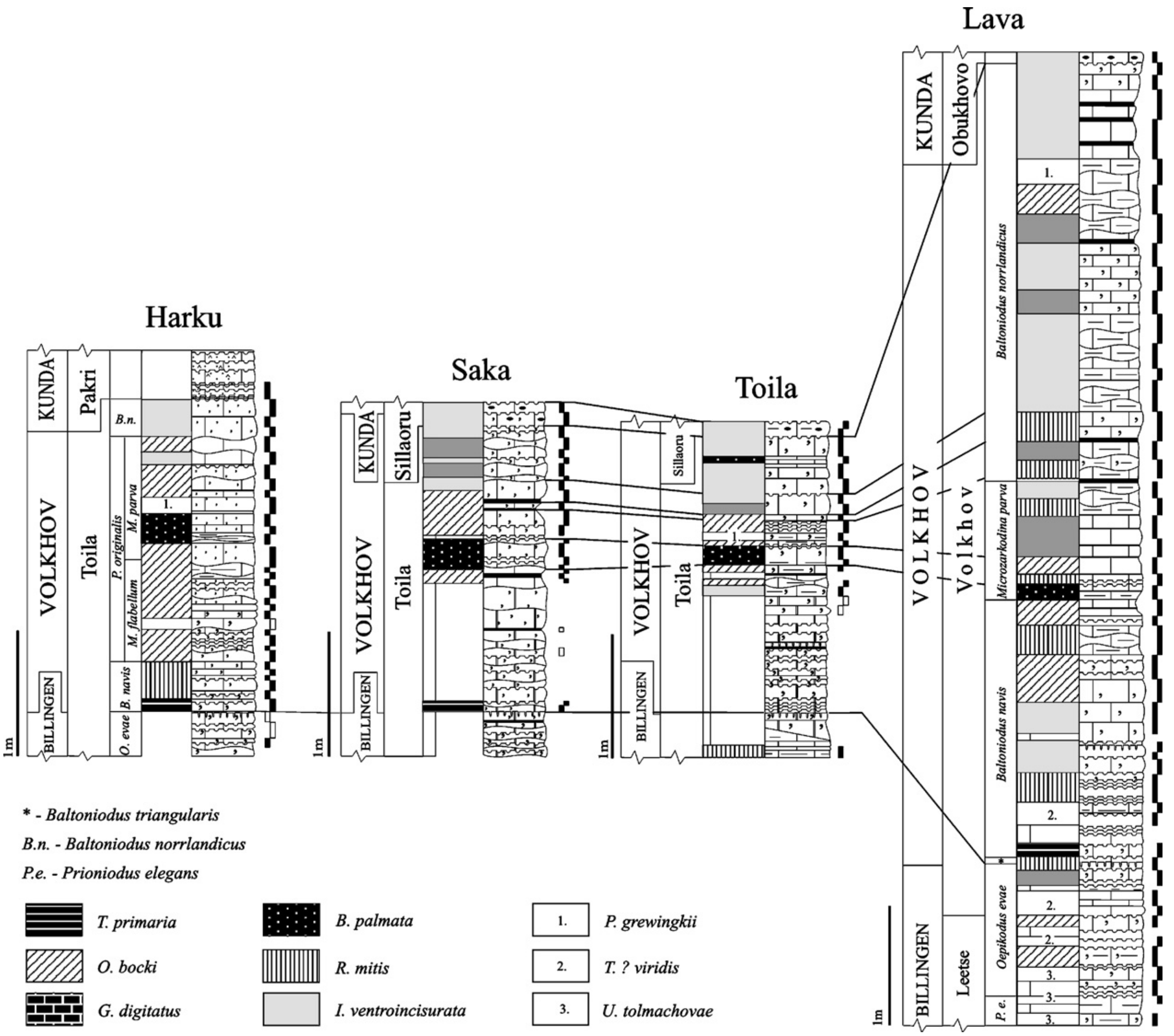


Fig. 12. Distribution of main ostracod biofacies in Harku, Saka, Toila and Lava sections. Conodont data for the Lava section by Tolmacheva and Fedorov (2001), for the Harku section correlated from the nearby Mäekalda section by Viira et al. (2001). Detailed bed-by-bed sedimentological and stratigraphical correlation from Dronov et al. (2000).

higher in Baltoscandia than in any other region where comparative data are available (Avalonia, Ibero-Armorica, Kazakhstan).

7.2. Palaeoenvironmental conditions

The environmental preferences of Palaeozoic neritic ostracods were primarily determined by water depth and resulting factors, such as temperature, salinity, water energy level, light conditions, bottom sediment character, oxygenation, etc. (Siveter, 1984). In the Arenig of Baltoscandia, distinct ostracod biofacies demonstrate probably depth-related distribution pattern, as was shown for the Upper Ordovician (Meidla, 1996). Available evidence suggests some influence of changing water energy level (Tinn and Meidla, 2001). The Arenig ostracod assemblage and biofacies analysis presented here does not offer clues to critical environmental factors but allows demonstration of broad facies control, general ecologic zonation — but only from late Volkhov time onwards.

The early to middle Volkhov age *R. mitis*, *T. primaria*, *B. palmata* and *O. bocki* assemblages occur in sections representing both the middle and outer ramp facies zones. At the same time, the sediments (type of substratum) of these zones were distinct, grading from mid-ramp packstones into calcareous mudstones of the outer ramp, and a similar pattern generally persists for the studied stratigraphic interval. It could be suggested, that depth differences between the palaeobasin facies zones were less distinctive during early and mid-Volkhov time than later, resulting in a remarkably wide facies distribution of early-middle Volkhov ostracod assemblages. The facies pattern changed during Volkhov time: upper Volkhov and Kunda stages show clear differentiation of biofacies zones. The outer ramp zone was inhabited by the *G. digitatus* assemblage, the middle ramp zone by the *I. ventroincisurata* assemblage and the inner ramp by the *O. variabilis* assemblage. This kind of differentiation apparently suggests a growing biofacies gradient in the palaeobasin, restricting the distribution of the particular ostracod assemblages.

7.3. Sea level changes

Different methods for reconstruction of sea-level changes in the Arenig Baltoscandian Palaeobasin have been used by Nielsen (1995, 2004), Dronov et al. (2003), and Tolmacheva et al. (2003). Reconstructions by Nielsen (1995, 2004) were based mainly on trilobite data from the Scanian and Bornholm areas, while those by Dronov et al. (2003) were based on detailed sedimentological data from fairly complete sections in the St. Petersburg area. Tolmacheva et al. (2003) studied the species diversity and community richness of various fossil groups — conodonts, brachiopods, ostracods, echinoderms, etc. also in the St. Petersburg area. However, in the latter work no correlation was found between small-scale variability in the diversity estimates and small-scale sea-level changes, reconstructed for the eastern part of the basin.

Sequence stratigraphic interpretations for Arenig strata in Baltoscandia have been proposed by Dronov and others (Dronov and Holmer, 1999; Dronov et al., 2003). According to this model, the sediments of the Billingen Stage represent a highstand system tract of the Latorp sequence and sediments of both the Volkhov and Kunda stages comprise the separate depositional sequences, respectively. The middle ramp *Ogmoopsis bocki* assemblage in the Lava section occupies a time of late highstand conditions in a relatively shallow sea. The regression event at the Billingen–Volkhov boundary (Latorp/Volkhov sequence boundary by Dronov et al., 2003; Basal Whiterock Lowstand by Nielsen, 2004) is represented by a noteworthy discontinuity surface throughout the Baltoscandian region (Ekdale and Bromley, 2001). The lower part of the Volkhov Stage is interpreted as a shelf margin system tract by Dronov et al. (2003). The transgression episode (transgressive surface) and the subsequent deepening of the sea in mid-Volkhov time (Dronov et al., 2003) is tracked by the *B. palmata* assemblage throughout the palaeobasin, especially in the northern Estonian sections.

The sediments of the upper part of the Volkhov Stage represent a highstand system tract with gradual marine regression (Dronov et al., 2003). The regression reached its peak at the Volkhov/Kunda stage boundary interpreted as major sequence boundary (Dronov and Holmer, 1999). In the westernmost part of the palaeobasin, in the shale-dominated Bornholm and Scania areas, the regression led to the westward shift of the carbonate facies, the Komstad Limestone (Nielsen, 1995, 2004). The inner-middle ramp sections in northern and central Estonia, on the other hand, show a remarkable sedimentary gap at the Volkhov–Kunda boundary interval. According to the present data, the sections in the St. Petersburg region (e.g. Lava section) show almost continuous sedimentary transition from the Volkhov to the Kunda Stage. During that regression event and following the lowstand period of the Kunda sequence, the outer ramp zone was inhabited by the *G. digitatus* ostracod assemblage and the middle ramp zone by the *I. ventroincisurata* ostracod assemblage. In the Siljan composite section, the lowstand sediments are marked by the *I. ventoincisurata* and *B. palmata* assemblages in the middle part of the Täljsten Layer, which is a bioclastic packstone–grainstone bed in between predominantly wackestone facies. The position of the Siljan area in the general depth zonation of the Baltoscandian basin has been debated for several decades, but the record of these ostracod assemblages here suggests that the area was located in deeper settings than the northern Estonian area (Tinn and Meidla, 2001).

In general, the ostracod assemblage-based reconstruction of sea-level changes in the studied area agree with the Dronov et al. (2003) sea level curve, made on the basis of sedimentological analysis of sections in the St. Petersburg region.

8. Conclusions

1. The Arenig ostracod fauna of Baltoscandia comprises about 50 ostracod species from seven suborders — palaeocopes, eridostracans, kloedenellocopes, metacopes, binodicopes, spinigeritiidae and leiocopes. The fauna is dominated by an eridostracan species *Conchoprimitia socialis*. The palaeocopes *Ogmoopsis bocki*, *Brezelina palmata*, *Rigidella mitis*, *Glossomorphites digitatus* and *Protallinnella grewingkii* are also very common. The only other

non-palaeocope, besides *C. socialis*, that is amongst the most abundant species is the eridostracan *Incisua ventroincisurata*. Although the number of studied species is relatively high, the ten most abundant ostracod species make up 90% of the total Arenig fauna. The remaining species are rare, occur in minor numbers, or are restricted to certain stratigraphic levels/biofacies. Some of the ostracod species are restricted to certain facies zones or have short stratigraphical intervals. There are also long-ranging species, recorded throughout the Arenig (the eridostracans *C. socialis* and *I. ventroincisurata*, the palaeocopes *O. bocki* and *P. grewingkii*, the kloedenellocope *Unisulcopleura punctosulcata* and binodicope *Laterophores ansiensis*).

2. Arenig ostracod diversity estimates for the Baltoscandian Palaeobasin are consistently low, with an average richness of 5.2. All calculated diversity measures show a gradual increase in diversity at younger horizons, diversity being lowest in the Billingen Stage with mean species richness of 2.6, and highest in the Kunda Stage, with mean richness up to 6.0. The generally low number of taxa is due to the early stage of evolution of the ostracod fauna in the Arenig.
3. Thirteen ostracod assemblages were distinguished in the Baltoscandian Palaeobasin. The *G. digitatus* assemblage is the most common of them, constituting about 30% of the studied samples. The next common assemblages are those of *O. bocki* and *I. ventroincisurata*. Ostracod assemblages show almost basin-wide distribution during early and mid-Volkhov time. Major distinctions between ostracod biofacies zones can be seen from the late Volkhov onwards, when the outer ramp was inhabited by the *G. digitatus* assemblage and the middle ramp by the *I. ventroincisurata* assemblage. Differentiation of ostracod biofacies marks the onset of major depth differences in the basin. The ostracod assemblage-based reconstruction of sea-level changes in the studied area agrees with the sea level curve (Dronov et al., 2003) and the sequence stratigraphic model (Dronov and Holmer, 1999).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2006.05.002.

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