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Faunal composition and dynamics in unconsolidated sediments: a case study from the Middle Ordovician of the East Baltic

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Abstract – The Volkhov Regional Stage (Middle Ordovician) in the East Baltic preserves diverse fossil assemblages dominated by epibenthic suspension feeders. Brachiopods, ostracodes, conodonts, echinoderms and bryozoans are the main components of palaeocommunities obtained from clay horizons in the Putilovo section (St Petersburg region, Russia), whereas trilobites, machaeridians, hyolithids, graptolites, benthic foraminifers and gastropods are rare or occur sporadically. Brachiopod bioclasts volumetrically dominate the debris of the studied sediments. Quantitative faunal data are used to assess species diversity patterns, as expressed by the species richness (total number of species in the standardized sample size) and by the evenness or equitability of the community. The numerical abundance of particular taxa in each standardized sample was used to evaluate the density of the fauna. The communities in the Volkhov Stage in Putilovo Quarry reveal a remarkable stability throughout the studied interval and are characterized by high density (1000–6000 specimens per 100 g), relatively moderate species richness (10–15 species) and a moderately variable equitability (0.3–0.7) for the dominant fossil groups (conodonts, ostracodes and brachiopods). Ostracodes significantly increase in numbers within the upper part of the section. This confirms a shallowing of the basin during the late Volkhov interval. Small-scale variability of the diversity estimates does not correlate with the small-scale sea-level changes reconstructed for this part of the basin. It may be connected with error in diversity measurement, or the result of undetected environmental parameters. Variability estimates for different faunal groups are poorly correlated because particular groups have different environmental tolerances.

Keywords: diversity, Conodonta, Brachiopoda, Ostracoda, Ordovician, Baltoscandia.

1. Introduction

Most studies on diversity patterns of fossil communities in relation to onshore–offshore gradients and sea-level changes have focused on broad geographic areas, and are rather coarse in stratigraphic resolution (Jablonski *et al*. 1983; Smith, Gale & Monks, 2001). The application of sequence stratigraphy and the use of parasequences and sequences as time units has made it possible to carry out such studies with higher stratigraphic resolution (Holland, 1997; Patzkowsky & Holland, 1999). However, only a few studies of fossil diversity patterns are comparable with such studies on modern faunas, mainly because of the very different methods of diversity evaluation in lithified and nonlithified sediments (Sageman & Bina, 1997; Peters & Bork, 1999; Conway Morris, 1986; Pokorný, 1971; Westrop, 1986).

Our present knowledge of the fauna from the condensed Lower and Middle Ordovician succession of Baltoscandia is mainly restricted to the diversity data on particular fossil groups and seldom concerns the diversity and evolution of whole communities. Nevertheless, the differences in the composition and sizes of skeletal remains in limestones from different parts of Baltoscandia have been recorded in many papers and moreover have been used partly as the basis for the recognition of 'Confacies' belts (Männil, 1966; Jaanusson, 1973, 1982; Lindström, 1979, 1984). A relatively poor benthic fauna is documented from the Ordovician sequences in Central Sweden, dominated by trilobites, closely followed by echinoderms, whereas small articulated brachiopods occur in minor proportions (Lindström, 1979, 1984). Ostracodes and gastropods are reported to be less common in the Arenig limestones in the western part of Sweden. The relative content of skeletal sand in the limestones increased toward the east, and similar patterns of temporal dynamics through the Volkhov and Kunda stages were documented in several sections in Central Sweden and Öland (Lindström, 1984).

The main aim of this paper is to study diversity changes in the Middle Ordovician faunas from the Volkhov Stage of the East Baltic (Russia), where samples from the unconsolidated parts of the carbonate/clay sequence contain a well-preserved fauna and readily available information on abundance and diversity. Diversity estimates were analysed for the major fossil

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groups (conodonts, brachiopods, ostracodes, echinoderms, bryozoans and gastropods), with regard to possible errors in species abundance and species density distribution, as demonstrated by Tolmacheva *et al.* (2001). The results of these analyses allow evaluation of faunal responses to the high-frequency environmental changes related to sea-level fluctuations implied by the existing sequence-stratigraphic model for the area.

2. Geological background

Lowermost Middle Ordovician deposits in Baltoscandia are characterized by very slow intermittent sedimentation in a rather shallow epicontinental sea, located within the temperate climatic zone (Jaanusson, 1973). During Early Ordovician times, Baltica was positioned approximately 60° south of the equator (Torsvik, 1998). The eastern part of the basin was characterized by predominantly siliciclastic deposition during the Late Cambrian and the Early Tremadoc, followed by the formation of fine-grained argillites and carbonate deposits in Late Tremadoc times. Continuous sedimentation of siliciclastic-starved carbonate sediments prevailed in the basin from the mid-Arenig onwards.

The Arenig sequence is exposed continuously over a distance of more than 350 km, along the Baltic–Ladoga Klint in northwestern Russia and northern Estonia (Fig. 1). It is one of the best-documented successions in Baltoscandia. The detailed lithostratigraphy of the carbonates, as well as various palaeontological studies from this interval are reported in numerous papers (Dronov *et al.* 1996, 2000; Egerquist, 1999; Melnikova, 1999). A first attempt at providing a sequence stratigraphic framework for this part of the region was recently proposed by Dronov & Holmer (1999), and the Volkhov Stage has been considered to represent a depositional third order 'Volkhov' sequence. The lower, middle and upper parts of the Volkhov Stage correspond to respective lowstand, transgressive and highstand system tracts (Fig. 2). Frequent changes in microfacies characteristics, such as size of bioclasts and sediment colour, have been considered as evidence

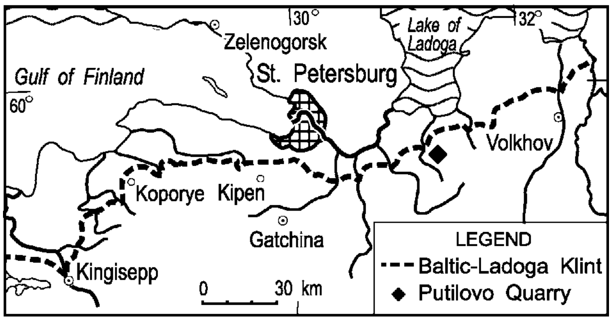

Figure 1. Location of Putilovo Quarry section in the St Petersburg region, Russia.

for sea-level changes during this stratigraphic interval and have helped to construct the proposed sea-level curve (Dronov *et al.* 1998; Dronov, 1999). A similar sea-level curve for the Volkhov Stage was also proposed by Nielsen (1992), based on the distribution of trilobite biofacies in southern Sweden and Bornholm.

Putilovo Quarry is located in the easternmost Klint area (Fig. 1). At this locality, the Volkhov Stage comprises approximately 7 m of calcareous packstones and wackestones with numerous soft clay intercalations (Fig. 2), representing thicker and more clay-rich deposits than are preserved in the central and western parts of the region. The lower part of the Volkhov Stage (BIIα Substage or Dikari Member) in the Putilovo section is 1.4 m thick and consists of 11 beds of limestones. The base of Dikari Member is marked by a distinct hardground surface ('Steklo'), which has been interpreted as the sequence boundary of the Volkhov cycle. The middle part of the Volkhov Stage (BIIβ Substage or Zheltjaki Member) is approximately 2 m thick and comprises six units of intercalated clays and limestones that are predominantly yellow and red in colour. The upper Volkhov (BIIγ Substage or Frizy Member) is 4 m thick and consists of intercalations of limestones and clays that are grey to green in colour. Carbonate beds in this unit are composed of bioclastic brachiopod-dominated wackestones and packstones. The clays are composed predominantly of thin ($\ll$0.001 mm) dioctahedral muscovite-type Al-hydromica, and are rich in bioclastic debris. In the fraction larger than 710 μ this type of debris makes up more than 15 % of the sample weight.

Dronov (1999) proposed a tempestite model for the deposition of the Lower/Middle Ordovician strata in the eastern part of Baltoscandia. He suggested that the limestone layers were deposited somewhat below the seasonal storm wave base during storm events of extraordinary magnitude, whereas the clay layers represent background sedimentation.

3. Methods

Standardized bulk samples averaging about 0.2 dm^3 were collected from the clay layers of the Putilovo section. The thickness of the sampled beds ranges generally from 3 to 10 cm. The lower part of the Volkhov Stage comprises mostly carbonate layers, however, comparative material was collected from two clay lenses within a mud mound located in the Putilovo Quarry (Tolmacheva, Fedorov & Egerquist, in press).

In the laboratory, samples were washed and the residues were sieved through a nest of three sieves for three minutes to split each sample into four fractions ($>$1 mm, 1–0.5 mm, 0.5–0.071 mm and $<$ 0.071 mm). The choice of the sieve mesh size can strongly influence the percent composition of the assemblage (Peters & Bork, 1999), and sieve mesh sizes were chosen to obtain maximum reliability of

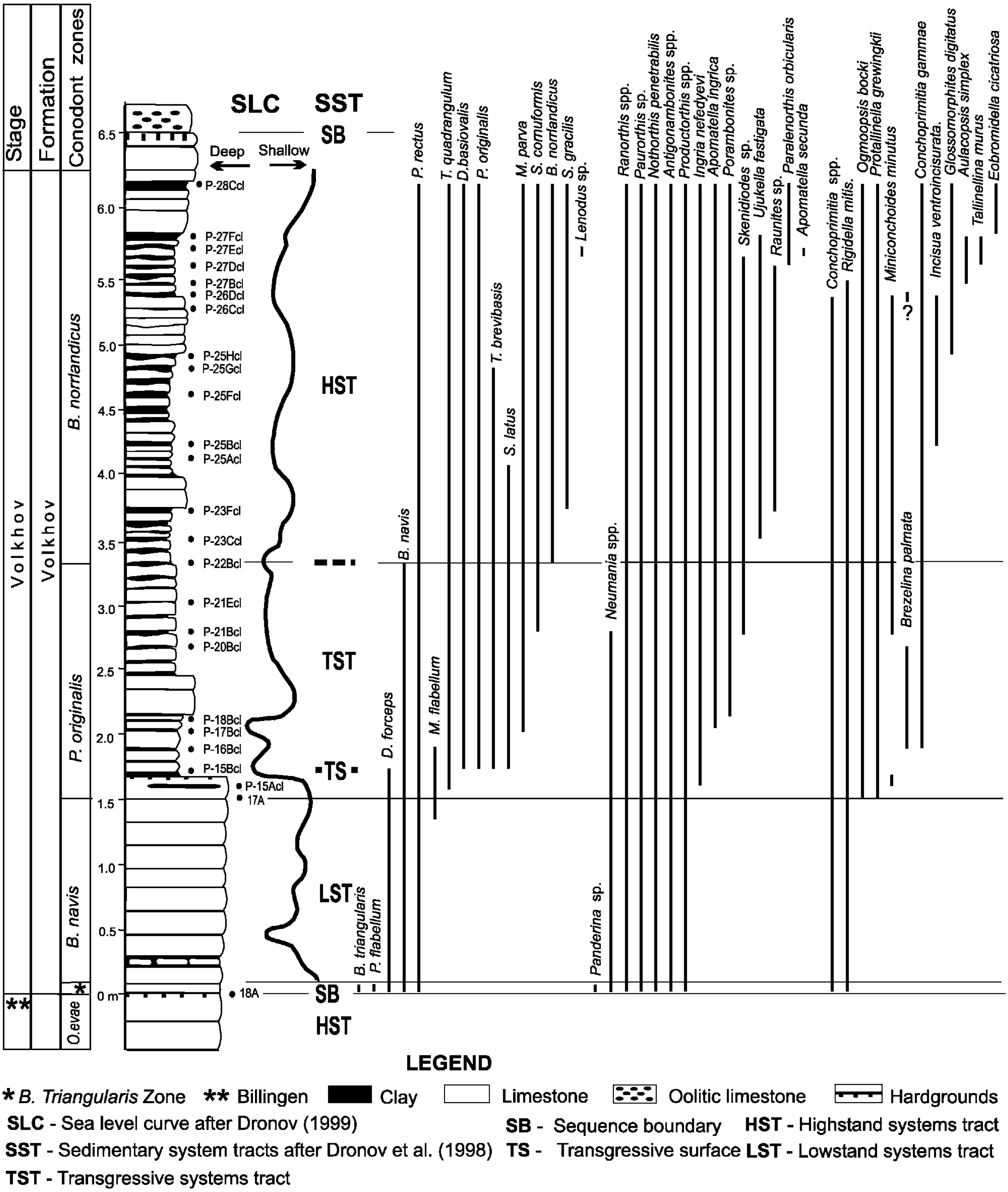

Figure 2. Stratigraphical column (weathering profile) of the Volkhov Stage exposed in Putilovo Quarry, with distribution of selected taxa of conodonts, brachiopods and ostracodes, sea-level curve and sequence stratigraphic units proposed for these strata (after Dronov, 1998, 1999).

the abundance estimates of species that are rather different in size.

The content of different fossil groups was estimated by counting identifiable skeletal elements in the fractionated residue. Comparative estimates were obtained for rhynchonelliformean brachiopods, ostracodes, conodonts, bryozoans and echinoderms. The definition of a counted 'specimen' differs from taxon to taxon. Below follows a brief description of the counting method, also given in detail by Tolmacheva *et al*. (2001).

Brachiopods, bryozoans and echinoderms were counted in the coarsest fraction (>1 mm). The total numbers of specimens of these taxa were calculated on separate valves, fragments of colonies, and pedicle columnals or thecal plates for the particular fossil group. Complete valves of ostracodes, or their large identifiable fragments were counted as specimens in a representative part of the 1–0.5 mm fraction. The number of conodont specimens was defined as the number of all identifiable conodont elements in a representative part of the 0.5–0.071 mm fraction. Brachiopod, conodont and ostracode remains were identified to the species level. The density of fauna was evaluated from the abundance of particular taxa per 100 g of the deposits.

Two estimates were used for evaluation of the diversity of fossil assemblages:

(1) Species richness (total number of species in a standardized sample size).
(2) Evenness or equitability expressed by Shannon-Wiener J' index ($J' = H'/H'_{\max}$, where $H'_{\max}$ is the Shannon/Wiener index calculated for a sample with equal proportion of species. Shannon/Wiener index is calculated as

$$H' = -\sum_{i=1}^{S} p_i \log_{10} p_i$$

where s = total number of species, and $p_i = n_i/N$ where n_i = number of individuals of the ith species, and N = total number of individuals (Pielou, 1974).

Since comparisons of species richness and equitability of the assemblages are made between samples of approximately the same size, the rarefaction method was not used.

4. Fossil assemblages in the Volkhov Stage of Putilovo Quarry

Epifaunal suspension-feeding brachiopods, echinoderms, bryozoans and ostracodes, as well as nektobenthic or nektonic scavenger-predatory conodonts are the most important and well-preserved members of the investigated faunal communities. Other fossils, such as trilobites, gastropods, graptolites, linguliformean brachiopods, machaeridians, hyoliths and benthic foraminifers occur sporadically through the section either as a result of a poor preservation (graptolites and gastropods) or because of extreme rare occurrences. Brachiopods are the volumetrically dominant component of the communities, whereas ostracodes, trilobites, echinoderms and conodonts are of much less importance.

The Volkhov Stage is characterized by relatively minor and gradual changes in the taxonomic composition of the studied faunal groups (Figs 2–5). The most important changes in the brachiopod fauna coincide with the base of Volkhov Stage (base of *Baltoniodus triangularis* Zone) (Egerquist, 1999). The taxonomic composition of the conodont assemblages also changes remarkably at this level, as well as at the upper surface of the 'Dictyonema' shales (*Cordylodus angulatus* Zone). These two particular levels are interpreted as sequence boundaries and correspond to significant gaps in the deposition. The distribution of ostracodes is correlated with the composition of the deposits, and the main faunal changes are associated with the boundary between the Mäekula and Vassilkovo members where the carbonate content of the sediments markedly increases.

Distribution and abundance data for the investigated groups (conodonts, brachiopods and ostracodes) are shown in Figures 2–5.

4.a. Conodonts

The conodont zonation for the Volkhov interval was previously established in the Swedish part of Baltoscandia (Lindström, 1954) and is now under considerable revision (Bagnoli & Stouge, 1997; Löfgren, 2000). We follow the scheme of Löfgren (1978, 2000), as zonal boundaries proposed by her are easily and unambiguously identifiable in the Russian part of Baltoscandia. Thus, the Volkhov Stage interval in the Putilovo Quarry encompasses the following four conodont zones: *Baltoniodus triangularis, Baltoniodus navis, Paroistodus originalis* and *Baltoniodus norrlandicus* (Fig. 2). The zones of *B. triangularis, B. navis* and *B. norrlandicus* are recognized by the first appearance of the nominal taxon, whereas the *P. originalis* zone is defined by a critical increase in the abundance of *P. originalis* and *Triangulodus brevibasis*.

The species of three conodont lineages strongly dominate the Volkhov Stage: *Baltoniodus, Drepanoistodus* and *Microzarkodina* usually comprise more than 80 % of the assemblage. Rasmussen & Stouge (1995) proposed several conodont biofacies (or communities) where the dominance of particular taxa is indicative for the relative sea-level of the basin. According to their model, the conodont communities of the Volkhov Stage in eastern Baltoscandia belong to the *Drepanoistodus* biofacies with the appearance of the more shallow wa–ter *Scalpellodus–Microzarkodina* biofacies in the uppermost Volkhov.

4.b. Brachiopods

The rhynchonelliformean brachiopod faunas of the Volkhov Stage include at least 18 different genera (Fig. 4). The most important members of the early Volkhov brachiopod communities are the wide-ranging genera *Ranorthis, Paurorthis* and *Antigonambonites*. *Porambonites* is rarely found in the clays of this interval, represented only by fragmentary, probably

Sample numbers	*Baltoniodus triangularis*	*Drepanoistodus* cf. *D. basiovalis*	*Semiacontiodus* sp.	*Scolopodus rex*	*Drepanoistodus forceps*	*Oistodus lanceolatus*	*Microzarkodina flabellum*	*Periodon flabellum*	*Baltoniodus navis*	*Protopanderodus rectus*	*Cornuodus longibasis*	*Decoriconus peselephantis*	*Drepanodus arcuatus*	*Drepanoistodus basiovalis*	*Trapezognathus quadrangulum*	*Paroistodus originalis*	*Scalpellodus latus*	*Triangulodus brevibasis*	*Drepanoistodus contractus*	*Microzarkodina parva*	*Semiacontiodus cornuformis*	*Baltoniodus norrlandicus*	*Scalpellodus gracilis*	*Lenodus* sp.	Total
P-28Ccl										2	3	|	1	57	1					12	|	68	11		155
P-27Fcl										8	1	1	16	52	2			1		40	12	122	6		261
P-27Ecl										5	1	|	1	87	1					20	3	74	|	1	192
P-27Dcl										8	1	|	5	89	1					7	1	81	|		193
P-27Bcl						1				16	|	|	1	67	|					4	2	71	4		166
P-26Dcl										21	|	|	5	72	|	1				37	4	57	3		200
P-26Ccl										22	3	1	|	39	1	|				29	2	80	4		181
P-25Hcl			*B. norrlandicus* Zone							22	|	|	|	48	|	|				68	1	39	5		183
P-25Gcl										12	|	1	4	33	|	4		11		54	1	50	|		170
P-25Fcl										10	2	|	3	38	1	1		7		60	5	62	3		192
P-25Bcl										5	1	|	1	63	1	|		11		47	1	44	4		178
P-25Acl				1						9	|	|	4	61	|	4	2	7		61	1	48	|		198
P-23Fcl				4						2	|	1	1	65	|	|	|	|		66	|	95	4		238
P-23Ccl										2	|	|	2	33	1	55	1	10		26	|	90			220
P-22Bcl										6	|	|	1	52	4	127	1	7		41	|	41			280
P-21Ecl									55	4	4	|	|	39	|	87	1	12		33	|				235
P-21Bcl									48	3	|	|	1	56	|	89	1	3	|	23	|				224
P-20Bcl			*P. originalis* Zone						63	3	1	1	2	66	1	96	|	15	1	16					265
P-18Bcl									86	1	|	|	3	47	|	18	|	10	|	20					185
P-17Bcl									61	2	1	1	1	39	6	85	1	12	|	18			1		228
P-16Bcl							10		65	9	5	1	5	115	5	19	1	13	1		2				251
P-15Bcl				6	37	1	160		166	11	|	|	3	232	10	69	6	34	3						738
P-15B			1	1	45	|	18		35	11	1	1	1	22	2	52	2	5							197
18 A	1	25		|	165	|	|	3	1	7	1	|	|					*B. triangularis* Zone							203

Figure 3. Data matrix of identified conodont taxa and quantities found in the Putilovo Quarry section.

allochthonous material. In the limestones, however, this genus occurs more commonly.

The lowermost part of the *B. navis* Zone is characterized by *Nothorthis, Glossorthis* and *Productorthis*, as well as a new species of *Neumania*, all of which appear at the base of the Volkhov Stage. *Apomatella, Raunites, Gonambonites, Ingria* and *Ujukella* first appear in the *P. originalis* Zone (Fig. 2), and a new orthid genus ranges from the middle *Oepikodus evae* Zone to the lowermost *P. originalis* Zone, where it was found in the carbonate mud mounds (Tolmacheva, Fedorov & Egerquist, in press). *Paurorthis* and *Ranorthis* are dominant throughout the whole Volkhov sequence. Other genera, which are less common but occur in most samples (together usually comprising less than 10% of the total number of individuals), are *Apomatella, Antigonambonites, Ingria* and *Ujukella*. *Raunites* is quite rare, whereas *Paralenorthis* is common in some samples but generally rare. Early representatives of the cosmopolitan genus *Skenidioides* were found in a few samples from the middle Volkhov Stage.

4.c. Ostracodes

Ostracodes in the clay intervals of the Volkhov Stage of the Putilovo Quarry are represented mostly by well-preserved single valves, which at certain levels show exceptional preservation. At some levels, however, the valves are slightly deformed and/or dolomitized. The taxonomic composition of the ostracode fauna is closely similar to that from studied sections from the western part of the Baltic/Ladoga Klint (Meidla *et al*. 1998). The fauna is dominated by several palaeocopid taxa, such as *Protallinnella grewingkii, Ogmoopsis bocki* and *Rigidella mitis*, but *Brezelina palmata* is rather abundant in some intervals (Fig. 5). The second largest group is the erisdostracan ostracodes, represented by *Conchoprimitia* sp. and *Miniconchoides*

Stage	Conodont zones	Sample numbers	*Panderina* sp.	New genus	*Neumania* spp.	*Ranorthis* spp.	*Paurorthis parva*	*Nothorthis penetrabilis*	*Antigonambonites* spp.	*Productorthis* spp.	*Ingria nefedyevi*	*Apomatella ingrica*	*Porambonites* sp.	*Porambonites reticulatus*	*Skenidioides* sp.	*Ujukella fastigata*	*Paralenorthis orbicularis*	*Raunites* sp.	*Apomatella secunda*	Others	Total
Volkhov	*B. norrlandicus*	P-28Ccl				54	33	6	2	1		6					6?				108
		P-27Fcl				4	50	2	21	2	1	7	1			7	19				114
		P-27Ecl				2	68	8	14	|	1		1			29	12		20		155
		P-27Dcl				48	58	15	3	|	6	9?	3	1	3	4	6	3?			159
		P-27Bcl				154	50	14	9	2	1	12	|			|		2			244
		P-26Dcl				51	68	36	9	2	2	8	1			1		5		3	186
		P-26Ccl				36	35	26	3	|	1	2	|			|		|			103
		P-25Hcl				316	40	51	23	3	2	14	1			|		|			450
		P-25Gcl				277	36	11	6	1	4	10	|			|		1			345
		P-25Ecl				832	81	|	9	4	3	34	|			|		|			963
		P-25Bcl				116	19	2	2	9	3	3	|			|		|			145
		P-25Acl				174	50	11	4	7	5	14	|			|		|			266
		P-23Fcl				147	202	16	7	|	4	10	1			|		1			388
		P-23Ccl				20	147	27	4	1	1	5	|			1					206
		P-22Bcl				14	115	9	10	20	1	8	|								177
	P. originalis	P-21Ecl				109	33	1	6	11	1	|	|								161
		P-21Bcl			6	30	69	9	4	8	3	1	|		54						184
		P-20Bcl			5	50	40	13	4	31	2	|	|								145
		P-18Bcl			3	12	233	11	7	4	1	|	1								272
		P-17Bcl			2	2	324	30	10	49	1	3									421
		P-16Bcl			7	83	29	45	2	3	|										169
		P-15Bcl			5	214	170	5	1	2	|										397
		P- 15Acl			19	|	416	2	2	|	1										440
		17A			3	756	81	10	2	173											1028
		18A		11	1	1270	14	73	4	27						*B. triangularis* Zone					1400

Figure 4. Data matrix of identified brachiopod taxa and quantities found in the Putilovo Quarry section.

minutus. Rare kloedenellid ostracodes are represented by occasional specimens of *Unisulcopleura punctosulca* and binodicopids by *Laterophores ansiensis*. The upper part of the studied sequence is characterized by rare finds of *Tallinnellina murus*, which has not been described previously from the Volkhov Stage of the eastern Baltic area.

5. Community properties

Faunal abundance and presence/absence data are strongly controlled by the preservation potential of faunas which in turn is related to palaeoenvironmental settings and most importantly to the rates of sedimentation (Parsons & Brett, 1991). Nevertheless, some observations on the preservational potential of modern shell assemblages indicate that relative abundance data may well illustrate the composition of the original communities (Kidwell & Flessa, 1996).

Taphonomic analyses of fossil assemblages in Putilovo Quarry indicate a more or less uniform environment for preservation of conodonts, brachiopods and ostracodes throughout the studied section (Tolmacheva *et al*. 2001). The type of preservation is consistent with a taphofacies characterized by low sedimentation rates, low environmental energy, and restricted or normal water oxygenation (Brandt, 1989). Calcitic shell material is relatively well preserved in the collection, although the shells are slightly corroded and commonly disarticulated. The overall fragmentation level of brachiopods and ostracodes is high, but size sorting of bioclasts is not apparent. The samples represent strongly time-averaged deposits and reveal significant spatial evenness of faunal diversity estimates (Tolmacheva *et al*. 2001). Thus the changes in fossil diversity through the Volkhov Stage can be expected to reflect the relative changes in the original benthic population structure.

Stage	Conodont zones	Sample numbers	*Conchoprimitia* spp.	*Tallinellina primaria*	*Rigidella mitis*	*Laterophores ansiensis*	*Laterophores*?	*Ogmoopsis* sp. nov.?	*Ogmoopsis bocki*	*Protallinella grewingkii*	*Miniconchoides minutus*	*Brezelina palmata*	*Conchoprimitia gammae*	*Incisua ventroincisurata*	*Glossomorphites digitatus*	*Aulacopsis simplex*	*Tallinellina murus*	*Eobromidella cicatriosa*	*Elliptocyprites nonumbonatus*?	Others	Total
Volkhov	*B. norrlandicus*	P-28Ccl							14	23			43		6			2		1	89
		P-27Fcl							8	11			115		5	9	5	1			154
		P-27Ecl							12	47			35		|	3	6				103
		P-27Dcl							11	13			66		1	1					92
		P-27Bcl			2				14	8			58		2						82
		P-26Dcl	61	1	13				51	6	19	2	|	1	|				3	1	158
		P-26Ccl	|	2	5				22	13	14		77	3	4						133
		P-25Hcl	6		40				13	35	5		|	|	1						100
		P-25Gcl	29		37				145	40	134		|	|					21		406
		P-25Fcl	|		9				10	17	11		36	|							74
		P-25Bcl	|		23				17	13	17		7	2							56
		P-25Acl	|	2	26				26	38	7		3								74
		P-23Fcl	2		47				53	4	149		|						3	1	259
		P-23Ccl	27		56				15	1	10		|								109
		P-22Bcl	|		2				10	83	5		6								104
	P. originalis	P-21Ecl	6		3				30	59	6		|								104
		P-21Bcl	|		9				28	37	3		15								83
		P-20Bcl	|	3	2				27	105		1	3								136
		P-18Bcl	|	7	5				3	4		72	20								99
		P-17Bcl	|		8				53	14		5	7								79
		P-16Bcl	|	5	31				23	5		16	2								46
		P-15Bcl	4	2	13		1	1	172	11	7										211
		17A	9		14	3			50	4											80
		18A	5	29	95							*B. triangularis* Zone									129

Figure 5. Data matrix of identified ostracode taxa and quantities found in the Putilovo Quarry section.

5.a. Density of fossil remains

The studied fossil assemblages are characterized by very high numerical density of the fossil remains, which might be due to high condensation of the deposits (Fig. 6, Table 1). The abundance of bioclasts per 100 g varies from 2000 up to 5000 or even more. Absolute values of bioclasts are poorly comparable with published data on fossil or modern faunal density, due to the different methods used to collect samples and density estimation. However, our results correspond with the empirical observation that the density of fossils is much more variable than the species richness in the sediments (Armentrout, Echols & Lee, 1991). Our previous studies confirmed the high lateral variability of fossil densities in the Middle and Upper Volkhov stages. We suggested that a vertical variation in fossil density less than 15–20 % for ostracodes, brachiopods and conodonts, and more than 50 % for echinoderms and bryozoans, may be connected with laboratory treatment, and/or small-scale lateral variations in the sediment, and should not be interpreted as true temporal variation (Tolmacheva *et al*. 2001). We also suggest that the variability in the density of brachiopods collected from a particular bed through the locality was more likely controlled by corrosion and amalgamation of the valves, whereas fragmentation of fossils and articulation appears to be almost the same in lateral transects of the locality (Tolmacheva *et al*. 2001).

The number of brachiopods shows little variation through the section of the Volkhov Stage, rarely exceeding 150 specimens per 100 g sample weight. In the major part of the section, the stratigraphic variability of brachiopods is less than the relative error connected with the heterogeneity in small-scale lateral distribution of fossil remains. Only at one stratigraphic level

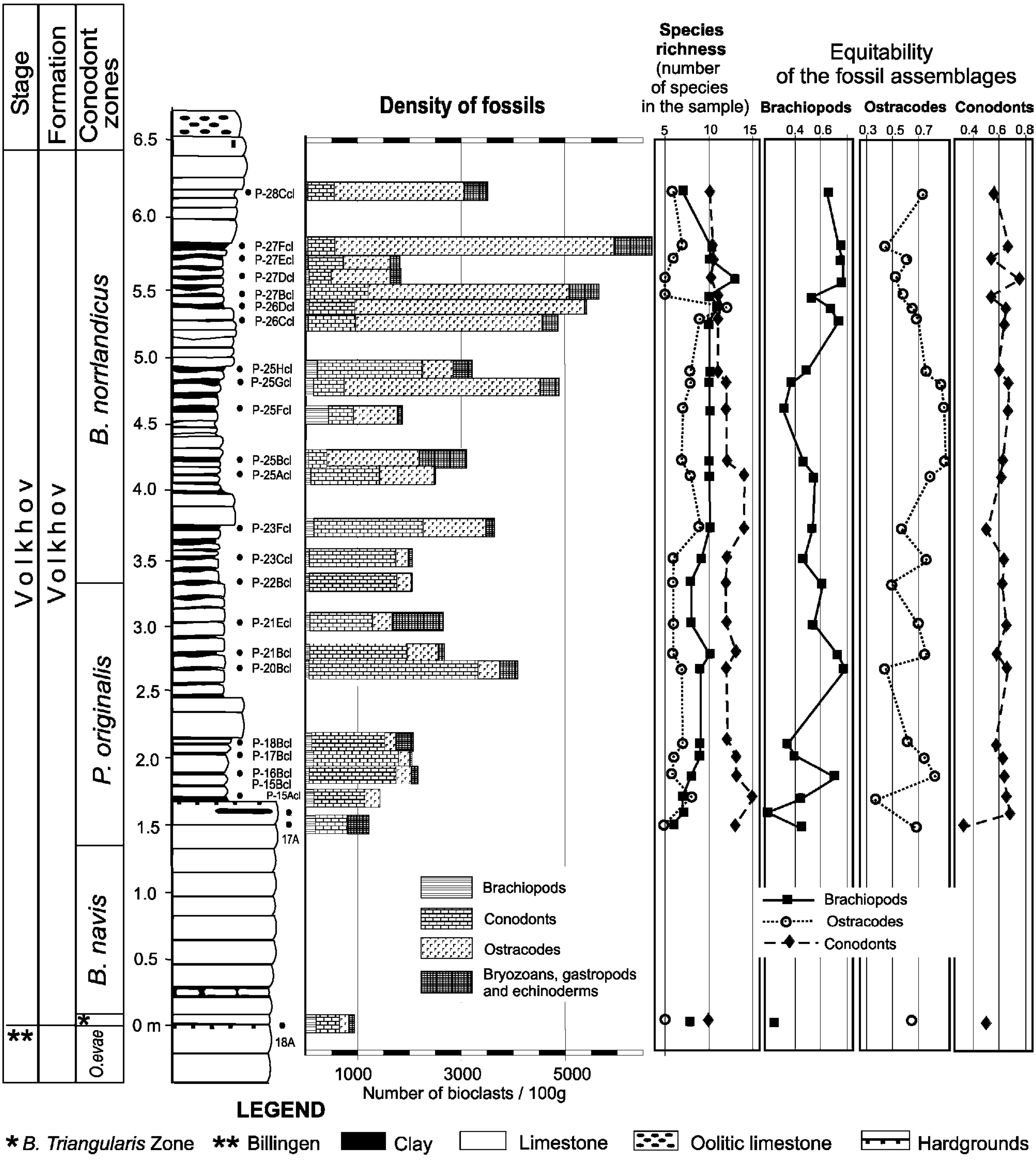

Figure 6. Stratigraphical column (weathering profile) of the Volkhov Stage with density values of fossil remains, species richness and equitability of fossil assemblages. Histograms show the density of fossils expressed as number of bioclasts per 100 g of the sediment.

(sample P-25Fcl), in which *Ranorthis* is extremely abundant (91 %), is the amount of brachiopods almost three times higher than in the other samples.

The ostracodes have variable but relatively low densities in the Lower, Middle and lowermost part of the Upper Volkhov stages. In the Upper Volkhov their abundance is ten times higher and often comprises more than 3000 specimens per 100 g, which is also reflected in the increase of coarse fractions at these stratigraphic levels. Despite the remarkable stratigraphic variability, the tendency for ostracode density to increase seems to be significant and may be connected with environmental changes in the basin (Fig. 6).

The density of conodonts gradually decreases through the Volkhov Stage from 2000 specimens per 100 g in the Lower Volkhov to 1000 specimens in the

Table 1. Data matrix of fossil remains in samples from the Putilovo Quarry section

Samples	Brachiopods	Conodonts	Ostracodes	Bryozoans	Gastropods	Echinoderms	Total
P-28C	39	514	2501	3	0	448	3505
P-27F	37	524	5393	8	0	746	6708
P-27E	49	678	902	0	0	186	1814
P-27D	68	419	1136	5	0	206	1835
P-27B	89	1110	3881	4	0	578	5663
P-26D	68	872	4438	0	0	44	5422
P-26C	46	913	3610	6	0	295	4870
P-25H	222	2019	595	1	177	164	3179
P-25G	152	587	3782	2	0	368	4891
P-25F	438	479	845	1	14	85	1862
P-25B	53	350	1779	0	6	918	3107
P-25A	108	1330	1052	0	10	11	2510
P-23F	154	2110	1203	3	3	167	3640
P-23C	70	1668	241	2	45	29	2054
P-22B	67	1692	282	6	0	16	2064
P-21E	80	1206	361	50	0	955	2652
P-21B	75	1876	602	7	2	110	2671
P-20B	64	3258	420	2	0	337	4082
P-18B	112	1406	170	59	0	331	2078
P-17B	149	1643	210	44	0	13	2058
P-16B	66	1673	290	14	129	17	2189
P-15B	158	987	285	1	6	14	1451
17A	190	600	10	4	0	410	1214
18A	200	445	180	1	0	110	936

upper part (Fig. 6). This decrease, however, could be a result of the increasing amount of coarse fraction in the clays that is connected with a higher number of ostracodes. The small fluctuations in the conodont density through the section do not exceed the variability of small-scale lateral variability of conodont density.

The density of echinoderms and bryozoans varies significantly through the section, but it is not possible to analyse the patterns in detail on account of the high lateral variability (68 % and 54 %, respectively). The only observable pattern is that the echinoderms have an approximately uniform density throughout the studied interval and that bryozoans are much more numerous in the Middle Volkhov as compared with the Lower and Upper Volkhov stages.

Gastropods are preserved as glauconitic moulds and therefore their numbers are strongly correlated with the content of glauconite in the sediments (Fig. 7).

5.b. Species richness

Species richness is specified as the total number of species in a standardized sample size. There has been considerable debate in the ecological literature concerning the correct methods of measuring species richness (e.g. Kowalewski, 1996). It has been shown that estimates of species richness are strongly affected by sample size, time averaging of sediments and heterogeneity in the completeness of fossil records, as well as by the quality of sampling and state of knowledge of particular faunal groups (Kowalewski, 1996). The fossil assemblages of the Volkhov Stage are more or less uniform in such factors as sample size, and nature of preservation throughout the section, although different faunal groups were considered at different taxonomic levels. Empirical observations on larger samples from some levels indicated that sample sizes used for the estimation of species richness were sufficient to obtain all taxa of the groups under discussion.

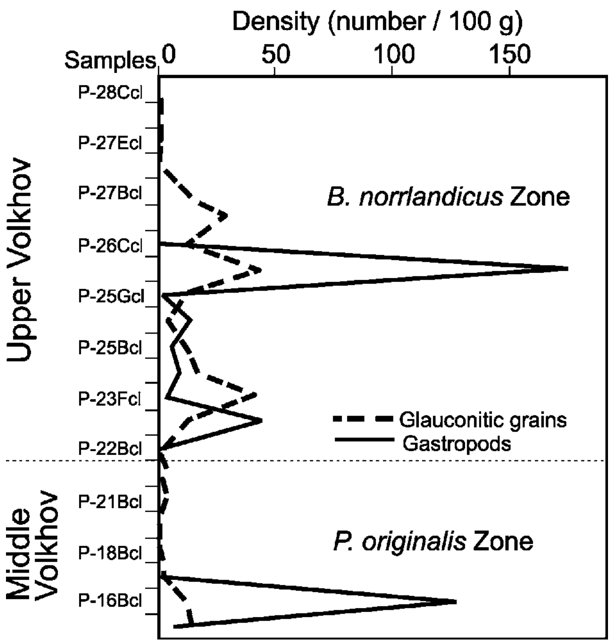

Figure 7. Distribution of glauconitic grains and gastropods in the Putilovo Quarry section. Note that gastropods are preserved as glauconitic moulds.

Conodonts demonstrate an insignificant gradual decrease in species richness from the Middle to the Upper Volkhov (Fig. 6), whereas the abundance of brachiopod genera is relatively higher in the Upper Volkhov Stage. The number of ostracode species gradually increases up to the upper part of the Upper Volkhov, where it was followed by a remarkable decrease.

5.c. Species diversity and equitability

Species heterogeneity, diversity or equitability describes how evenly individuals are distributed among the recorded species. High values of equitability occur when the species present are equal or virtually equal in abundance.

The conodont communities in the studied section are relatively even, with a small-scale stratigraphic fluctuation that in the major part of the section is mostly less than the lateral variations in the equitability of the conodonts through the section (Tolmacheva *et al.* 2001). Only the samples from the lowermost beds of the Volkhov Stage are characterized by communities with a strong dominance of *Drepanoistodus forceps* and thus have low values of equitability (Fig. 6, Table 2).

The equitability of ostracodes varies more significantly and its average value is higher than that of the conodont communities.

Brachiopods demonstrate lower average values of equitability with more significant variability than the other studied groups (Fig. 6). Usually the assemblages show strong dominance (up to 90 %) by one genus, either *Ranorthis* or *Paurorthis*. These taxa usually do not dominate together but display a well-pronounced negative correlation in their abundance. Changes in domination in the brachiopod assemblages are common and can be recognized at least 12 times in the clays during the Volkhov. However, the correlation between these events and environmental changes expressed in the sediments is obscure. Generally brachiopod communities show more even composition in the Upper Volkhov Stage.

There is no correlation between the equitability trends of different faunal groups, which probably reflects different environmental responses from taxa with different life modes. However, at some stratigraphic intervals, for example, the lowermost Middle Volkhov, ostracodes and brachiopods demonstrate similar patterns of equitability dynamics, with a significant decrease followed by an increase in the next two levels. On the other hand these groups show a strong negative correlation in the upper part of the Volkhov Stage.

Table 2. Equitability values for the faunal groups

Samples	Brachiopods H'/H'_{max}	Ostracodes H'/H'_{max}	Conodonts H'/H'_{max}
P-28Ccl	0.67	0.73	0.57
P-27Fcl	0.72	0.49	0.65
P-27Ecl	0.74	0.61	0.53
P-27Dcl	0.74	0.54	0.75
P-27Bcl	0.54	0.60	0.53
P-26Dcl	0.68	0.67	0.64
P-26Ccl	0.73	0.69	0.63
P-25Hcl	0.50	0.76	0.60
P-25Gcl	0.38	0.85	0.67
P-25Fcl	0.30	0.90	0.67
P-25Bcl	0.46	0.91	0.62
P-25Acl	0.54	0.80	0.61
P-23Fcl	0.53	0.58	0.50
P-23Ccl	0.47	0.76	0.62
P-22Bcl	0.62	0.50	0.61
P-21Ecl	0.54	0.70	0.65
P-21Bcl	0.72	0.76	0.57
P-20Bcl	0.79	0.44	0.63
P-18Bcl	0.32	0.63	0.58
P-17Bcl	0.40	0.74	0.64
P-16Bcl	0.70	0.82	0.64
P-15Bcl	0.48	0.37	0.66
P-15Acl	0.16		0.68
17A	0.45	0.69	0.29
18A	0.22	0.27	0.50

6. Comparison of diversity estimates from limestones and clays

Diversity data on faunal communities from limestone and clay are comparable in species richness and equitability of the assemblages, although they cannot be evaluated by exactly the same methods. The differences between faunal communities from clays and limestones exist but are not significant when studied in detail. The brachiopod communities in the clays of the Volkhov Stage are usually dominated by *Paurorthis* or *Ranorthis*, whereas *Paurorthis* almost consistently dominates in the limestones. This difference between limestones and clays, however, could be due to different preservational potential of these brachiopod genera. Variation in preservational conditions and different sample sizes could also be responsible for the more frequent records of *Porambonites* from the limestones.

The taxonomic composition of ostracodes from limestones and clays is approximately the same, but with a higher proportion of fragile taxa in clay samples. This difference may result from different laboratory treatment of the limestone and clay samples, and better preservation of robust specimens than fragile ones in limestones.

Conodont elements of *Baltoniodus* were slightly more numerous in limestone samples than clay samples but this could also be due to the laboratory treatment. Usually, the variability in relative abundance of taxa between collections from tempestites is related to size sorting (Westrop, 1986), but our collections show no obvious size sorting.

7. Interpretation of diversity data

The fossil assemblages of the Volkhov stage are characterized by:

(1) A high density of faunal remains that increase from the Middle to Upper Volkhov. Generally the Volkhov assemblages display an increase in the density of ostracodes and tentatively some decrease in bryozoan density. Other fossil groups demonstrate more or less stable densities through the same interval.
(2) Moderate faunal richness, for all studied groups throughout the section. Conodont assemblages became less rich in the Upper Volkhov, which is the opposite of brachiopods and ostracodes. Ostracode richness is more variable but has relatively low values in the uppermost Volkhov Stage.
(3) The equitability of the conodont assemblages varies only slightly through the section, whereas brachiopods and ostracodes are more dominant and reveal more complicated fluctuations of equitability.

In general, diverse communities that exist under conditions of environmental stability have high richness and equitability values. Communities that exist under physically or chemically stressed conditions and/or experience low levels of environmental stability show low values of equitability and species abundance (Peters & Bork, 1999). The faunal communities from the clay deposits of the Volkhov Stage are generally characterized by moderate values of species richness and equitability (Fig. 6). These diversity characteristics indicate communities that experienced stable but somewhat stressed conditions, which is expected for a basin with low productivity like that in Baltoscandia (Jaanusson, 1973).

Two types of environmental change can be invoked to explain the dynamics of diversity estimates as described in the following sections.

7.a. Gradual environmental changes or sequence stratigraphic framework

The faunal communities of the Volkhov Stage demonstrate a distinct gradual change through the sequence. This is expressed in a decrease in the diversity of the pelagic/nektobenthic component of the community (conodonts) and an increase in the diversity of benthic organisms.

The diversity of faunal communities is generally strongly depth-related (Karakassis & Eleftheriou, 1997; Flach & de Bruin, 1999, and references therein). However, the relationship between marine biodiversity and water depth remains uncertain, as it is strongly affected by the heterogeneity of the ecological landscape, that is not always positively correlated with a depth decrease (Gray *et al*. 1997). That shallow water environments are more diverse is borne out by a number of empirical surveys (Karakassis & Eleftheriou, 1997), and confirmed by investigations of palaeocommunities where time averaging smooths the effect of short-lived heterogeneity on the landscape (Kidwell & Flessa, 1996). Thus, onshore settings usually have higher species richness as well as a higher density of fauna, which is more sharply pronounced, in the regions of siliciclastic-sediment starvation. According to the sequence stratigraphy paradigm, the highest diversity is expected to occur around sequence boundaries or at the beginning of the transgressive system tracts, and the lowest diversity will coincide with the highstand system tracts (Brett, 1998). Clusters of first and last occurrences are expected at major flooding surfaces in the transgressive systems tracts and at sequence boundaries (Holland, 1995).

Variation in fossil density and richness within the studied section only partly corresponds with the well-known patterns of faunal diversity predicted by the sequence stratigraphic framework. The beginning of the transgressive tract is marked by a slightly higher diversity of conodonts but lower diversity of ostracodes. Conodont communities are extremely uneven at the beginning of the lowstand tract (*B. triangularis* Zone), whereas the highstand tract (Upper Volkhov) is characterized by increased brachiopod diversity and ostracode densities through the parasequence. Ostracodes are rather sensitive to environmental changes. They may occupy a wide range of habitats but tend to be particularly abundant in shallow hypersaline or brackish environments and are interpreted as indicating a low-energy restricted or peritidal environment (Benson, 1959). Thus, the progressive decrease in ostracode species richness and increase in the density of individuals upward through the sequence may be the result of the gradual shallowing of the basin in the uppermost Volkhov Stage. Ostracode communities that have been studied from the more shallow-water Volkhov interval of the carbonate sequences in Estonia are relatively diverse and rich, and reveal similar patterns of population dynamics through the Upper Volkhov (Meidla *et al*. 1998). Bryozoans, the distribution of which are depth as well as temperature controlled (Franseen *et al*. 1997; Walter, 1989), are more abundant in the Middle Volkhov, but decrease in density upwards in the section, possibly due to a gradual shallowing during the Volkhov period.

In general the faunal communities of the Volkhov Stage are stable and represented by a single biofacies reflecting the relative environment quiescence. The area experienced comparatively little temporal variation in environmental factors, and depositional conditions appear to have been uniform during the Volkhov.

7.b. Small-scale environmental changes

Small-scale variations in the diversity estimates show no correlation with the small-scale sea-level changes reconstructed for this part of the basin, but seem to reflect the error component of the diversity measurements or to result from unknown environmental parameters. It is also likely that complex, as yet unknown, environmental changes are responsible for the changes of dominant taxa in the brachiopod communities, but these changes are not correlated with variability in the diversity structure of the assemblages. It is widely proposed that the most volumetrically abundant components of the community are not necessarily of the greatest environmental significance in microfacial analyses (Spence & Tucker, 1999), and that changes in composition rather than in abundance are significant in characterizing microfacies in the context of high frequency relative sea-level changes.

Thus, it may be suggested that the dominant elements of the studied palaeocommunity, like brachiopods, ostracodes and conodonts, were not sensitive to small-scale sea-level changes and other environmental changes of high frequency.

8. Conclusions

Studies of fossil distribution patterns in a single section cannot determine the complete history of the original diversity patterns of a region, but some observations concerning the diversity and temporal dynamics of the palaeocommunities can be made:

(1) Faunal communities of the Volkhov Stage in Putilovo Quarry were diverse and relatively stable during this part of Middle Ordovician times. Rhynchonelliformean brachiopods are the volumetrically dominant members of the community throughout the Volkhov Stage. Ostracodes became significantly more numerous in the Upper Volkhov.

(2) Small-scale variability in the diversity estimates does not correlate with the small-scale sea-level changes reconstructed for this part of the basin and seems to be connected with the error component of diversity measurements or to result from undetected environmental parameters.

(3) Within this section, variation in fossil density and species richness does not correspond well with known patterns of the sequence stratigraphic framework or with the sequence stratigraphic constraints suggested for this region. However, diversity dynamics of brachiopods and ostracodes confirm the relative upward shallowing of the basin into the Upper Volkhov.

(4) There is almost no correlation between the variability in diversity estimates for different faunal groups. Thus, community structure was not tightly integrated and species responded to environmental changes according to their individual environmental tolerances.

(5) The gradual increase of bioclast content in the clays through the Volkhov interval corresponds well with data reported by Lindström (1984), who documented the relative increase of the amount of bioclasts obtained from point counting of thin sections from a contemporaneous interval in central Sweden and Öland.

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