Conodonts and brachiopods from the Volkhov Stage (Lower Ordovician) microbial mud mound at Putilovo Quarry, north-western Russia

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Microbially mediated clay mud mounds are widely developed in the Lower Ordovician succession east of St. Petersburg (Russia) and are associated with a diverse and abundant fauna of brachiopods, ostracodes, echinoderms, bryozoans and conodonts. The lithology of one such mud mound in Putilovo Quarry has previously been studied, but the faunas associated with the mounds have not been investigated to date. Clay lenses in the Putilovo mud mound yield conodont assemblages belonging to the *Baltoniodus triangularis* and lowermost part of the *Paroistodus originalis* zones and these stratigraphical intervals are much thicker in the mud mound than in the coeval Lower Ordovician succession lateral to the mound. The compositions of the conodont and brachiopod assemblages are generally the same in the mud mound as in contemporaneous beds. The occurrence of relatively fewer conodont elements in the mud mound than in the surrounding successions probably indicates the higher rate of accumulation of the mud mound clays. Juvenile brachiopods are more numerous in the clays of the mud mound than outside the build-up, supporting the hypothesis that the mounds included ecologically stressed environments.

Key words: Microbial mud mounds, conodonts, brachiopods, Lower Ordovician, Russia.

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Microbial mud mounds with a clay core were discovered in the upper part of the Lower Ordovician of the East Baltic at the beginning of the last century, but they have only recently been studied and described in detail (Dronov & Fedorov 1994; Fedorov & Dronov 1998; Fedorov *et al.* 1998; Fedorov 1999). More than 15 mud mounds of different sizes are now known from quarries and natural outcrops along the Baltic - Ladoga Klint from the Narva to the Syas rivers in the vicinity of St. Petersburg and in Estonia. The smallest mud mounds occur as clay lenses, not more than 1 m across, covered by a micritic crust, whereas the largest Simonkovo mud mound is approximately 250–350 m wide, 4–5 m high, and has a complex inner structure. One of the best exposed of the large mud mounds is located in the central part of Putilovo Quarry (Fig. 1).

Lamination in the clays and sparitic layers in the Putilovo mud mound indicates that this build-up, like other similar structures in the region, was formed as a result of biotic activity (Fedorov 2003). The clay sediments of the mud mound contain a diverse and abundant fauna of brachiopods, ostracodes, echinoderms, and bryozoans together with rarer taxa such as conodonts and graptolites. The architecture of the Putilovo mud mound was described in detail by Fedorov *et al.* (1998); however, the faunas have not previously been investigated in detail. This paper compares the composition of brachiopod and conodont assemblages in the mound with that elsewhere in the adjacent Lower Ordovician successions.

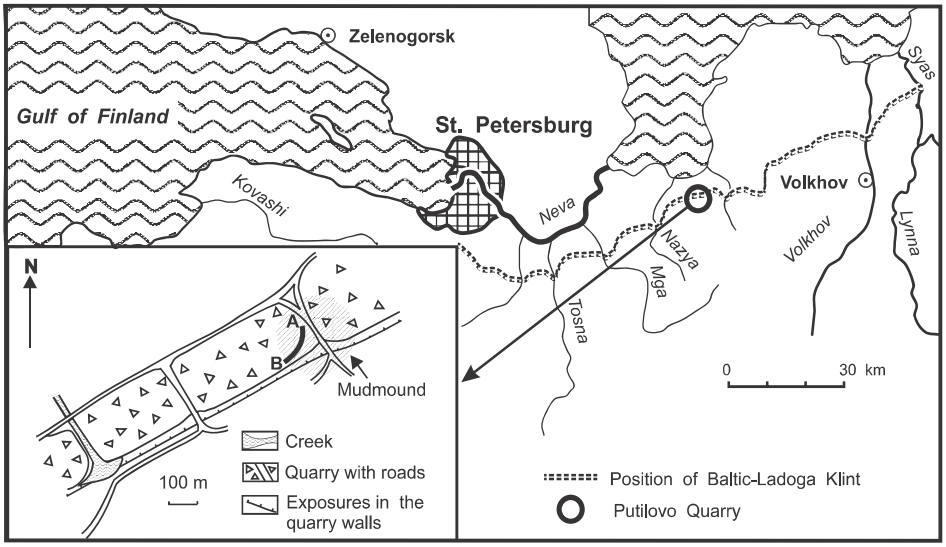


Fig. 1. Schematic map of the East Baltic with the position of Putilovo quarry. Sketch of the quarry shows the location of the mud mound.

Geological settings and lithology of the mud mound

Putilovo Quarry is one of the classic Lower Ordovician localities in the vicinity of St. Petersburg where the lithostratigraphy of the Volkhov Stage is well documented (Dronov *et al*. 1995; Dronov *et al*. 1996; Dronov & Fedorov 1995). The base of the Volkhov Stage is marked by a distinctive hardground, the 'Steklo' surface, which is emphasized by borings and glauconitic enrichment. The lower part of the Volkhov Stage (Dikari Member) has a thickness of approximately 1.4 m, and includes eleven recognizable lime-

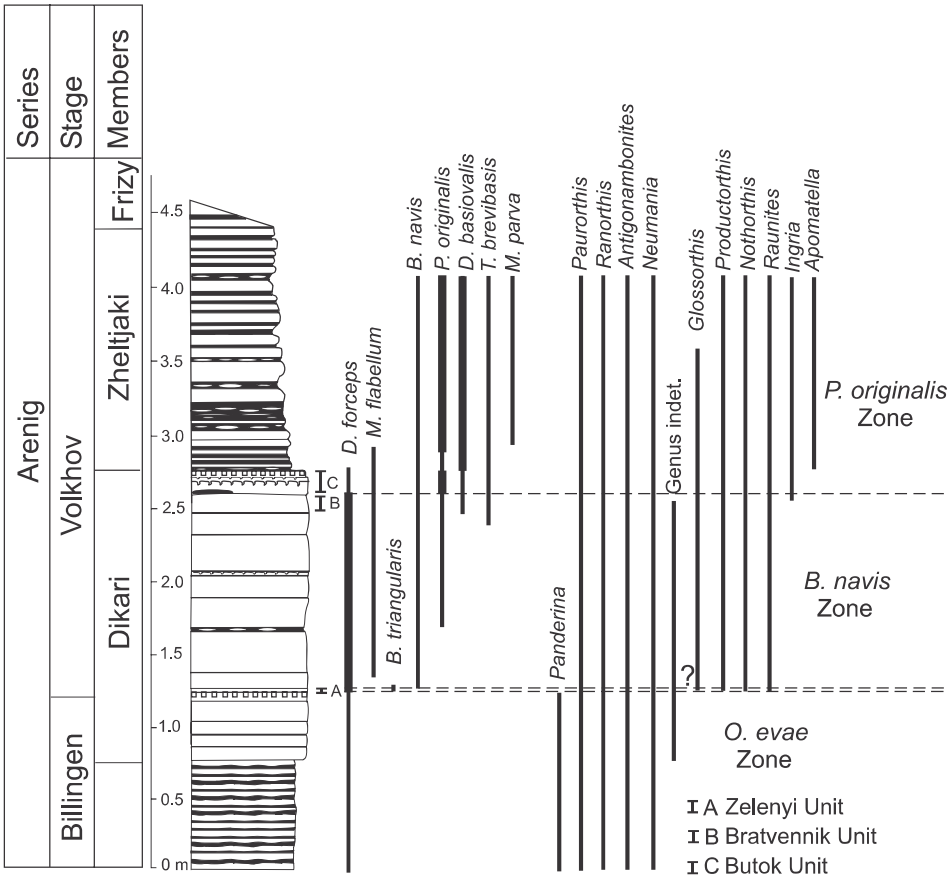


Fig. 2. Distribution of selected conodonts and brachiopods in the Lower – Middle Volkhov Stage of the Putilovo Quarry section. Bold lines mark the intervals of dominance of particular species.

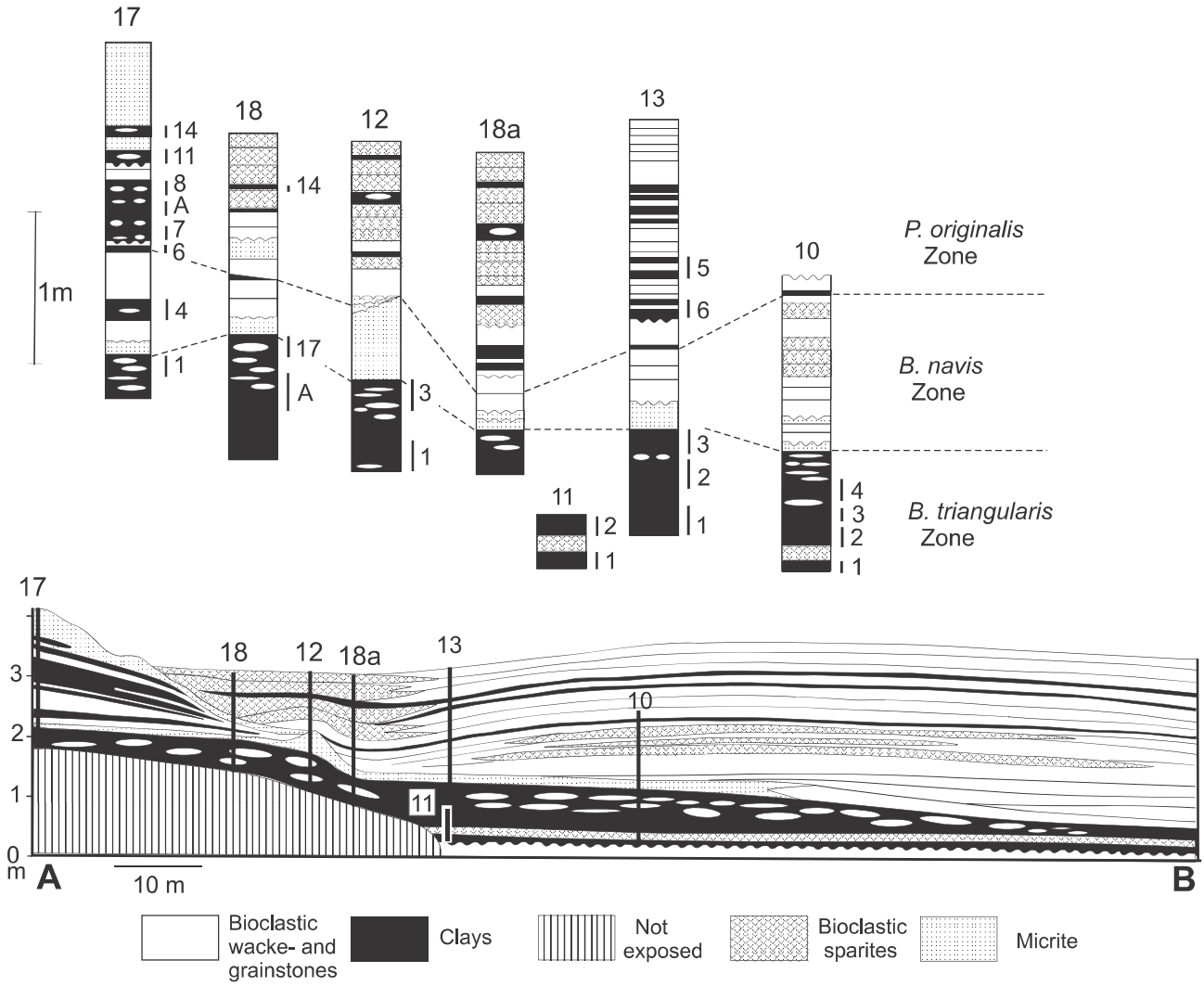


Fig. 3. Cross section of the Putilovo mud mound with the location of sections and sampled levels.

stone beds. The Middle Volkhov (Zheltjaki Member) is approximately 1.7 m thick and is composed of seven units of intercalated clays and limestones (Dronov & Fedorov 1995; Fig. 2). The Lower – Middle Volkhov interval encompasses three conodont zones: *Baltoniodus triangularis, Baltoniodus navis* and *Paroistodus originalis* (Fig. 2).

The entire Volkhov sequence is remarkably constant in thickness, clay content and other lithological features, and extends for several hundred km along the Baltic-Ladoga Klint. In contrast, the mud mounds are associated with very rapid lithological changes, indicated by a significant increase in clay content and the upward displacement of some limestone beds. The area affected by the mud mound is marked by the appearance of a thin clay layer on the 'Steklo' surface and the increased thickness of the lowermost bed of the Volkhov Stage (Zeljenyj Unit), which can be observed for a distance of 100–150 m outside the mud mound. In the surrounding successions, the Zeljenyj Unit usually is not more than 7 cm thick, whereas close to the mud mound it becomes as thick as 25 cm.

The mud mound is more or less isometric in plan view, but the north-eastern part of the structure is not exposed (Fig. 1). A detailed lithological description of this mud mound was given by Fedorov *et al*. (1998) and only a brief description is provided here. The mud mound is composed of two clay lenses with the lower lens situated on the 'Steklo' hardground surface and laterally more extensive than the upper one (Fig. 3).

The peripheral part of the mud mound is composed of two micritic layers and the lower clay lens that wedges into the more typical 'standard' succession of the surrounding Dikari limestones. In the exposed part of the central structure, the lower clay lens is approximately 1.5 m thick. The upper part of this clay

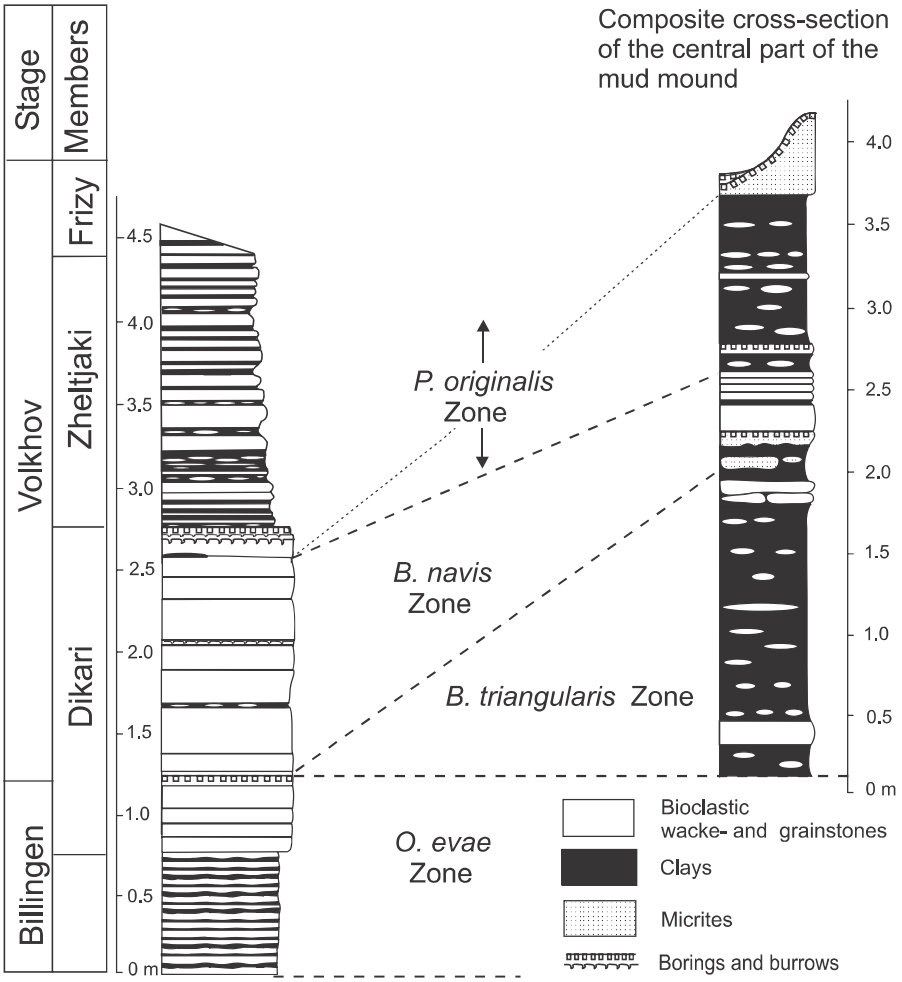


Fig. 4. Comparison between the biostratigraphic units of the standard sections in Putilovo Quarry and the section through the central part of the Putilovo mud mound (section 17).

lens contains numerous, lens-shaped limestone pebbles which are more abundant towards the edge of the structure. A 15 cm thick layer of striped sparites can be traced through all the exposed central part of the lower clay lens dividing it into two parts. The clay below the sparite layer is violet-grey and contains numerous small glauconite grains, and minute brachiopod and ostracode valves, while the clay above the sparite layer is green and enriched with calcareous fossil fragments. The thin layer above the sparites contains abundant graptolite detritus with identifiable fragments of *Expansograptus hirundo* (T. Koren', personal communication). The upper part of the clay lens is bioturbated, whereas the lower part is weakly laminated.

The upper clay lens is significantly smaller in overall size and is mainly restricted to the central part of the mud mound (Fig. 3, section 17). The clay contains abundant carbonate nodules and fossil fragments. The micritic crusts, which cap the clay lenses, are composed of cryptocrystalline, possibly cryptic, microbial carbonates. They contain fine-grained brachiopod and ostracode detritus as well as rare monaxone sponge spicules. The lower crust in the Putilovo mud mound consists of two micritic beds, which are closely spaced and correspond to two bioclastic wackestone layers covering the marginal part of the structure. The upper surfaces of the micritic crusts, as well as small bioherms on the crusts, are characterized by hardgrounds with numerous *Trypanites* borings. The bioherms, and the hardgrounds between them, contain many holdfasts of echinoderms and bryozoans.

Methods and material

Six cross sections through the exposed part of the mud mound were sampled for conodonts and rhynchonelliformean brachiopods (Fig. 3). The stratigraphical distribution and numerical composition of the assemblages are given in Tables 1 and 2. Brachiopods from the upper part of the Dikari Member and lower part of the Zheltjaki Member of the standard successions

Section numbers	Sample numbers	*Drepanoistodus forceps*	*Drepanoistodus* cf. *D. basiovalis*	*Scolopodus rex*	*Oistodus lanceolatus*	*Cornuodus longibasis*	*Protopanderodus rectus*	*Decoriconus peselephantis*	*Periodon flabellum*	*Baltoniodus triangularis*	*Baltoniodus navis*	*Trapezognathus quadrangulum*	*Semiacontiodus sp.*	*Drepanoistodus basiovalis*	*Microzarkodina flabellum*	*Microzarkodina parva*	*Paroistodus originalis*	*Triangulodus brevibasis*	*Scalpellodus latus*	Others	Total
13	**5**	7				1	1				48	2	1	37		34	47	14			192
13	**6**	32		2		2	8				24	2		14	7		26	2	1		120
17	**11**	32					15				30			32	18		25	1	1		154
17	**8**	43						1	6		26			37	9		42	2			166
17	**A**	44		*P. originalis* Biozone			4				11			62	5		36	1			163
17	**7**	52					6				21		1	10	12		33				135
17	**6**	29					8	2	1		9	1		15	2			1			68
17	**4**	29		1			4	1			9			7	9		*B. navis* Biozone				60
18	**17**	107	25	1			9			5		3									150
18	**A**	165	25		1		7		3	1											202
17	**1**	126	0			1	15		1	5		1								2	151
12	**3**	127	0				6		3	1											137
13	**3**	120	9			1	6	1	3			1									141
10	**4**	117	16	1	1	1	29		4	1		1									171
12	**1**	94	12			1	10	1	1	2		1									122
13	**2**	80	4	1		1	11	1	3	1				*B. triangularis* Biozone							102
10	**3**	156	0				10		5												171
13	**1**	185	0		2	2	9	1	8	2										1	210
11	**2**	75	10		2		8		8	1											104
10	**2**	124	0	1		1	10		4												140
10	**1**	117	6	1	4	1	2		17	1											149
11	**1**	106	15		2	1	6		11	2											143

Table 1. Conodont element distribution in the samples from the Putilovo mud mound.

outside the mud mound were additionally sampled and studied. Two samples (18-A and 17-A from the upper part of the lower clay lens and from the upper clay lens respectively) were used for evaluation of the bulk composition of the fossil assemblage, including bryozoans, echinoderms and ostracodes. These two samples were processed by the method proposed for estimation of faunal diversity in clays (Tolmacheva *et al.* 2001). The content of bioclasts per 100 g of sediment was used as a measurement of the relative abundance of different faunas in the two clay lenses.

The distribution of conodonts and brachiopods in the successions of the Hunneberg and Volkhov stages of the Putilovo Quarry as well as the numerical composition of their assemblages have been partly presented in other papers (Egerquist 1999; Tolmacheva *et al.* 2001). Here, these data are used to compare the fossil assemblages in the surrounding Lower Ordovician strata with the assemblages from the coeval successions of the mud mound.

Biostratigraphic correlation of the mud mound and the surrounding deposits of the Volkhov Stage

The Putilovo mud mound was formed during the *B. triangularis*, *B. navis* and the beginning of *P. originalis* biozones (Fig. 4; Table 1). However, the thickness of the zones and therefore the rates of sedimentation of

Section numbers	Sample numbers	*Panderina* sp.	*Paurorthis parva*	*Ranorthis* sp. nov.	*Ranorthis* sp.	*Antigonambonites* sp.	*Neumania costata*	*Neumania* sp. nov.	New genus	*Glossorthis schmidti*	*Productorthis aculeata*	*Productorthis obtusa*	*Nothorthis penetrabilis*	*Ingria* sp.	*Apomatella ingrica*	*Raunites* sp.	Others	Juveniles (unidentified)	Total
13	**5**		187		2	2		3			1	87	3		7				292
13	**6**		55								1		4						60
17	**11**		57			*P. originalis*		Biozone					114						171
17	**8**		2	51							14			1					68
17	**A**		81	756		2		3			173		10					1060	2088
17	**7**		30	46							66		21						163
17	**7&8**		28	1			1 ?		4		80		5						119
17	**4**		2							29	8		2		*B. navis* Biozone				41
18	**17**		27	82							26								135
18	**A**		14	1270		4	1?		11		27		73					2409	3809
17	**1**		5	78		2		1	15		5		9						115
12	**3**		6	16			4	1	1		40		1				2		71
13	**3**		2		93				9		5?		22					123	250
10	**4**		10	55		1			21		5?		14					6	112
12	**1**		37	341*		1	1?		28		12		89			5?		50	564
13	**2**		6		149	1			3		3?							6	168
11	**1**	4			160	2	2?			1?	3?				*B. triangularis*				177
10	**1**	2	3	199									9		Biozone				213

*probably both *R. trivia* and *R.* sp. nov.

Table 2. Brachiopod distribution in the clay samples from the Putilovo mud mound.

the mud mound and surrounding deposits in Putilovo Quarry are markedly different.

In the standard section, the *B. triangularis* Zone has been identified only in the upper 2–3 centimetres of the Zeljenyj Unit. The same zone in the mud mound is up to 1.5 m thick in the central part and comprises the entire lower clay lens. The conodont assemblage of the *B. triangularis* Zone is strongly dominated by *Drepanoistodus* species, which constitute more than 80% of the assemblage. The relative abundance of *Protopanderodus rectus* and *Periodon flabellum* varies significantly through the clay lens (16–10% and 10–5% respectively), but does not reveal any obvious structure-related trend.

In the standard section in Putilovo Quarry the *B. navis* Biozone has a thickness of 1.2 m and comprises almost all the Volkhov part of the Dikari Member with the exception of the lowermost Zeljenyj Unit and the two uppermost limestone units. However, the thickness of the *B. navis* Biozone gradually decreases to 0.5 m in the central part of the mud mound, due to the reduction of the lower part of the zone.

The lower boundary of *P. originalis* Biozone in the Putilovo Quarry section is based on the increase in abundance of *P. originalis*. The first appearance of *Triangulodus brevibasis*, or its consistent occurrence in the medium-size samples, is widely used for recognition of the lower boundary of *P. originalis* in other parts of Baltoscandia (Löfgren 1978, 1995). However, in the Putilovo Quarry section this taxon appears below the acme of *P. originalis* in the middle part of the Dikari Member and very gradually increases its abundance through the section such that it is impossible to choose any level of critical significance. The increasing abundance of *P. originalis* in the uppermost layer of the Dikari Member (Butok Unit) coincides with higher proportions of *Drepanoistodus basiovalis*. In the overlying beds of the Zheltjaki Member *D. basiovalis* strongly dominates over *Drepanoistodus forceps* (Fig. 2).

The conodont assemblages from the upper clay lens of the Putilovo mud mound comprising *T. brevibasis*, abundant *D. basiovalis* and *D. forceps*, correspond well to the assemblage composition of the uppermost bed of the Dikari Member outside the mud mound. Here this interval has a thickness of approximately 20 cm

whereas the upper clay lens of the mud mound is more than 1.2 m thick. Limestones overlying the mud mound contain *Microzarkodina parva* indicating the middle part of the *P. originalis* Biozone.

In the standard Putilovo succession outside the mud mound, the brachiopod genus *Productorthis* outnumbers *Paurorthis* in the lowermost part of the *P. originalis* Biozone (Bratvennik Unit), whereas in the overlying bed (Butok Unit), *Paurorthis* is the most abundant of these two genera. Considering the lateral invariability of dominance of particular taxa in the same bed over several tens of meters (Tolmacheva *et al*. 2001) or even kilometres, dominating taxa in the mud mound assemblages are assumed to be the same as in the surrounding contemporary clays. Calculations of the brachiopods in section 17 (Table 2) suggest, that the upper clay lens of the mud mound, with a dominance of *Productorthis* over *Paurorthis*, correlates with the deposits below the Butok Unit. This correlation, however, is not firmly confirmed by sedimentological evidence and the possibility that environmental stress during deposition of the mud mound could produce heterogeneity in the brachiopod communities should not be neglected.

Composition of fossil assemblages in the mud mound

In microbial build-ups, the micro and macro faunas are usually preserved as autochthonous inhabitants and dwellers on ancient mats or as allochthonous elements (mostly planktonic) (Seong-Joo & Golubic 1999; Morris *et al.* 1997). The fossil assemblages of the Putilovo mud mound comprise all components of the surrounding Lower Ordovician fauna including conodonts, brachiopods, ostracodes, echinoderms, and bryozoans. Conodonts, being part of the nektonic fauna, represent the allochthonous elements in the mud mound, whereas the benthic brachiopods, echinoderms, ostracodes and bryozoans represent the autochthonous fauna. Echinoderms are the most abundant taxon in the sparitic lenses and flanks of the mud mound, and a strong enrichment of crinoids, as well as the appearance of crinoidal sparites in the ordinary limestone beds, are well-known indications of mud mound proximity. Ostracodes probably have more complicated preferences since their numbers differ significantly in the mud mound samples as well as through the whole Putilovo Lower Ordovician section (Tolmacheva *et al*. in press). A comparison of the fossil composition between the two clay lenses in the mud mound shows an increase in sessile organisms such as bryozoans and echinoderms upwards through the sequence. Both of these taxa are almost four times as abundant in the upper clay lens than in the lower one. The ostracodes show an opposite trend, with 180 ostracode specimens per 100 g of sample in the lower clay lens, and only 10 specimens per 100 g in the upper clay.

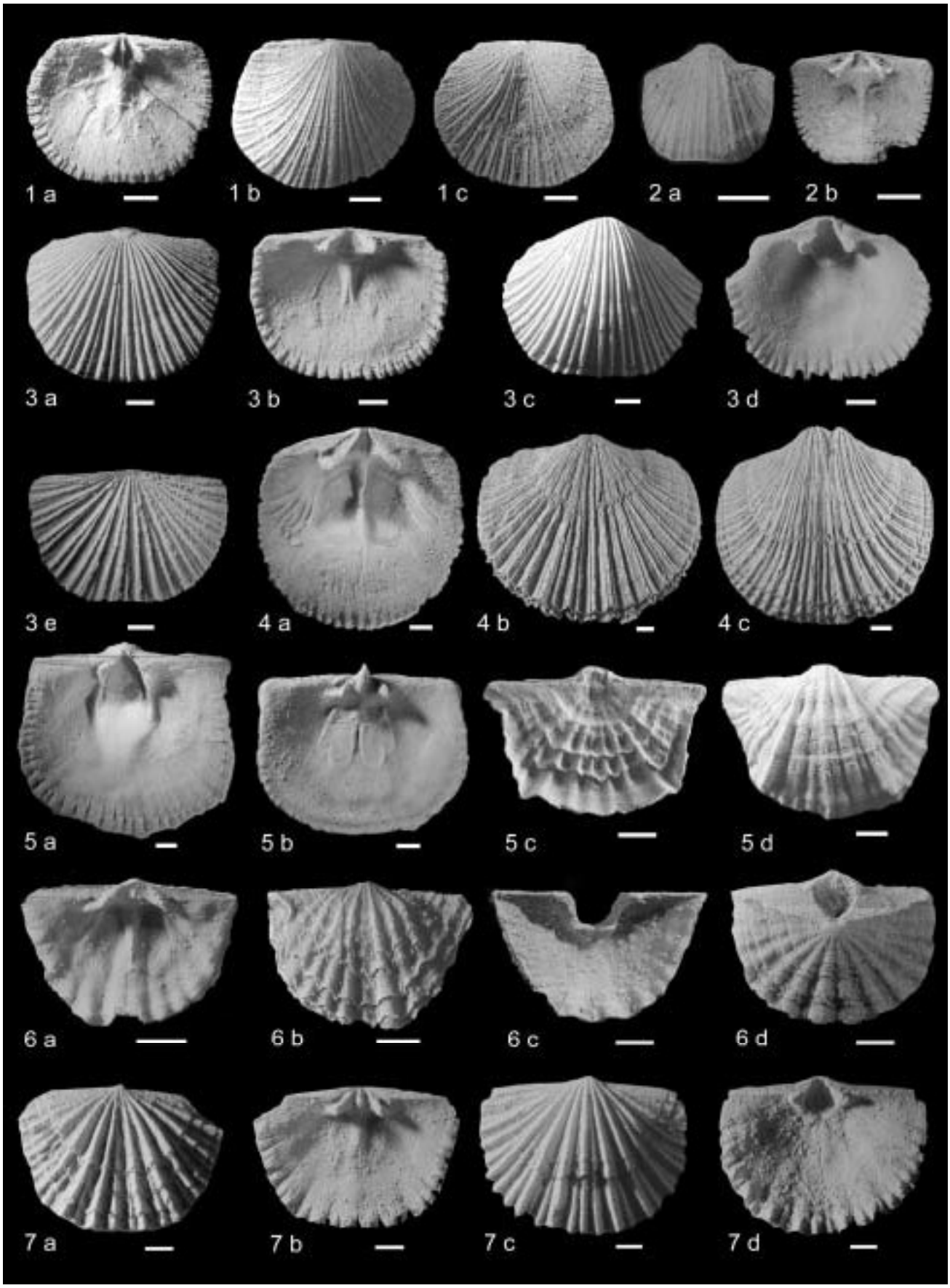
Brachiopods

The abundance of brachiopods is more or less equal in the two clay lenses. The composition of the brachiopod assemblage in clay lenses does not differ much from that in the clays of the surrounding strata, although in the lower clay lens (*B. triangularis* Biozone) comparison is not possible due to lack of coeval strata in the area. The only obvious difference is the larger number of juveniles in the clay lenses. Over 50% of the brachiopods in the mud mound represent juveniles, whereas the surrounding clays usually do not yield more than 20% juveniles.

The mud mound is dominated by the genus *Ranorthis* (most of them probably belonging to a new species) with a relative abundance of about 90% in the basal part of the lower clay lens and slightly decreasing numbers upwards in the sequence. Only in sample 17.4, just above the lower micritic layer, the dominating taxon is *Glossorthis*, comprising 70% of the brachiopod assemblage (Table 2). The brachiopod assemblages usually include *Paurorthis parva, Nothorthis penetrabilis, Productorthis,* and *Antigonambonites*. *Productorthis* is represented by *P. aculeata* below the micritic crust, above the crust both *Productorthis aculeata* and *P. obtusa* are present. *Productorthis* occurs throughout the section except for the lowermost *B. triangularis* Biozone where *Panderina* was found instead. Characteristic brachiopod species from the Putilovo mud mound are shown in Figure 5.

The clays of the mud mound are characterized by the presence of a very coarsely ornamented *Nothorthis penetrabilis*, which has been found together with the normal, more finely ornamented, morphotype. Adult specimens of this taxon that have been sampled outside the mud mound have usually 40 ribs or more at the margin, whereas the mud mound variant mostly has less than 30 ribs. It seems inappropriate to distinguish these two morphotypes, because of the highly variable number of ribs characterizing this species, but the coarser ribbed morphotype may possibly represent a new subspecies or an environmentally adapted variant.

Two new brachiopod taxa have been found in the clays of the mud mound. One is a previously undescribed orthid genus, which was also recorded from the middle part of the *Oepikodus evae* Biozone at the


1 a
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7 a
7 b
7 c
7 d

Popovka River. The other represents a new species of *Neumania*, and was collected from the lower and upper clay lenses of the mud mound, and from the clays of the surrounding successions of the *P. originalis* Biozone. (For description see Egerquist, in press).

Conodonts

The taxonomic compositions of the conodont assemblages are mainly similar in the mud mound samples and in the surrounding coeval layers. However, conodonts are less abundant in the mud mound samples than in the clays of the surrounding strata. Especially the micritic crusts are poor in conodonts; their abundance is here not more than 1000 elements per 1 kg sediment. The lower number of conodont elements in the mud mound indicates a higher rate of sedimentation of the clay forming the mud mound lenses.

The conodonts from the *B. triangularis* Biozone are much better preserved in the mud mound clay deposits than in the thin coeval limestone bed outside the structure. Moreover, clay samples contain conodont assemblages of the unmixed *B. triangularis* Biozone that rarely occur in samples of the surrounding succession. The clearly dominating species in the conodont assemblages of the *B. triangularis* Biozone is *D. forceps*, which is significantly more abundant than all other conodont species. A similar numerical composition of conodont taxa is typical for the *B. triangularis* Biozone reported from other regions of Baltoscandia e.g. in Närke (Löfgren 1995) and in northern Öland (Bagnoli & Stouge 1997). However, the dominance of *D. forceps* is even more significant in the studied locality in the eastern part of Baltoscandia, thus reflecting the small difference in conodont biofacies that occurred in the basin during this time. Typical conodonts of this zone are illustrated in Figure 6.

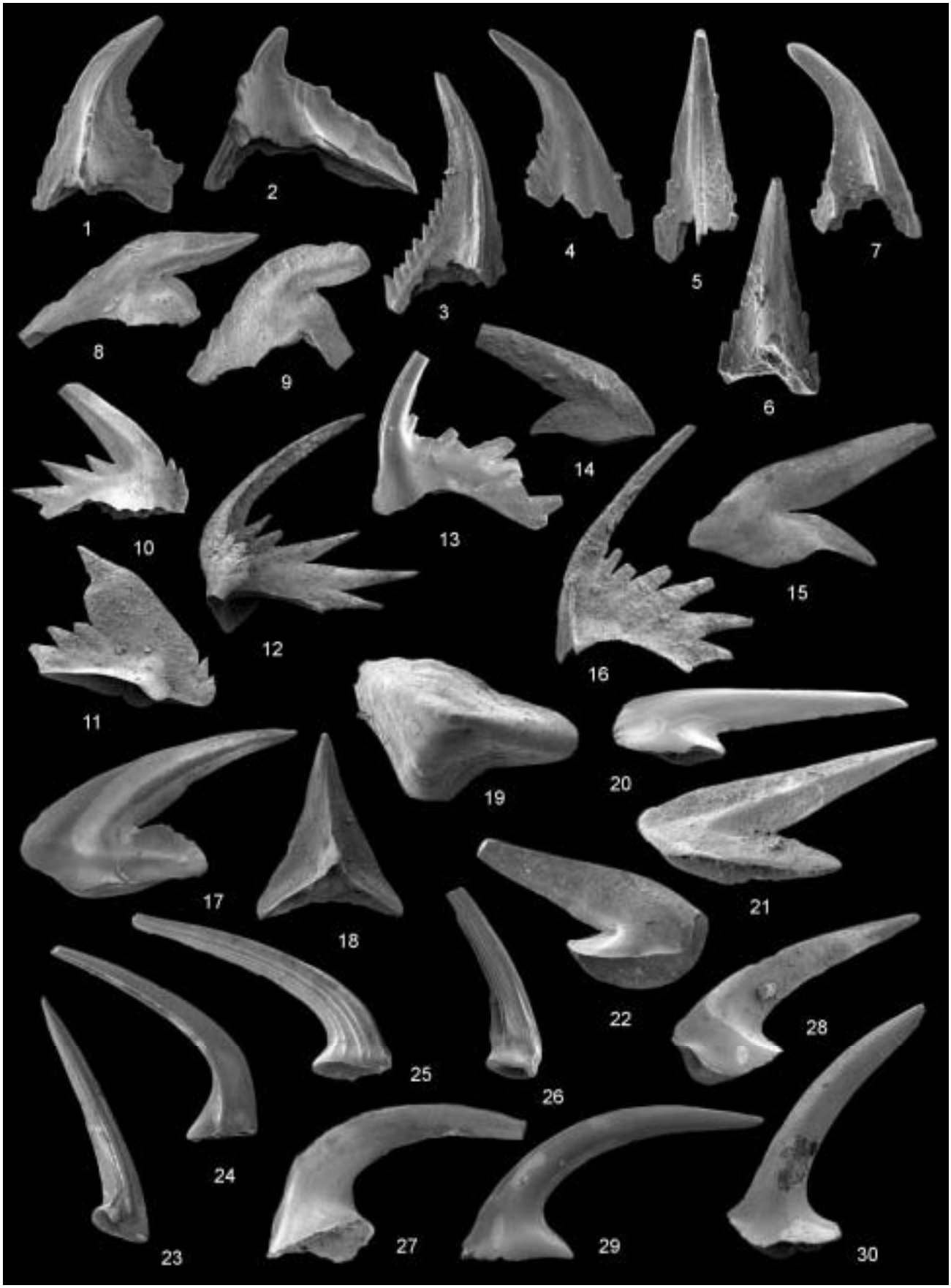
Discussion and results

The clay lenses of the Putilovo mud mound yield conodont assemblages of the *B. triangularis* and the lowermost part of *P. originalis* biozones; these intervals are much thicker in the mound than in the surrounding succession. The clay deposition and formation of clay lenses was favoured by the trapping of terrigenous particles by microbial mats. On the other hand, the mat and its dwellers prevented later erosion and levelling of irregularities of the seabed and re-deposition of reworked fossil fragments.

The sedimentation rate of the clay in the mud mound was relatively low but nevertheless higher than that in the Middle and Upper Volkhov sequences, which is indicated by the lower abundance of conodonts in the mud mound. The rate of mat growth was also high enough to be detrimental for the continued ontogeny of juvenile brachiopods, since these are more numerous in the mud mound clays than in clays from outside the structure.

Evidence of primary lamination in mud mound clays is poor and is preserved in the lower and middle parts of clay lenses only, as the surface of mats was permanently disturbed by the invasions of bioturbators (Fedorov *et al. 1998).* In spite of the slightly higher sedimentation rate of the mud mound clay, the number of bioclasts in the clay samples is high and comparable with the richest samples from the surrounding sections. A high faunal density is typical for microbial mounds, which usually provide complex ecosystems that are optimally situated with regard to illumination, nutrients, and source of terrigenous material, all resulting in high organic productivity (Gerdes *et al.* 1985a; Horny 1995). On the other hand, the mats sometimes represent ecologically stressed environments for many species. This is substantiated by the low species diversity and general absence of mature individuals (Gerdes *et al.* 1985b;

Fig. 5. Representative brachiopods from the Putilovo mud mound. Scale bar 1 mm.
1. *Ranorthis* sp. nov., a, dorsal interior, PMU In 179; b, c, ventral and dorsal exterior of conjoined specimen, PMU In 180 (sample Pmm 16, *B. triangularis* Zone).
2. *Ranorthis trivia* Rubel, a, ventral exterior, PMU In 96; b, dorsal interior, PMU In 97 (sample 754/4, *O. evae* Zone).
3. *Nothorthis penetrabilis* Rubel, a, b, dorsal exterior and interior, PMU In 103; c, d, ventral exterior and interior, PMU In 104 (sample P-21Bcl W, *P. originalis* Zone); e, dorsal exterior of the coarse ribbed morphotype, which is common in the mud mound, PMU In 211 (sample Pmm 12;1, *B. triangularis* Zone).
4. *Paurorthis parva* (Pander), a, dorsal interior, PMU In 207 (sample P-25Bcl W, *B. norrlandicus* Zone); b, dorsal exterior PMU In 98 (sample 578, *M. parva* Zone); c, ventral exterior PMU In 99 (sample R93 21:1, *P. originalis* Zone).
5. *Productorthis aculeata* (Pander), a, ventral interior, PMU In 197; b, dorsal interior, PMU In 199 (a, b sample Pmm16, *B. triangularis* Zone). c, dorsal exterior, PMU In 100; d, ventral exterior, PMU In 102 (c, d sample R93 21:1, *P. originalis* Zone).
6. *Neumania* sp. nov., a, c, dorsal interior and exterior of specimen PMU In 107 (sample P-18Acl W, *P. originalis* Zone); b, ventral interior, PMU In 108 (sample P-18Acl W, *P. originalis* Zone); d, exterior of conjoined specimen PMU In 109 (sample P-20Bcl W, *P. originalis* Zone).
7: Gen. et sp. nov., a, b, exterior and interior of dorsal valve, PMU In 110; c, d, exterior and interior of ventral valve, PMU In 111 (sample Pmm17-7 and 8, *P. originalis* Zone).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Morris *et al.* 1997). The fossil assemblages of the Putilovo mud mound illustrate both these features, yielding a high density of macrofauna and a large number of juvenile brachiopods in the mud mound clays. However, the composition of the brachiopod assemblages in the mud mound and in the coeval beds outside were generally the same. This indicates that brachiopods were not permanent inhabitants of the mud mound but recurrently colonized the mats. The similarity in taxonomic composition between the conodont assemblages in the mud mound and those in the surrounding, coeval, strata is probably due to their pelagic mode of life resulting in a distribution not influenced by the heterogeneity of the seafloor.

The Early Ordovician shallow-water basin of Baltoscandia was characterized by extreme stability and very low sedimentation rates during more than 10 Myrs. Being located mainly within the limit of one facies, large mud mounds exhibit an example of small-scale environmental short-term heterogeneity of the evolving seafloor. Although this paper is mainly concentrated on brachiopods and conodonts, it is clear that these taxa are not the most significant members of the faunal community of a mud mound. It is more likely that bryozoans and echinoderms played a crucial role in the evolution of the mud mounds, but these elements of the faunas are still awaiting study.

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References

Bagnoli, G. & Stouge, S. 1997: Lower Ordovician (Billingenian–Kunda) conodont zonation and provinces based on sections from Horns Udde, North Öland, Sweden. Bolletino della Societa Paleotologica Italiana 35, 109–163.

Dronov, A.V. & Fedorov, P.V. 1994: New data on a structure and distribution of Hecker-type mud mounds in Lower Ordovician deposits of St.-Petersburg vicinity. Vestnik Sankt-Peterburgskogo Universiteta, series 7: Geologia, Geographia 14, 89–93 (in Russian).

Dronov, A.V. & Fedorov, P.V. 1995: Carbonate Ordovician in the St. Petersburg region: the stratigraphy of "Zheltiki" and "Frizy". Vestnik Sankt-Peterburgskogo Universiteta, series 7: Geologia, Geographia 2, 17–26 (in Russian).

Dronov, A.V., Koren', T.N., Popov, L.E., Tolmacheva, T.Ju. & Holmer, L.E. 1995: Uppermost Cambrian and Lower Ordovician in north-western Russia: sequence stratigraphy, sea level changes and bio-events. In: Cooper, J.D., Droser, M.L. & Finney, S.C. (eds.): Ordovician Odyssey: short papers for the Seventh International Symposium on the Ordovician System. The Pacific Section Society for Sedimentary Geology (SEPM), 319–322.

Dronov, A.V., Savitsky, J.S., Fedorov, P.V. & Tsyganova, E.A. 1996: Detailed lithostratigraphy of the Ordovician Lower Volkhov limestone along the eastern part of the Baltic-Ladoga Glint, north-western Russia. GFF 118, 19–24.

Egerquist, E. 1999: Early Ordovician (Billingen–Volkhov stages) Brachiopod faunas from the NW Russia. Acta Universitatis Carolinae, Geologica 42, 341–343.

Fig. 6. Conodonts from the lower clay lens of the Putilovo mud mound. All elements are from the sample 18A, *B. triangularis* Zone.
1-8. *Baltoniodus triangularis* (Lindström), 1, Pa element, PMU In 66, ×65, 2, Pb element, PMU In 67, ×57, 3, Sb element, PMU In 68, ×58, 4, Sc element, PMU In 69, ×78, 5, Sd element, PMU In 70, ×76, 6, Sa element, PMU In 71, ×68, 7, Sd element, PMU In 72, ×73, 8, M element, PMU In 73, ×75.
9. *Trapezognathus* sp., M element, PMU In 74, ×85.
10-16. *Periodon flabellum* (Lindström), 10, P element, PMU In 75, ×54, 11, P element, PMU In 76, ×45, 12, Sa element, PMU In 77, ×58, 13, Sc element, PMU In 78, ×61, 14, juvenile M element, PMU In 79, ×89, 15, M element, PMU In 80, ×73, 16, Sb element, PMU In 81, ×65.
17-18. *Oistodus lanceolatus* Pander, 17, P element, PMU In 82, ×44, 18, Sa element, PMU In 83, ×48.
19. *Pseudooneotodus* sp., PMU In 84, ×63.
20. *Drepanoistodus contractus* (Lindström), oistodiform element, PMU In 85, ×47.
21. *Drepanoistodus forceps* (Lindström), oistodiform element, PMU In 86, ×56.
22. *Drepanoistodus* cf. *D. basiovalis* (Sergeeva), oistodiform element, PMU In 87, ×62.
23-24. *Protopanderdus rectus* (Lindström), 23, asymmetrical element, PMU In 88, ×67, 24, symmetrical element, PMU In 89, ×65.
25. *Scolopodus rex* Lindström, scandodiform element, PMU In 90, ×54.
26. *Decoriconus* sp., PMU In 91, ×96.
27. *Scandodus furnishi* Lindström, scandodiform element, PMU In 92, ×58.
28-30. *Drepanoistodus forceps* (Lindström), 28, drepanodiform element, PMU In 93, ×64, 29: drepanodiform element, PMU In 94, ×58, 30, suberectiform element, PMU In 95, ×56.

Egerquist, E. in press: New brachiopods from the Lower – Middle Ordovician (Billingen–Volkhov stages) of the East Baltic. Acta Palaeontologica Polonica.
Fedorov, P.V. 1999: Hecker-type organic mud mounds from the Lower Ordovician of the East Baltic. Acta Universitatis Carolinae, Geologica 43, 139–142.
Fedorov, P. V. 2003: Lower Ordovician mudmounds from the St. Petersburg Region, north-western Russia. Bulletin of the Geological Society of Denmark 50, 125–137.
Fedorov, P.V. & Dronov, A.V. 1998: Early Ordovician organic build-ups from north-western Russia. 1. Hecker-type mud mounds in «Dikari» member of Babino flagstone quarry. Vestnik Sankt-Peterburgskogo Universiteta, series 7: Geologia, Geographia 14, 81-87 (in Russian).
Fedorov, P.V., Dronov, A.V. & Zavarzin, I.V. 1998: Early Ordovician organic build-ups from north-western Russia. II. Hecker-type mud mounds in Putilovo quarry. Vestnik Sankt-Peterburgskogo Universiteta, series 7: Geologia, Geographia 14, 27–36 (in Russian).
Gerdes, G., Krumbein, W.E. & Reineck, H.E. 1985a: The depositional record of sandy, versicolored tidal flats (Mellum Island, southern North Sea). Journal of Sedimentary Petrology 55, 265–278.
Gerdes, G., Krumbein, W.E. & Reineck, H.E. 1985b: Distribution and geological importance of marine microbial mats in the North Sea tidal flats. Facies 12, 75–96.
Horny, R.J. 1995: Gastropod assemblage from the Lodenice limestone (Lower Devonian, Pragian) at Branzovy near Lodenice, Bohemia. Casopis Narodniho Muzea Rada Prirodovedna 164, 3–10 (in Czech).
Löfgren, A. 1978: Arenigian and Llanvirnian conodonts from Jämtland, northern Sweden. Fossils and Strata 12, 129 pp.
Löfgren, A. 1995: The middle Lanna/Volkhov stage (Middle Arenig) of Sweden and its conodont fauna. Geological Magazine 132, 693–711.
Morris, P.A, von Bitter, P.H. & Schenk, P.E. 1997: Effects of microbial activity on bryozoan colony development in a Lower Carboniferous vent community, Big Cove Formation, Codroy Group, Port au Port Peninsula, western Newfoundland. Geological Society of America, 1997 Annual Meeting, Salt Lake City, Utah, abstracts with programs, 194. Boulder, Geological Society of America.
Seong, J.L. & Golubic, S. 1999: Microfossil populations in the context of synsedimentary micrite deposition and acicular carbonate precipitation; Mesoproterozoic Gaoyuzhuang Formation, China. Precambrian Research 96, 183–208.
Tolmacheva, T., Egerquist, E., Meidla, T. & Holmer, L. 2001: Spatial variations in faunal composition, Middle Ordovician, Volkhov Stage, East Baltic. GFF 123, 65–72.
Tolmacheva, T., Egerquist, E., Meidla, T., Tinn, O. & Holmer, L. in press: Faunal composition and dynamics in unconsolidated sediments: a case study from the Middle Ordovician of the East Baltic. Geological Magazine.