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Ordovician
(Billingen and Volkhov stages)
brachiopod faunas of the East Baltic
Abstract
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Lower-Middle Ordovician (Arenig) successions in the East Baltic have been investigated for more than one hundred
and fifty years. Nevertheless detailed sampling still yields new species and better knowledge of the environment in
which these organisms lived. The successions are well suited for bed by bed sampling because of the lack of tectonic
disturbance and because the sequences are well documented.

This study analyses collections of Billingen-Volkhov age mainly from the St. Petersburg region, but also from
Estonia. A great deal of the material was obtained from the marly to clayey, soft sediment that intercalates the
compact packstones and wackestones in the succession. Twenty-nine of these clay horizons were used for diversity
estimates on the fauna through the succession. The most thoroughly investigated groups for this investigation were
rhynchonelliformean brachiopods, conodonts and ostracodes. The results indicate that variances in diversity and
abundance levels for these groups were not correlated, either to each other or to the small-scale sea level fluctuations
that have been suggested for the region. However, diversity dynamics of brachiopods and ostracodes confirm the
large-scale upward shallowing of the basin into the Upper Volkhov. Comparison with fossils from the limestones
did not reveal any differences in faunal composition between the two preservation modes.

The detailed sampling, coupled with sampling of the recently described mud mounds that occur in several
outcrops, yielded large numbers of specimens. This enabled revision of earlier poorly known rhynchonelliformean
genera such as *Ujukella* Andreev, as well as better known genera such as *Porambonites* Pander. In total the
examined faunas include 31 genera assigned to 53 species of rhynchonelliformean brachiopods. Of these
*Leoniorthis* and *Eoparabreinonites* are defined as new genera, and the following new species are described: *Neumania
paucicostata*, *Ranorthis rotunda*, *Orthidium gambolovensis*, *Orthidium lavensis*, *Skenidioides minutus*, *Tetralobula
peregrina*, *Idiostrophia prima* and *Idiostrophia tenuicostata*.

Keywords: Early Middle Ordovician, Billingen Regional Stage, Volkhov Regional Stage, Diversity, Brachiopoda,
Conodonta, Ostracoda, Estonia, Russia.

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VII Egerquist, E. Manuscript. Early-Middle Ordovician (Billingen – Volkhov stages) orthid and protorthid brachiopods from East Baltic.

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Authorship statement
In addition to contributing to the research and participating in the general preparation of the articles where more than one author is involved, I have been responsible for descriptions, numerical data and calculations on rhynchonelliformean brachiopods discussed in articles I, II and III.
Ordoviciska brachiopodfaunor från St. Petersburgområdet och Estland

Brachiopoder (armfotingar) är en i dag relativt ovanlig djurgrupp. Under paleozoikum var den däremot både artrik och vanlig. Denna avhandling behandlar de kalkskaliga (Rhynchonelliforma) brachiopodfaunor som man hittar rester av i Estland och västra Ryssland i lager från tidig till mellanordovicisk ålder (billingen- och volkhovetagen för c:a 475-485 miljoner år sedan). De ordoviciska lagren i Baltikum och västra Ryssland är väl undersökta, allt ifrån den fössil faunan till tolkningar av den miljö där de olika sedimenten har avsatts. Andå finns mycket kvar att upptäcka, till stor del tack vare de tektoniskt ostörda sedimenten och de ofta mycket välbevarade fössila lämningarna.

Material och undersökningsområde

Materialet till avhandlingen kommer från ett flertal lokaler i området mellan Tallinn i Estland och floden Lynna i nordvästra Ryssland (Fig. 1). Alla dessa lokaler ligger utmed en kalkstensklint, kallad ”the Baltic-Ladoga Klint”, som sträcker sig längs Estlands norra kust, in i Ryssland till södra kanten av Ladoga (Fig. 4). De plant liggande lagren är ofta lätt urskiljbara och enskilda lager går i vissa fall att spåra tiotals mil. De hårda sedimenten utgörs mestadels av märglig kalksten med inslag av glaukonit, framförallt i de lägre lagren. Mellan kalkstenslagren finns ofta lösa ler- och siltavlagringar insprängda särskilt i volkhovlagren i S:t Petersburgområdet. En stor del av materialet till avhandlingen kommer just från dessa ler/siltavlagringar.

Tidig och mellanordovicisk sedimentation i Östersjöområdet

Under ordovicium var stora delar av landområdena kring Östersjön och i Ryssland täckta av ett förhållandevis grunt epikontinentalhav tillhörande den dåvarande kontinenten Baltica, som vid denna tid omfattade större delen av Skandinavien, Ryssland och nordöstra Centraleuropa. Det dåvarande grundhavet har indelats i olika så kallade konfaciesbälten (Jaanusson, 1982), vilka representerar olika djup och sedimentationsförhållanden (Fig. 4). Det i den här avhandlingen behandlade området tillhör det nordestniska konfaciesbältet och anses tillhöra den grundare delen av bassängen.

Under sen cambrium till tidig tremadoc avsattes här huvudsakligen sandiga till finklastiska sediment, följt av avsättning av ler- och kalkavlagringar, där det terrigena inslaget var litet. Lagerföljden i den därpå följande arenigepoken utgörs huvudsakligen av kalkstenar med silt/lerinslag, mellan vilka lösa siltiga -leriga sediment är insprängda. Sedimentationen har varit ytterligt långsam, med kanske bara några få millimeter under tusen år (Jaanusson, 1982) (Fig. 5).
Under den första halvan av ordovicium låg undersökningssområdet på ungefär 40-50 grader sydlig bredd i ett troligen tempererat klimat (Fig. 3). Ett flertal försök har gjorts att bedöma temperaturen i det grundhav som omgav kontinenten, bland annat genom att mäta olika syreisotoper i fossil kalk. Dessa mätningar har dock givit skiftande resultat, från +8°C till runt +20°C (t. ex. Lindström, 1984; Dorofeeva et al. 1997). Djupet i bassängen har fluktuerat väsentligt över den tidsrymd som omspännas av billingen- och volkhovetagen. Under billingen blev havet successivt grundare, något som kuluminerade i och med bildandet av en enormt utbred och lått igenkännlig diskontinuitetsyta. Denna har i Ryssland fått namnet "Steklo" av lokala stenhuggare, medan den i Sverige kallas "Blommiga bladet”. Härefter inleds volkhovetagen med en transgression, som med smärre fluktuationer varar till slutet av detta etage, där vattendjupet återigen sjunker drastiskt och en ny diskontinuitetsyta bildas vid gränsen mellan volkhov och kunda (Dronov et al. 2003) (Fig. 5).

En stor del av de bioklastiska kalkstenarna, som bildades i volkhov, har föreslagits vara så kallade tempestiter, vilka avlagrats vid extrema stormar. De lösa mellanliggande sedimenten skulle däremot vara avsatta under lugnare förhållanden (Dronov & Fedorov 1995; Dronov 1998).

Enligt denna teori borde vattendjupet i bassängen ha legat någonstans mellan vägbasen för extrema stormvågor och den för normala stormvågor. Med tanke på det förmodat öppna läget mot väster, och att vindarna troligen var västliga på dessa breddgrader under ordovicium liksom idag, så kan en försiktig uppskattning av djupet röra sig mellan sextio och hundra meter.

De fossila lämningarna av den fauna som levde på dessa lugna, svagt sluttande mjukbottnar, utgörs volymermässigt huvudsakligen av brachiopoder. Tillsammans med dessa hittar man också ostrakoder, bryozoer, tagghudingar, snäckor, conodonter och machaerider.

### Brachiopodfaunans diversitet

Den fossila brachiopodfaunans genomgår en markant förändring vid det sedimentationsavbrott som utgör gränsen mellan billingen och volkhov (Fig. 5). I materialet från billingen har 19 olika släkten hittats. Av dessa har 10 försvunnit i volkhov, där de i stället ersätts av 12 nya, så att det totala antalet släkten i detta etage uppgår till 21. I billingen tillhör 53% av släktena (10 st.) ordningen Orthida, medan pentamerider, billingsellider och plectambonitider vardera representeras av 4, 3 och 2 släkten. Av de 21 släktena i volkhov däremot, tillhör endast 38% orthiderna. Ordnningen Protorthida introduceras med ett släkte, pentamerider och plectambonitider representeras av 2 släkten vardera, medan billingselliderna har ökat i antal så att de nu är lika diversifierade som orthiderna med 38% av släktena. Orthidersas relativta dominans tyder på att vattentemperaturen var relativt låg snarare än den höga temperatur som vissa av resultaten från syreisotopmätningarna pekar på(Benedetto, 2001). Den lägre dominansen av orthider i volkhov beror på diversifieringen av de för Baltica typiska clitambonitidera, därför är dessa värden troligen inte jämförbara med värden från andra områden. Det är vårt att notera att ett flertal släkten, så som orthiderna *Apheo-orthina*, *Prantlina*, *Orthidium* och *Angusticardinia*, liksom även *Tetralobula*, försvarer redan en tid före övergången från billingen till volkhov, medan andra som *Plectella* och *Panderina*, försvarer vid eller strax ovanför sedimentationsuppehållet. Detta samtmanfaller med den föreslagna snabba regression som påbörjades i övre delen av billingen, och vars maximum utmärks av den redan omtalade diskontinuitetsytan Steklo (Fig. 5). Relativt snart efter att den efterföljande transgressionen hade inletts, invandrade ett antal nya släkten till området. En del av dem tycks ha varit ganska kortlivade och försvarna nära gränsen mellan de traditionella epokerna dikari och zheltjaki. Vid denna tid samebor therien en ny snabb transgression med upptärdandet av en andra grupp nykomlingar, så som *Ingrina*, *Gonambonites*, *Apomatella* och djupvattensbrachiopoden *Skenidioides*. *Skenidioides* uppträder talrikt i några få prover från zheltiakiepo-ken, men avtar sedan och försvarer igen i den grundare översta delen av volkhov.
Den “trumpetande” brachiopoden

De påpekade emellertid att man ännu inte kunnat fastställa hur den skall klassificeras hos släktet Antigonambonites, eftersom man hittat så få juvenila individer av detta släkte. Ett flertal små exemplar, som hittats i material från ansamlingar av finsediment, de flesta från den så kallade ”Sablino mud mound” vid floden Tosna, tyder på att det hos Antigonambonites inte rör sig om ett deltium. De juvenila exemplaren har en tydlig pedikelöppning omgiven av en trumpetformad pedikeltub (Fig. 7 & 9: 1-3). Tuben tycks till en början vara mer eller mindre fri från resten av skalet, men växte tidigt ihop med detta, även öppningen tillslöts på ett tidigt stadium (Fig. 8). Även hos vuxna individer går det att spåra rester av bildningen. Nedre bilden i figur 8 visar ett itusågat och polerat vuxet exemplar, där gränsen mellan pedikeltubben och skalets ventralsida är tydligt skönjbar.
Introduction

Early-Middle Ordovician ( Arenig) successions in the East Baltic region have been investigated for more than one hundred and fifty years. Nevertheless detailed sampling of, especially the soft, clayey sediments in the succession, still yields new species and better knowledge of the environment in which these organisms lived. The successions are well suited for bed by bed sampling because of the lack of tectonic disturbance (Fig. 1) and because they are well-documented (e.g. Dronov et al. 2000).

Research area and localities

This work mainly deals with rhynchonelliformean brachiopod faunas from the Billingen and Volkov stages. The material comes from several localities in the vicinity of St. Petersburg in Russia and from two localities in Tallinn, Estonia (Fig. 2) The Volkov Stage material is mostly based on bed by bed sampling of the unconsolidated sediments at the Putilovo quarry and detailed sampling from a large mud mound from the same locality. All sampled localities are within the outcrop area of the so-called Baltic – Ladoga Klint, a more than 350 km long escarpment with numerous exposures of Ordovician deposits in the East Baltic area.

Figure 1. Frizy Unit at Putilovo quarry, showing the undisturbed horizontal layers in the succession.
Geological background

Lowermost Middle Ordovician deposits in Baltoscandia are characterised by very slow intermittent sedimentation in a rather shallow epicontinental sea, located within the temperate climatic zone (Jaanusson, 1973). The eastern part of the basin was characterised by predominantly siliciclastic deposition during the late Cambrian and early Tremadoc, followed by the formation of fine-grained argillites and carbonate deposits in the late Tremadoc to early Arenig. Continuous sedimentation of siliciclastic-starved carbonate sediments prevailed in the basin from the mid Arenig onwards.

The Arenig succession is exposed continuously along the Baltic-Ladoga Klint, an erosional cliff, which extends from Lake Ladoga in north-western Russia and along the northern coast of Estonia (Fig. 1). The deposits along the Klint are, spatially, remarkably homogenous and undisturbed and consist of horizontal, easily recognizable units of calcareous packstones and wackestones alternating with soft silt/clay horizons. It is one of the best-documented successions in Baltoscandia (e.g. Dronov et al., 2000). The boundary between the Billingen and Volkhov regional stages is marked by a distinct hardground surface (“Steklo”) which it is also possible to trace into Sweden, where it is known under the local name “Blommiga bladet”.

In addition to the standard section several mud mounds of different size are found in some of the outcrops. These are, more or less circular, probably sponge mediated, build-ups consisting of thick clay lenses which are covered by micritic crusts (Fedorov 2003). In Putilovo quarry a large mud mound sits upon the Steklo surface and the lower clay lens is within the *Baltoniodus triangularis* conodont Biozone, which is otherwise missing in this outcrop (Fedorov and Dronov, 1998; Tolmacheva, Fedorov & Egerquist, 2003, Paper III).
Palaeoenvironment
During the Early-Middle Ordovician the research area was covered by a shallow epicontinental sea, and positioned approximately 40 - 50 degrees south of the equator on the palaeocontinent Baltica (e.g. Torsvik et al. 1998), (Fig.3). The continent was, rather rapidly, moving northwards, and probably experienced a temperate climate. However, several attempts to estimate water temperature using $\delta^{18}O$ measurements on different carbonate sources have yielded a wide range of data from +8°C annual surface water temperature (Lindström 1984) to values around +20 degrees (e.g. Dorofeeva et al. 1997). The deposits along the Baltic-Ladoga Klint belong to the North Estonian confacies belt (Fig. 4) which is considered to be the shallowest part of the basin (Jaanusson, 1982), with the most shallow part in Estonia and slightly deepening towards the eastern part of the klint. The water depth has undergone quite extensive fluctuations during the Billingen-Volkhov time span. During the Billingenian the sea became successively shallower, which culminated at the sequence boundary with the “Steklo” hardground surface. The Volkhov Stage is regarded as a transgressive episode, with a complete cycle of relative sea-level changes forming a well developed depositional sequence, shallowing again in the upper part to form a new erosionally truncated surface at the Volkhovian/Kundan boundary (Dronov et al, 2003), (Fig. 5).

The depth in the basin is another matter of discussion. It has been suggested that a significant part of the bioclastic limestones in the Volkhov Stage represents proximal tempestites, deposited during major storm events somewhat below the seasonal storm wave base, whereas the soft silt/clay beds represent background deposits (e.g. Dronov 1999). According to this model an estimated depth of the basin should range between normal storm wave base and extraordinary storm wave base. Reconstructions of the palaeo-continent show a vast epicontinental sea facing southwest and probably exposed to a west-wind drift and quite extraordinary waves even at normal storms. If there were no sheltering island arcs, the waves could probably grow as high as 10 meters and as long as 150 to 200 meters. Calculating the wave base to approximately half the wavelength the estimated depth in the basin is likely to fall within at least 60-100 meters.

The fossil remains of the fauna, which inhabited these predominantly calm and gently sloping shelves, is volumetrically dominated by a moderately diverse brachiopod assemblage, together with ostracodes, echinoderms, bryozoans, gastropods, conodonts and machaeridians (Tolmacheva et al. 2003, Paper II).

Brachiopod diversity
The rhynchonelliformean brachiopods in this region show a marked shift at the sequence boundary between the Billingen and Volkhov stages (Fig. 5). In Billingen Stage 19 genera are present in the investigated samples. Of these 10 have disappeared in Volkhov, where, in stead 12 new genera appear so that the total number of genera in this stage is 21. In the Billingen assemblage 53% (10 genera) belong to the Order Orthida, whereas pentamerids, billingsellids and plectambonitoids are represented by 4, 3 and 2 genera respectively. In Volkhov Stage the assemblage contains 21 genera, of which the orthids constitutes 38%.
The Order Protorthida is represented by a single genus, whilst the pentamerids and plectambonitoids are represented with two genera each and the billingsellids have increased their number so that they now are as diverse as the orthids with 38% of the genera.

The relative orthid dominance indicates a cool water temperature rather than the high values obtained by some of the oxygen isotope investigations (Benedetto, 2001). The lower relative orthid dominance in the Volkov stage is due to the diversification of the typical Baltic clitambonitoids and is probably not comparable with similar estimates from other regions.

Figure 5. Stratigraphic column of the Billingen – Volkov succession in St. Petersburg region, also showing the distribution of found brachiopod genera and sea level curve. The dashed lines for Oslogonites and Platystrphia indicate very few, widely spaced finds. Legend: 1) Limestones with iron oolites; 2) Bioclastic wackestones and packstones; 3) Thalassinoides burrowing systems; 4) Marls; 5) Clays; 6) Quartz sandstones; 7) Quartz sandstones with scattered glauconite grains; 8) Black shales; 9) Hard ground surface with Trypanites-like borings; 10) Hardground with pencil-like borings; 11) Uneven hardground surface evolved from firmground; 12) “Steklo” hardground surface with Gastrochaenolites oelandicus borings; 13) Planolites and other trace fossils; 14) Bergaueria at the bottom surface of the beds. Modified after Dronov et al, 2003.
It is noteworthy that the decline of several genera, such as the new plectambonitoid genus as well as *Prantlina, Orthidium* and *Angusticardinia*, which starts somewhat before the end of the Billingenian, as well as *Plectella* and *Panderina* which disappear at or slightly above the sequence boundary, seem to coincide with the suggested rapid sea level fall that began in the upper part of the *O. evae* conodont Biozone, the maximum of which is marked by the Steklo discontinuity surface at the sequence boundary (Fig. 5). Soon after the subsequent transgression had started, a number of new genera migrated into the region, some of which were rather short lived and disappeared close to the boundary between the two traditional units Dikari and Zheltiaki. At this time a new rapid transgression occurred, coinciding with a second group of newcomers such as *Ingria, Gonambonites, Apomatella* and the deep-water brachiopod *Skenidioides*. *Skenidioides* is abundant in a few samples in the Zeltiaki Unit, but decreases and disappears again at the shallow upper part of the Frizy Unit. This turnover pattern is even more obvious when looking at species level (Fig. 6).

The Billingen brachiopod fauna

Plates 1 & 2; fig. 6

The brachiopod fauna of the Billingen Regional Stage include at least 24 species referred to 19 genera (Fig. 6). The fauna is strongly dominated by orthids, which include 13 species. Billingsellids and pentamerids include 4 species each and the strophomenids 3 species. The strophomenids are represented by two genera: *Plectella* Lamansky and a new, not yet published, genus. *Plectella* is morphologically very homogenous; however, there are three different distinctive shell ornamentations, probably indicating that they represent different species or subspecies (Plate I: fig. 1 A-F). The new genus was found at three localities, Volkho, Tosna and Syas rivers, in lowermost Dikari Member (*Oepikodes evae* conodont Biozone). It is a moderately large, on average 6.5 mm wide and 5.5 mm long, concavo-convex and semicircular plectambonitoid, with short dental plates, simple cardinal process, low platform and no side septa. The ornament is unequally costellate. (Plate I: fig. 2 A-D). The pentamerids are represented by *Tetralobula peregrina* sp. nov., *Idiostrophia prima* sp. nov., *Eoparambonites latus* (Pander) and *Porambonites intermedius* Pander, all of which are discussed in paper VI. The billingsellids, not yet as diverse as in the following stage, are represented by three genera. *Antigonambonites* Öpik, and *Neumania* Harper, each with one species, are rather common, whereas *Oslogonites* Öpik only was found at one locality. Among the orthids *Panderina* is one of the most dominating genera. Several species of *Panderina* were described already in the nineteenth and early twentieth centuries; however, measurements on a large amount of specimens indicate that two of the described species, *P. tetragonum* (Pander) and *P. lata* (Pander) are junior synonyms to the type species *Panderina abscissus* (Pander) (Paper VII). Following this classification only *P. abscissus* is present in the material. Other dominating taxa are the dalmanelloid species *Paurorthis resima* (Rubel) as well as the plectorthoid genus *Ranorthis* Öpik, which is represented by three species including *Ranorthis rotunda* sp. nov. described here (Paper VII). Two new species of the wide spread genus *Orthidium* Hall & Clarke are also quite common in some samples. *O. gambolovensis* sp. nov. first occurs in the lowermost Mäekula Member and *O. lavensis* in lowermost Vassilkovo Member. They coexist until lower Dikari Member where they both disappear. Finally, I mention *Leoniorthis robusta* Egerquist which is sparsely present at a few levels in Vassilkovo Member but numerous in the mud mound at Putilovo quarry (upper Dikari Member). (Paper IV).

The Volkhov brachiopod fauna

Plates 3, 4 & 5; fig. 6

The brachiopod fauna of the Volkhov Regional Stage include at least 33 species distributed in 21 genera (Fig. 6). The fauna is dominated by the orders Orthida (14 species) and Billingsellida (13 species), whereas strophomenids and pentamerids are of minor importance.

The strophomenids are represented by two plectambonitoid species; *Ingria nefedyevi* (Eichwald) is present from the *P. originalis* conodont Biozone and upwards, whereas the newly revised species *Ujukella fastigata* (Rubel) (paper V) first appears in the *B. norrlandicus* Biozone, where it is quite numerous especially in the upper part of the section.
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**Traditional units and bed indexes**

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<td>Pranitina incurvata</td>
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<td>Apheorhina sp.</td>
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<td>Tetralobula peregrina</td>
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<td>Idiostrophia cf. digitata</td>
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*Figure 6. Range chart for species found in the material. All finds of *Porambonites* is referred to *P. elegans* for reasons discussed in the text.*
Among the clitambonitidines the genus *Neumania* Harper is represented by two species: *N. costata* Pander and *N. paucicostata* Egerquist both of which are present already at the bottom of the Volkhov Stage. *N. costata* is quite rare, whereas *N. paucicostata* is present in most samples up to the Frizy Unit where it disappears. *Apomatella ingrica* (Pahlen) is the most frequent species of its genus; it appears in the lowermost Zheltiaki Unit and continues throughout the entire stage. *A. secunda* Öpik is much sparser and is present only in the Frizy Unit.

Genera such as *Lacunarites* Öpik, *Hemipronites* Pander and *Raunites* Öpik are usually preserved as fragments only, which make their recognition somewhat difficult. However, the distinct ornamentation enables a fairly accurate classification. *Lacunarites* occurs throughout the Frizy Unit (*B. norrlandicus* Zone), whereas only one fragment referred to *Hemipronites imbricata* (Öpik) have been found in the upper part of this unit. *Raunites* is represented by four species: *R. wolkowiana* (Öpik), *R. janischevskyi* (Lesnikova), *R. venusta* (Öpik), and *R. strophomenoides* (Öpik). Among these *R. wolkowiana* is the most common species occurring throughout the Volkhov Stage, whereas *R. strophomenoides* is restricted to the Frizy Unit. From this unit comes one find of *Oslogonites* as well.

A new species of the protorthid *Skenidioides* Schuchert & Cooper (Paper II) occurs first, with a few specimens, in the clay between beds 17 and 18 in the lower part of the Zheltiaki Unit (BIIβ), large numbers occur in a clay horizon in bed 21, also BIIβ. After that the genus decreases in abundance but reoccurs again in three clay horizons in the upper Frizy Unit.

The orthids are represented by three superfamilies: Orthoidea Woodward, Plectorthoidea Schuchert & Le Vene, and Dalmanelloidea Schuchert. Among the orthoids *Panderina* Schuchert & Cooper, *Glossorthis* Öpik and *Leoniorthis robusta* (paper V) are restricted to the Dikari Unit (BIIα), and have only been found in the large mud mound at the Putilovo Quarry (*B triangularis* and *B. navis* zones). *Productorthis* Kozlowski is represented by three approximately successive species: *P. aculeata* (Pander), *P. obtusa* (Pander) and *P. parallela* (Pander).

Within the super family Plectorthoidea *Ranorthis* Öpik, and *Nothorthis* Ulrich & Cooper are the dominating genera throughout the whole Volkhov Stage, together with the dalmanelloid *Paurorthis parva* (Pander). *Ranorthis* is represented by three species, of which *Ranorthis rotunda* sp. nov. (paper VII) occurs in BIIα and BIIβ, whereas *R. carinata* Rubel and *R. norvegica* Öpik occurs in BIIβ and BIIγ. A few fragmentary specimens of probable *Platystrophia* King were found in the Zheltiaki and Frizy units. Pentamerid brachiopods are represented by the genera *Porambonites* Pander and *Idiostrophia* Ulrich & Cooper, of which the latter occurs with two new species: *I. tenuicostata* sp. nov. and *I. digitata* sp. nov. (paper VI) in the upper part of the Frizy Unit. *Porambonites* is present in the Zheltiaki and Frizy units; it is mostly fragmentary which makes classification difficult, except for *P. reticulatus* Pander with its characteristic pitted pattern on the shell surface. However, the few complete specimens found, which do not belong to *P. reticulatus*, all belong to the species *P. trigonus* Pander, the shell surface of which is smooth. Thus probably the other smooth shell fragments also belong to this species, and they are tentatively classified as such in the range chart (Fig. 6).
Some aspects on the development of the delthyrial cover in *Antigonambonites*

A large number of well-preserved juvenile shells of *Antigonambonites* can possibly shed some light on the enigmatic delthyrial cover in this genus. The development of the clitambonitidine delthyrial cover was discussed by A. Wright and M. Rubel (1996). They generally considered it as a deltidium that was formed by the deltidial plates and usually with a visible line of junction between them. However they point out that *Antigonambonites* is still problematic in this respect because of lack of evidence from juvenile specimens. Öpik (1934 p. 12, 151) mentions that the deltidium is perforated with a narrow foramen which is sealed already in young specimens and that the sealed knob probably served as a holdfast for young specimens. However he does not discuss the development of the structure. Juvenile and young specimens of *Antigonambonites* picked from soft sediment samples of volkhovian age, gives a hint of the development of the delthyrial cover in this genus. The material comes mainly from Sablino mud mound at Tosna river. The juveniles have a clearly visible pedicle foramen surrounded by a trumpet formed pedicle tube (Fig. 7 & 9: 1-3). This structure fuses quite early with the spondylium at the ventral side, and usually ends with a chevron formed tip. The posterior part, on the other hand, continues to grow as the interarea grows, the lateral edges underlying the edges of the delthyrium, and finally fusing to the sides of the spondylium (Fig. 8 & 9: 4).

![Figure 7. Pedicle tubes on specimens PMU In 531 and PMU In 533.](image)

![Figure 8. Adult specimen PMU In 538 with marked delthyrial cover, damaged specimen PMU In 537 with visible suture between the delthyrial cover and the spondylium, and sectioned adult specimen PMU In 539 with visible sutures between the pseudodeltidium and the ventral valve.](image)
The specimen on figure 9: 6 obviously died before the cover was completely fused with the spondylium. After death the compaction of the overlying sediment caused the two structures to separate, thus beautifully demonstrating the construction.

The distal end of the tube is often differently shaped in different specimens, indicating that the tube was formed with the substrate, to which the larva was attached, as a template. When the brachiopod is about 5 to 6 mm wide, the pedicle foramen is already closed. However the distal surface of the tube still reflects the shape of the attached surface, although in many specimens there is a central pitch in it. It is difficult to say whether the brachiopod still was attached or not when the foramen was closed, with the sealed knob serving as a holdfast. However, the smooth and often well-preserved distal surface of the tube indicates that the brachiopods may have turned into a free lying mode of life already at this stage.

Figure 9. Pseudodeltidium in *Antigonambonites*. Scale bar 1 mm. 1-3: Juvenile specimens showing open pedicle tube. 1: PMU In 529; 2 A-B: PMU In 532; 3 A-C: PMU In 530; all from Sablino mud mound, Zheltiaki Member. 4: magnification of delthyrial cavity on adult specimen, showing the suture between the pseudodeltidium and the spondylium as described in the text, PMU In 538, Putilovo quarry, Frizy Member. 5: Specimen with loose pseudodeltidium, PMU In 536, Sablino mud mound, Zheltiaki Member. 6: Same specimen as on figure 8 without guidelines.
Summary of papers

Sample size and fidelity of calculations


For this paper the easily recognised clay and marl horizons in Putilovo quarry were used for estimating the fidelity of calculations made on small sample size. Five clay beds were sampled and from each clay bed five samples of about the same size were taken in some distance from each other. All samples were treated in the same way: they were weighed, washed and then sieved into four fractions. The samples were then investigated on different criteria such as mineralogy, proportion of sediment fractions, degree of corrosion, amalgamation and fragmentation of the shell fragments, and composition of the faunal communities. Taxa investigated were brachiopods, ostracodes, conodonts, bryozoans and echinoderms. The investigation indicates that for quantitative palaeontological studies in the region, a sample size of about 200 specimens gives a relative error that is less than 10%. This error is less than the error related to the laboratory treatment of the samples of the same sizes, which is estimated to 12%, calculated on conodonts. Other conclusions that may be drawn from this investigation is that the relative error in the relative abundance of taxa that is connected with the small-scale spatial homogeneity is around 10 to 15%, that is to say that gradients in relative abundance of taxa, either lateral or vertical can be considered reliable if they exceed this value.

Diversity and faunal dynamics


This study is an attempt to map the patterns of diversity and density of different taxa from Volkhov successions at Putilovo quarry. Although studies of fossil distribution patterns in a single section cannot discern the complete history of the original diversity of a region, some observations concerning the diversity and temporal dynamics of the palaeocommunities can be made. Twenty-nine clay horizons were investigated on six different organism groups, of which conodonts, brachiopods and ostracodes were the most thoroughly investigated taxa. Estimates made on each of these taxa were: density of fossil remains, species richness, and equitability (which quantifies whether the fauna is dominated by one or a few species or if the different species are evenly distributed in the assemblage). The diversity estimates from the clays were compared with estimates made on limestones from the same locality in order to discover possible differences between the two preservation modes. The limestones in this region have been interpreted as tempestite deposits by sedimentologists whereas the clays were interpreted as background sedimentation in shallow waters somewhat below normal storm wave base. However, there is no significant difference between the faunas in the limestone and clay beds, and there is no obvious size sorting, which does not correspond with such an interpretation. The three organism groups show no obvious correlation concerning the different estimates, which indicates that the community structure was not tightly integrated and that species responded to environmental changes according to their individual environmental tolerances. Furthermore, there is no obvious correlation between the small-scale variability in the diversity estimates and the suggested small-scale sea level curve for the region, which is supported by sedimentological and trilobite data. Thus, it may be suggested that the dominant elements in the studied palaeocommunity, like conodonts, brachiopods and ostracodes, were not sensitive to small scale sea level changes and other environmental changes of high frequency. However, diversity dynamics of brachiopods and ostracodes confirm the large-scale upward shallowing of the basin into the Upper Volkhov.
Mud mound faunas


Clay 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, conodonts, bryozoans and echinoderms. The lithology of one such mud mound in Putilovo quarry was previously studied, but not the faunas associated with the mound. The clay lenses in the Putilovo mud mound yield conodont assemblages belonging to the *Baltoniodus triangularis* and lowermost *Paroistodus originalis* conodont biozones, the stratigraphical intervals of which are much thicker than in the coeval Arenig successions 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.

*Leoniorthis robusta* and *Neumania paucicostata*


Two new rhynchonelliformean brachiopods, *Leoniorthis robusta* gen. et sp. nov. and *Neumania paucicostata* sp. nov., are described from the Billingen and Volkhov stages of the Baltic-Ladoga Klint area. All specimens were washed out from unconsolidated sediments that were sampled in Tallinn, Estonia and at three localities in St. Petersburg district, Russia. Numerous specimens were found in the large mud mound at Putilovo quarry, the lower part of which is within the *Baltoniodus triangularis* conodont Biozone, otherwise usually missing in this area. *Leoniorthis robusta* is more or less restricted to the mud mound, whereas *Neumania paucicostata* is common also in the clays higher up in the surrounding standard section. (Plate 3: fig. 3 A-C; Plate 4: fig. 1 A-D)

Revision of the brachiopod *Ujukella* and related genera


New material of the poorly known plectambonitoid brachiopod *Ujukella fastigata* (Rubel) is described from the Middle Ordovician (Upper Volkhov) of Lava river and Putilovo quarry, St. Petersburg district. To enhance comparison new descriptions are also provided for the closely related brachiopods *Ujukella? geometrica* (Kutorga) from slightly younger strata (Kunda Regional Stage) in the same region, for *Ujukella* sp. from contemporaneous deposits on Öland, Sweden, and for *Ujukella alexandracea* Andreev of Llanvirn age from Tuva, Siberia, close to the Kazakhstan border. M. Rubel, 1961 tentatively described two specimens from Lava river, with only exteriors preserved, as *Eostrophomena? fastigata*. The new specimens, which are externally very similar to Rubel’s specimens, but with several nicely preserved internal features, show that this brachiopod is not an orthid but a plectambonitoid, and thus can not be referred to the genus *Eostrophomena*. Furthermore, the close resemblance to the Siberian brachiopod *Ujukella alexandracea* shows that the two brachiopods belong to the same genus. A cladistic analysis based on 10 taxa and 20 characters supports this conclusion and indicates affinity to the Family Leptestiidae. (Plate 3: fig. 2A-D).
Syntrophidiine brachiopods from Early and Middle Ordovician


Syntrophidiine brachiopods are a rare and poorly known component of Ordovician faunas in Baltoscandia. In the East Baltic region they appear in the Billingenian (lower Arenig) as part of the earliest known benthic assemblages dominated by elements of the Palaeozoic Evolutionary Fauna. The fauna includes bryozoans, ostracodes, the earliest known porambonitoids, strophomenids and endopunctate orthids together with genera such as *Idiostrophia* and *Orthidium* which later became characteristic of the Whiterockian brachiopod assemblages in Laurentia, but by that time had completely disappeared from Baltica. The superfamily Syntrophioidea reappears in the Baltoscandia only in the mid Caradoc. By contrast, Porambonitoidea remained the integral part of the Baltoscandian brachiopod associations through the Ordovician. *Porambonites*, herein redefined on the basis of restudy of the type species *P. intermedius*, includes only smooth porambonitoids; taxa with distinctive ornament of radiating rows of pits first appeared in the group in the mid Arenig and are probably not congeneric with *Porambonites*. The taxa *Eoporambonites* gen. nov., *Tetralobula peregrina* sp. nov., *Idiostrophia prima* sp. nov. and *Idiostrophia tenuicostata* sp. nov. are newly established. (Plates 2 & 5).

Orthid and protorthid brachiopods of Billingen and Volkov age

Early-Middle Ordovician (Billingen – Volkov stages) orthid and protorthid brachiopods from East Baltic. Egerquist, E. Manuscript. (Paper VII).

Three new species of the orthid genera *Orthidium* Hall & Clarke, 1892 and *Ranorthis* Òpik, 1939 and one new species of the protorthid genus *Skenidioides* Schuchert & Cooper, 1931 are described from the Arenig succession (Billingen and Volkov stages) of Estonia and north-western Russia. Detailed biometric study of an extensive material of *Panderina* Schuchert & Cooper, 1931, indicates that some of the earlier established species in reality represent intraspecific variants. Preliminary investigations of the genus *Antigonambonites* indicate a similar pattern. In contrast, other brachiopods, such as *Orthidium* and *Skenidioides*, group into more morphologically distinctive groups, and it would seem that the latter taxa mostly represent widespread or cosmopolitan forms. (Plates 1 & 4).

Acknowledgements

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Last, but not least, I want to acknowledge the staff at Rudbeckianska Gymnasiet, Västerås, who have provided me with a working schedule that enabled my work in Uppsala, and my family who has always encouraged and helped me.
References


Plate 1

Scale bar 1 mm if nothing else is stated.


3. *Prantlina incurvata* (Lamansky). A: dorsal interior, PMU In 526, B: ventral exterior of conjoined specimen, PMU In 525, both specimens from Harku trench, Estonia, Mäekula Member.


5. *Orthidium lavensis* sp. nov. A: interior of dorsal valve, holotype, PMU In 480, Popovka river, Vassolkovo Member. B: dorsal view of conjoined specimen, PMU In 483, Syas river, lower Dikari Member.

6. *Orthidium gambolovensis* sp. nov. A: interior of dorsal valve, holotype, PMU In 489, Sablino mud mound, Vassilkovo Member. B: exterior of ventral valve, PMU In 495, Popovka river, Mäekula Member.
Plate 2
Scale bar 1 mm if nothing else is stated.

1. *Lycophoria lamanskii* Rubel. Ventral view of conjoined specimen, PMU In 454, Babino quarry, Vassilkovo Member.
4. *Neumania erecta* (Pander). A: ventral view of conjoined specimen PMU In 527. B: lateral view of ventral valve, PMU In 528, both specimens from Volkhov river, Mäekula Member.
8. *Idiostrophia prima* sp. nov. A-C: ventral, dorsal and lateral views of conjoined specimen, holotype, RM Br 137126, Popovka river, Vassilkovo Member.
Plate 3
Scale bar 1 mm if nothing else is stated.

1. *Ingria nefedyevi* (Eichwald). A: ventral exterior of conjoined specimen, PMU In 456, Lava River, Frizy Unit. B: ventral interior of specimen PMU In 457 from the mud mound (Volkhov Formation) at Volkhov River.
5. *Oslogonites* Öpik. A & B: ventral interior and exterior of specimen PMU In 499 from Frizy Unit at Lava River.
Plate 4

Scale bar 1 mm if nothing else is stated.


5. *Ranorthis norvegica* Ópik. Interior of dorsal valve, PMU In 474, Zheltiaki Unit, Putilovo Quarry.


7. *Skenidioides minutus* sp. nov. A: interior of dorsal valve, holotype, PMU In 510. B: exterior of ventral valve, PMU In 515, both specimens from Putilovo Quarry, Zheltiaki Unit.

8. *Nothorthis penetrabilis* Rubel. A: dorsal exterior of a coarsely ribbed morphotype, PMU In 211, Dikari Unit, Putilovo mud mound. B & C: exterior and interior of dorsal valve, PMU In 103. D: ventral interior, PMU In 104. The two latter specimens from Zheltiaki Unit, Putilovo Quarry.

9. *Paurorthis parva* (Pander). A: dorsal interior of specimen with well developed mantle canals, PMU In 207. B: dorsal interior of specimen with pits on the internal surface of the shell, PMU In 477. Both specimens from Frizy Unit, Putilovo Quarry. C: exterior of dorsal valve with well developed pseudopunctae, PMU In 98, Frizy Unit, Lava River. D: internal of ventral valve with pitted inner surface, PMU In 478, Frizy Unit, Putilovo Quarry.
Plate 5

Scale bar 2 mm

   A, C & E: ventral, anterior and front view of conjoined specimen, PMU In 452, Frizy Unit, Lynna River.
   B & D: dorsal and posterior view of conjoined specimen, CNIGR 23/13101, loose sample in Volkhov Formation, Putilovo Quarry.

   Dorsal fold with characteristic ornamentation, PMU In 451, Volkhov Formation, Putilovo Quarry.

3. *Idiostrophia tenuicostata* sp. nov.
   A & B: dorsal and ventral view of conjoined specimen, CNIGR 15/13101, loose sample in Volkhov Formation, Volkhov River.