

Review of the Ordovician rhynchonelliformean Brachiopoda of the East Baltic: Their distribution and biofacies

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Analyses of the distribution, in time and space, of approximately 300 Ordovician rhynchonelliformean brachiopods in the East Baltic allow the development of a faunal template for the Baltic Province (*sensu stricto*) within the context of the European Realm. Two different brachiopod magnafacies, the upper and lower ramp associations, are monitored through time. Changes in the brachiopod fauna through uppermost Hunneberg to the Porkuni stages are demonstrated from different drill core sections and some bedrock exposures located in facially contrasting areas across the region. The main developmental trends within the brachiopod biofacies of the shallower part of the palaeobasin (North Estonian facies belt) are characterized by relatively continuous changes in taxonomic composition including the evolution of endemics and the establishment of relatively persistent associations, especially during the later Ordovician. In the deeper parts of the palaeobasin (Central Baltoscandian confacies belt including the Livonian Tongue) the several different types, clearly determined by changes in environment, occur: Relatively low diversity associations in the red-coloured sediments, a well-defined assemblage associated with black shales and more diverse associations in the argillaceous carbonate deposits. The appearance and distribution of some short-lived associations including immigrants to the Baltic (*Dactylogonia* and *Rhynchotrema* during the Keila-Oandu event, the *Holorhynchus* association during the mid-Ashgill and the *Hirnantia* fauna during the late Ashgill) are probably associated with climatic and sea-level changes in the palaeobasin.

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Over 300 species of rhynchonelliformean Ordovician brachiopods belonging to about 150 genera are known from the East Baltic. The lists of Baltic Ordovician brachiopods and the data on their distribution have been published in a series of reviews, together with data presented in papers dealing with the stratigraphical problems (see for example, Hints 1990; Hints & Rõõmusoks 1997; Männil 1966; Paškevičius 1997, 2000; Rõõmusoks 1967a, 1970). The most complete species-level data were reported in the monographic studies by Öpik (1930, 1934), Rõõmusoks (1967, 1970), Alikhova (1953, 1969), Rubel (1963), Hints (1975), and others. Nevertheless many species recorded under open nomenclature in some publications (for example in Rõõmusoks 1970), in addition to new species cited in manuscripts (Rõõmusoks 1967b), suggests that the real number of brachiopod species is probably somewhat greater.

The biofacies differentiation of the Ordovician faunas, including that of the brachiopods, in the East Baltic, was first demonstrated by Männil (1966) who also established the main facies belts within the Baltic Palaeobasin. Since the 1960s the main distributional trends of brachiopod faunas within the European Realm, including the Baltoscandian faunas, have been analysed by a number of authors (e.g., Williams 1969, 1973; Jaanusson 1973, 1976; Sheehan 1987). Nevertheless despite the excellence of preservation of the East Baltic faunas and the detailed data available on their distribution, the differentiation of the brachiopod faunas within the Baltic Palaeobasin has been addressed in relatively few papers (e.g., Jaanusson 1973, 1984; Harper & Hints 2001).

In summary, the main trends in the temporal and spatial evolution of the brachiopod faunas in the shallow part (upper ramp facies) of the Baltic Palaeoba-

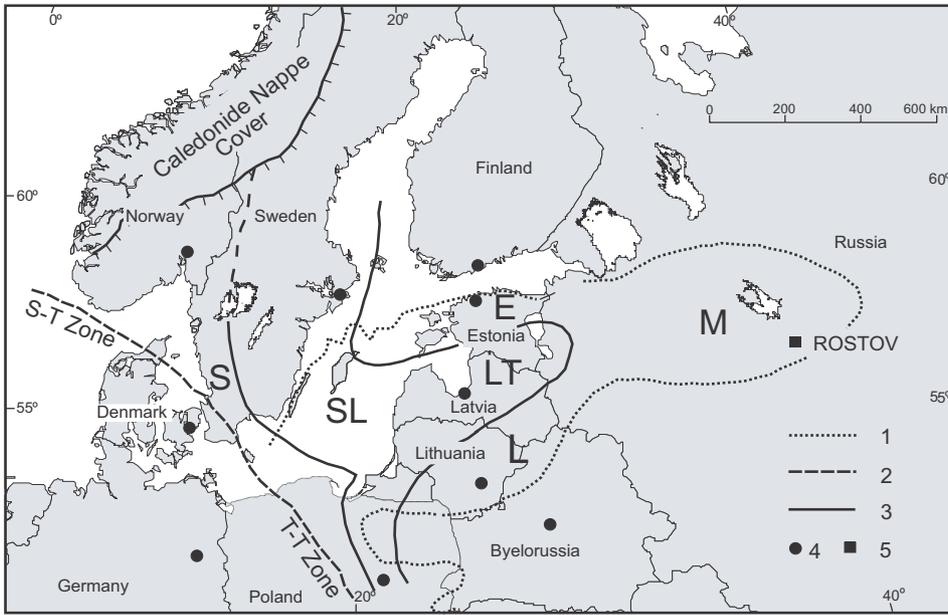


Fig. 1. Confacies belts of the Baltoscandian Basin (modified by Jaanusson 1995, Nölvak 1997 and Nestor & Einasto 1997 for the northwestern part of Baltica: E – Estonian, L – Lithuanian, SL – Swedish–Latvian (Central Baltoscandian), S – Scanian Confacies Belt, LT – Livonian Tongue of SL, M – Moscow Syncline (Moscow Palaeobasin). Caledonian Nappe Cover and the main fault Tornquist–Teisseyre (T–T Zone) and Sorgenfrei–Tornquist (S–T Zone) zones following Tuuling 1998. Legend on the lower right corner: 1 – the outer limit of the area with continuous distribution of Ordovician rocks, 2 – the fault zones, 3 – boundary of facies belt, 4 – capital of country, 5 – location of drill core.

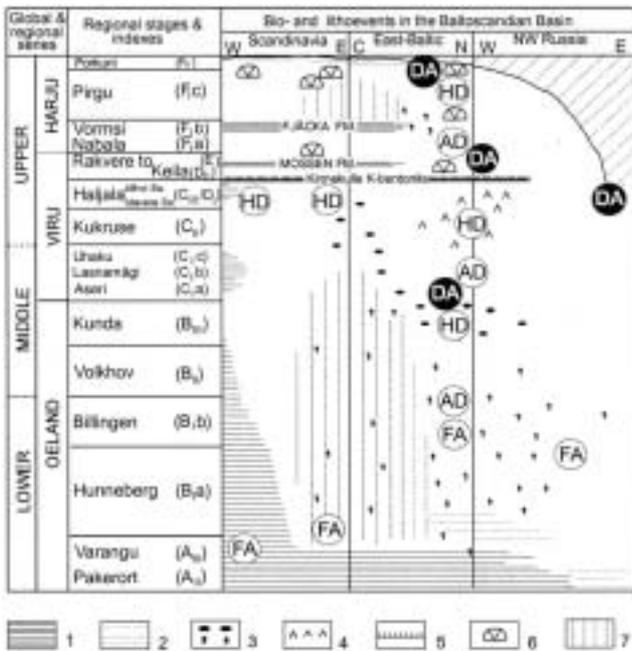


Fig. 2. Stratigraphical chart, showing some bioevents and characteristic features of the Ordovician successions in the various parts of the Baltoscandian Palaeobasin. The vertical scale corresponds roughly to the time scale of Webby 1998. Lithological features: 1 – shale, 2 – sandy deposits, 3 – oolites (above), glauconite (below), 4 – kukersite kerogen, 5 – K-bentonite, 6 – reefs, 7 – red-coloured rocks; FA – first appearance of rhynchonelliformean brachiopods. Dynamics of rhynchonelliformean brachiopods: AD – indicates appearance of many new taxa, HD – high diversity levels, DA – disappearance of many taxa (See A/D ratio and trends in brachiopod diversity on Fig. 3). W – West, E – East, N – North, C – Central part; Ss. – substage. The Oandu Stage (D_{III}) between the Keila and Rakevere stages is not shown in the table.

sin (North Estonian facies belt; see Fig. 1) are characterized by a relatively continuous turnover of their taxonomic composition, including the extensive evolution of endemic stocks or the relative persistence of associations, particularly during the latest Ordovician. The continuity of these faunas, distributed in more-or-less argillaceous carbonate deposits, is interrupted at some levels by stratigraphical gaps in the sequence. In the lower ramp facies in the central part of the region (Livonian Tongue of the Baltoscandinavian facies belt) the brachiopod composition changes in accordance with sudden changes in environment, evident by the intercalation of red- and grey-coloured mudstones, argillaceous limestones or black shales all characterised by their own faunal associations (see Fig. 2). Such environments were less suitable for habitation by brachiopods.

The distribution of some short-lived associations comprising immigrants from other provinces (e.g., *Rhynchotrema*, *Dactylogonia*, *Holorhynchus*, *Hirnantia* and others) occur in the Baltic areas during intervals associated with major geological events (Keila-Oandu event and the end Ordovician event) accompanied by changes in sea level.

This overview aims to present the main biofacies and differences in the various brachiopod faunas across the Baltic Palaeobasin, showing faunal changes through facies transects for the separate regional stages. In addition, the relationships of the East Baltic brachiopod faunas with faunas in the easternmost (Moscow Palaeobasin), and westernmost parts of the

palaeobasin (Scandinavian part), are analyzed. The role of brachiopods in the composition of benthic faunas across the region is indicated by data from drill core sections.

Material and methods

This overview of Ordovician articulated brachiopods is based on data from outcrops in Norway and Sweden, northernmost East Baltic and NW Russia and from drill core sections, mostly from the East Baltic. The limited amount of rock material and fossils in the drill core sections makes direct comparisons between drill-core data and outcrops impossible. For example, the diverse and abundant brachiopod fauna from northern Estonia has been collected and studied for more than 150 years. Nevertheless despite a great number of drill cores their data cannot hope to match those known from intensive studies of exposures. This is also emphasized when outcrop sections were processed and studied using methods employed for extracting fossils from rock. The most effective method for the disintegration of rock samples is their repeated heating and cooling with sodium hyposulphite (the method most commonly used for extracting ostracodes) or by treating clay samples with hydrogen peroxide. The occurrence of abundant shelly faunas in core sections is generally unusual (see Põlma, Sarv & Hints 1988, figs 7, 14, 15, 18). Their frequent occurrence (in some sections in northern Estonia, Southern Lithuania and Russia) presumably

shows a high population density or indicates concentrations in particular environments and settings (e.g., storm accumulations).

The most diverse and abundant brachiopod fauna within the Baltic Palaeobasin was developed during the later Mid and early Late Ordovician (Harper & Hints 2001). Data from six sections demonstrate the role of brachiopods within the shelly faunas during this interval. These sections were studied through bed-by-bed sampling and the frequency of each fossil taxon was determined as the number (per cent) of specimens in relation to the total number of specimens from any one stage. Thus the composition of each shelly fauna is considered in terms of both shells and shell particles, which supposedly can be identified at the species, genus or family level. The small fragments (commonly less than 2–3 mm) were considered as a constituent part of the skeletal sand (biodetrit) of the rocks themselves.

Trends in the turnover of the brachiopod faunas are characterized by the ratio of appearances to disappearances of genera per stage (Turnover Index). On the figures below, the total range of selected brachiopods in the drill core sections is shown as the interval between the first and last occurrence. The stratigraphical frame, provided by the regional stages and some specific lithological features within the Ordovician successions in different parts of the Baltic Palaeobasin are shown on Figure 2. The difficulties of correlation of the Keila to Rakvere interval (see Ainsaar & Meidla 2001; Ainsaar, Meidla & Martma 1999) complicate interpretations of the brachiopod faunas of the Blidene and Mossen formations whose stratigraphi-

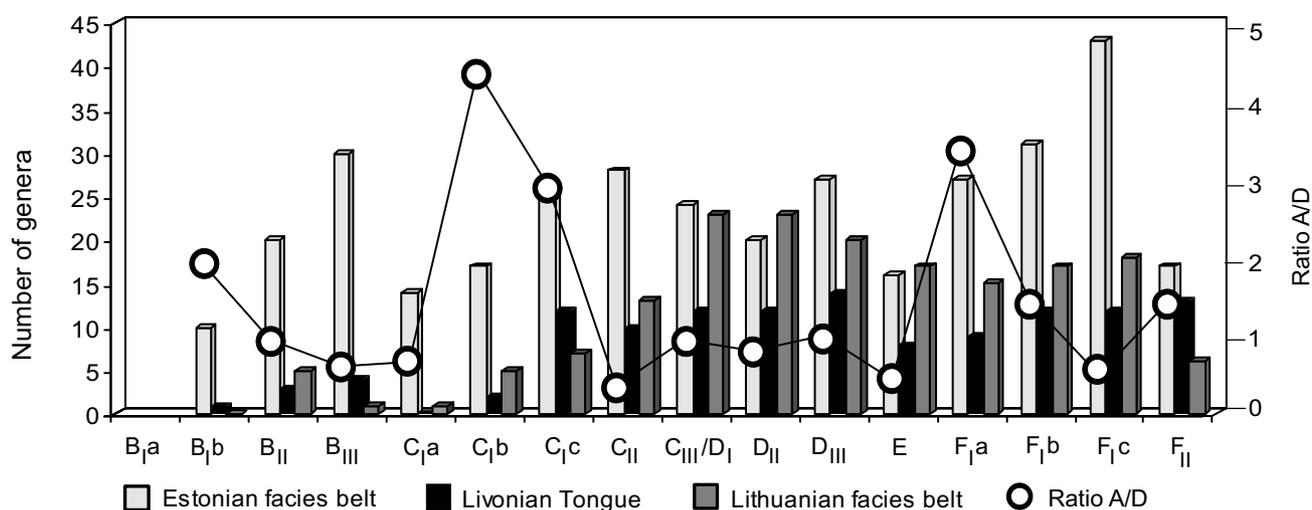


Fig. 3. Taxonomic diversity of brachiopods: Number of genera in the Estonian and Lithuanian facies belts (upper ramp) and in the Livonian Tongue (lower ramp) (See Fig. 2), and ratio of appearances (A) and disappearances (D) of genera in the Estonian facies belt (data from Hints & Rõõmusoks 1997; Paškevičius 1997; partly unpublished data for the Livonian Tongue). Indexes of stages see Fig. 2.

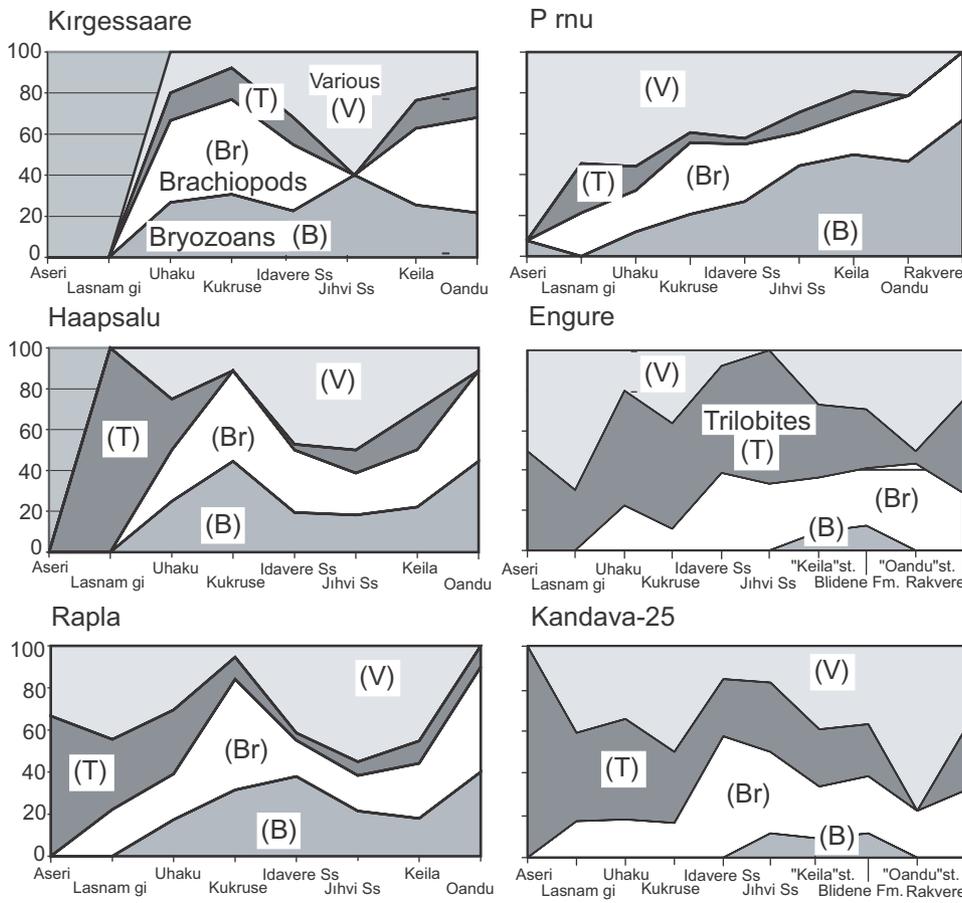


Fig. 4. Composition of the shelly fauna of the Viru Series (later Mid and early Late Ordovician) based on data from six drill core sections. Kõrgessaare, Haapsalu and Rapla cores are located in the Estonian Confacies Belt, Engure and Kandava-25 in the Livonian Tongue and Pärnu in the transitional area between the main facies belts. Location of sections, see Fig. 6. Due to correlation difficulties the Blidene Formation (Fm.) is shown separately between the Keila (*sensu stricto*) and Oandu stages (st.). The data for the Haljala Stage are shown in substages (Ss).

cal position in the central East Baltic has been the subject of debate by different authors.

The brachiopod component of the shelly fauna

The East Baltic occupied a central position within the Baltic Palaeobasin (Fig. 1) during most of the Ordovician Period; its faunas have close relationships with those in the west (Scandinavia) and those in the east (e.g. Moscow Palaeobasin); both regions developed a greater individuality from the beginning of the Late Ordovician. The Ordovician rhynchonelliformean brachiopods first appeared in the East Baltic in shallow-water environments during the latest Early Ordovician, when the siliciclastic sedimentation was replaced by predominantly carbonate facies.

The standing brachiopod diversity and temporal trends are clearly apparent by reference to the number of genera per regional stage across the different facies belts (Fig. 3). Three high-diversity intervals characterize northern Estonia. The earliest brachiopod fauna, dominated by Baltic endemics, achieved its highest diversity in the Kunda Stage (B_{III}) (end of

the regional Oeland Series; middle of the Middle Ordovician). After a fall in diversity during the Aseri Stage (C_{Ia}), diversity again climbs to reach a peak in the Uhaku (C_{Ic}) and Kukruse (C_{II}) stages at the Middle-Upper Ordovician transition. In Lithuania, high brachiopod diversities characterize the higher stratigraphical levels, particularly the Haljala ($C_{III}-D_I$) and Keila (D_{II}) stages, which consist of argillaceous limestones and marls. In the northern East Baltic the third diversity peak occurs within the Pärnu Stage (F_{Ic}) (middle of the Harju Series, uppermost Upper Ordovician). In the Livonian Tongue (the central East Baltic) brachiopods are less diverse than in other parts of the East Baltic, except for three stages (B_{III} , C_{Ic} , F_{Ic}) (Fig. 3). As noted previously, the dynamics of brachiopod fauna can also be shown by the ratio of number of appearances (A) and disappearances (D) of genera (Fig. 3). Values of the A/D ratio over unity in northern Estonia show that appearances prevail over disappearances in the Billingen (B_{Ib}), Lasnamägi (C_{Ib}) and Nabala stages (F_{Ia}) (Fig. 3). In these three cases, turnovers (the high value of the A/D ratio) brachiopod composition clearly anticipated the three levels of highest diversity (Fig. 3). Thus the development of high diversity takes place approximately two stages

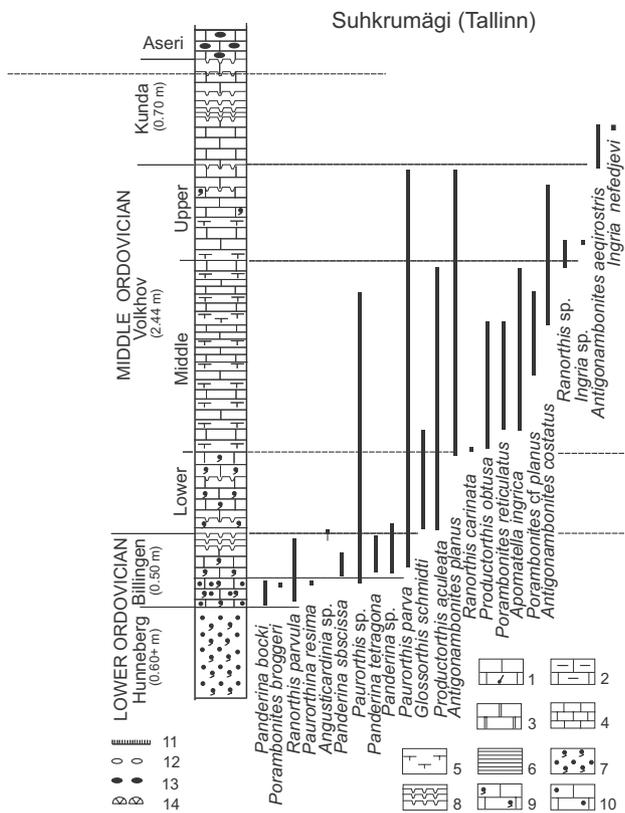


Fig. 5. Distribution of brachiopods in the Suhkrumägi (Tallinn) section. Legend for Figs 5 – 9: 1 – limestone and limestone with pyritized skeletal sand (lower row), 2 – argillaceous limestone, 3 – dolomite, 4 – micritic (aphanitic) limestone, 5 – marl, 6 – shale, 7 – glauconitic sand, 8 – limestone with discontinuity surfaces, 9 – glauconitic limestone, 10 – sandy limestone, 11 – K-bentonite bed, 12 – carbonate ooids, 13 – goethitic ooids, 14 – reef. Left of the log - global series, regional stages and substages.

after the turnover. By contrast with the brachiopods, the most marked turnover in trilobite composition takes place earlier, during the Aseri Stage (See Rõõmusoks 1997).

The brachiopods in relation to other components of the Ordovician shelly fauna are analysed through the interval from Aseri to Rakvere, which comprises the transition from the Middle to Upper Ordovician; this boundary falls close to the junction between the Uhaku and Kukruse stages; data from six core sections located in the different facies belts are presented (Fig. 4). In the northernmost sections, Kõrgessaare to Rapla, the frequency of brachiopods tends to increase during the Viru Series, that is during the late Mid and early Late Ordovician. (The apparent decrease in the Kõrgessaare sections is due to the restricted thickness of the Jõhvi Substage). In the two southernmost sections, Engure and Kandava, the trilobites are the most common shelly fossils up to Keila Stage.

The earliest Ordovician brachiopod faunas

The oldest brachiopods in Baltoscandia occur in the Hunneberg and Billingen stages, but appear in different parts of the region at different times, during a 10 million year interval from the mid Tremadoc to the mid Arenig (see Fig. 2).

In northern Estonia, the first articulated brachiopods appear in the glauconitic, calcareous sandstones of the Mäeküla Member in the lower part of the Billingen Stage. The orthides *Ranorthis* and *Paurorthis*, in the Mäeküla Member of the Suhkrumägi section represent widely-distributed taxa, which also occur in the younger beds of the Volkhov Stage (Fig. 5). Particular early Billingen (Mäeküla) species of the genera *Plectella*, *Angusticardinia*, *Apheoorthina* are quite rare and are known from only a few sections (see Öpik 1933; Rubel 1961). The presence of *Angusticardinia* in the lowermost Volkhov Stage in the Suhkrumägi section is recorded from a small pebble of older (Billingen) rocks. *Ranorthis parvula* (Lamansky) is apparently the only species, which occurs abundantly at some levels in the glauconitic carbonate sandstones of the Mäeküla Member, northern Estonia.

The earliest brachiopods in the NW part of Russia are discussed in several papers, the most complete overview is that of Egerquist (1999). She has identified in the lowermost Ordovician, including the Volkhov Stage, representatives of 27 genera. Sixteen of them are of Billingen age which indicates that the earliest brachiopod fauna is more diverse in NW Russia than in Estonia. This is supported indirectly by the fact that many species have holotypes from NW Russia. Somewhat more detailed data on the stratigraphy and distribution of some fossils is presented by Dronov, Koren, Popov & Tolmacheva (1998, p. 38) for the section on the Lava River near the village of Vassilkovo. In this section the first articulated brachiopods *Ranorthis* and *Panderina* appear in the Lakity Member, which is correlated with the upper part of the Hunneberg Stage (Holmer & Popov 1996/98). This correlation is supported by the fact that these two brachiopods occur together in the middle part of the *P. proteus* conodont Biozone, just below the first occurrence of *Tetragraptus phyllograptoides* (Dronov et al. 1998). Consequently the earliest articulated brachiopods in NW Russia are from the upper part of the Hunneberg Stage, earlier than those in northern Estonia. In the Moscow Palaeobasin, the first articulated brachiopods (*Ranorthis* sp., *Paurorthis?* sp.; unpublished data) occur in the upper part of the *T. phyllograptoides* Biozone (see Kaljo 1974).

Dronov (in Dronov et al. 1998) has also concluded that the boundary between the Lakity and Nazya members represents a gap corresponding to the

Hunnebergian trilobite *M. (E.) armata* and the lower part of the *M. planilimbata* biozones in Scandinavia. In Sweden, the lowest zone comprises the brachiopods *Lycophoria? laevis* Stolley, *Archaeorthis? suedica* Tjernvik and *Nanorthis? billingensis* Tjernvik (Tjernvik 1956; Löfgren 1994, fig. 2), but the oldest brachiopods (*Archaeorthis christianiae* Brøgger) in Baltoscandia are recorded from the glauconitic Ceratopyge Limestone in the Oslo-Asker district of Norway (Bockelie 1982; Harper 1986), which belongs to the most oceanward part of Baltoscandia (Bruton & Harper 1988). This limestone is of Varangu age in terms of the East Baltic stratigraphy.

Somewhat unusual is the occurrence of *Plectella* and associated brachiopods in the lowermost Volkhov Stage in Lithuania recorded by Paškevičius (2000). In Poland, close to the Lithuanian border, *Plectella* is noted from the pre-Volkhov rocks (Modlinski 1973). The age of the *Ranorthis carinata*-*Plectella uncinata* Community of Paškevičius is in need of refinement and a more detailed correlation with the conodont biozonation is required.

The Oeland (Early and early Mid Ordovician) brachiopod faunas

The interval discussed here comprises the succession from the Billingen to Kunda stages represented by more-or-less argillaceous carbonate rocks with glauconite grains or goethitic ooids formed in the shallow-water upper ramp facies (Estonian and Lithuanian facies belts).

Within the limits of the lower ramp facies (Livonian Tongue), mainly red-coloured argillaceous carbonate rocks were deposited (Fig. 2). The diverse brachiopod fauna was distributed in the upper ramp area, and in the easternmost part of the epicontinental Moscow Palaeobasin (Alikhova 1969). Only some rare articulated brachiopods (*Ranorthis* sp. and *Paurorthis* sp.) occur in the red-coloured sediments in the drill-core sections of the Central East Baltic. Trilobites were the most common inhabitants of this part of palaeobasin.

The brachiopod fauna of the Oeland Series is quite similar across the upper ramp facies of Estonia and NW Russia, but in the latter area the sequence is more complete. *Paurorthis*, *Panderina*, *Ranorthis* and *Antigonambonites* appear first in the Billingen Stage but become more common in the younger strata of the Volkhov or both the Volkhov and Kunda stages. Orthides together with clitambonitidines and small numbers of strophomenides dominate the brachiopod fauna of the first half of the Ordovician Period. The

orthides *Productorthis obtusa* (Pander) and *Paurorthis parva* (Pander) were considered by Alikhova (1960) to represent the nominal (eponymous) taxa for the local brachiopod zone comprising the Volkhov Stage, but unfortunately the distribution ranges of these species do not correspond to the whole stage (see Rubel 1961).

The most complete Volkhov–Kunda transition is represented in NW Russia. In one section on the Lynna River, close to its confluence with the Sjas' River in the easternmost part of Leningrad district, diverse brachiopod associations have been reported (see Hansen & Harper 2003). The most common taxon in the upper part of the Volkhov Stage is *Paralenorthis orbicularis* (Pander) which occurs in 34 of the 44 samples collected from the 3.15 m thick uppermost Volkhov Stage. *Paralenorthis* (see Jaanusson & Bassett 1993) occurs together with the plectambonitoids *Ingria* and *Ahtiella*, which are also common in Avalonia faunas. In the Lynna section both plectambonitoids occur at the same stratigraphical interval (commonly in the same samples) together with the endemic brachiopod genera *Antigonambonites*, *Gonambonites* and *Ladogiella*.

Within Lithuania, the *Paralenorthis orbicularis*-*Orthambonites majuscula*-*Lycophoria nucella* association was established for the Kunda Stage (Paškevičius 2000). The bizarre genus *Lycophoria* appears in the middle of the Volkhov Stage in northern East Baltic, Sweden and SW Russia and, somewhat later, in the Kunda Stage it occurs all over Baltoscandia (Rubel 1961).

The brachiopod fauna described above, tentatively named the *Productorthis* fauna (Harper & Hints 2001) disappeared at the end of the Kunda Stage. Several genera appearing in the Oeland Series (*Clitambonites*, *Estlandia*, *Glossorthis*, *Nicolella*, *Cyrtonotella*, *Platystrophia* and *Porambonites*) become more widely distributed in younger rocks. *Lycophoria* is one of the most characteristic Oelandian brachiopods also represented in post-Kunda rocks.

The Oeland-age brachiopod faunas in the Moscow Palaeobasin consist mainly of taxa common in the Baltic areas. *Ranorthis carinata* Rubel, *Paurorthis parva* (Pander) *Antigonambonites planus* (Pander), *Panderina tetragona* (Pander), *Apomatella ingrlica* (Pahlen), *Ingria nefedjevi* (Eichwald), *Lycophoria nucella* (Dalman), *Orthambonites calligramma* (Dalman), *Iru concava* (Pander) together with a number of other species have been recorded from sections in the easternmost part of the Moscow Palaeobasin (Alikhova 1969; Dimitrovskaja 1991; Melnikova & Dimitrovskaja 1997).

The Viru (late Mid and early Late Ordovician) brachiopod faunas

The Viru Series (*sensu stricto*: from the Aseri to Keila stages) is represented in most parts of the palaeobasin by calcareous sediments with increased clay material and decreased bioclastics in an offshore direction (Nestor & Einasto 1997). The distribution of oil shales in northern Estonia and NW Russia and the occurrence of numerous K-bentonites all over Baltoscandia characterize this stratigraphical interval. The Oeland-Viru transition is characterized by a decrease in brachiopod diversity and there are only two species of brachiopods common to both the Kunda and Aseri stages, *Clitambonites adscendens* (Pander) and *Glossorthis verneuili* (Rubel) (Rõõmusoks 1970, table 3). The Aseri brachiopod fauna is of low diversity and sparse in upper ramp as well as lower ramp environments where the deposition of red-coloured rocks continued (see Figs 2 and 3). *Leptestia*, *Leptoplium* and *Christiania* appear as new genera together with new species of *Plectambonites*, *Panderites* (*Oepikina* in older publications) within this Middle Ordovician brachiopod fauna. *Christiania oblonga* (Pander) has served as the diagnostic species for the Lasnamägi Stage (Alikhova 1960), but at least one specimen occurs in the Aseri Stage in Northern Estonia (Savala drill core section). The frequent occurrence of *Christiania* in NW Russia (in the dolomites of the Duboviky quarry) and its appearance in drill-core sections (Fig. 6, in the Kõrgessaare and Rapla sections) shows its wide distribution in the upper ramp facies during the Lasnamägi. In the lower ramp facies, the genus is represented at different stratigraphical levels (Fig. 6, Ikla section) up to the Pirgu Stage (lowermost Ashgill) (see also Spjeldnæs 1957).

Several early Viru (late Mid and early Late Ordovician) brachiopods, e.g. *Hesperorthis*, *Cremnorthis*, *Vellamo*, *Sowerbyella*, *Leptelloidea*, *Bekkerina* (= *Oepikina*), *Kiaromena* (= *Estonomena*), appear in the Lasnamägi Stage (Fig. 3). The most complete overview of the brachiopods of the Viru Series was presented for northern Estonia by Rõõmusoks (1970), for Lithuania by Paškevičius (1997, 2000) and for the Moscow Palaeobasin by Alikhova (1969). Unfortunately the lists of species given by stages are difficult to use because of changes to stadial boundaries by later authors. In particular, the boundary between the Lasnamägi and Uhaku stages has been modified. Recent stratigraphical studies (Nõlvak 1997) following Männil (1970) have suggested that the lower boundary of the Uhaku Stage is correlated with the level of the appearance of the graptolite *Gymnograptus linnarssoni* (Moberg). This level is in fact within the upper half of the lower substage of the Lasnamägi Stage, as defined by Rõõmu-

soks (1970, fig. 11; compare with Männil 1970, fig. 2), somewhat above the last occurrence of *Christiania oblonga*. Thus species ascribed by Rõõmusoks to the upper substage of the Lasnamägi Stage [e.g. *Apatorthis jugata* Öpik, *Hesperorthis inostrantzeffi inostrantzeffi* (Wysogorski), *Porambonites laticaudatus* Bekker, *Sowerbyella* (*Sowerbyella*) (= *Viruella*?) *orvikui* and *Vellamo* aff. *ultima* Öpik] may have their first appearances in the Uhaku Stage as currently recognized.

Many of the Baltic brachiopods also occur in the Moscow Palaeobasin and only a few new species [*Glossorthis lavensis* Alikhova, Vavilov in coll.; *Sowerbyella* (*Sowerbyella*) (= *Viruella*) *bystrovi* Nikanorova, S. (S.) *orechovensis* Nikanorova and some others] are restricted to that palaeobasin (Alikhova 1969; Dimitrovskaja 1991). To these species can also be added new species of *Platystrophia* described from NW Russia (Zuykov 1995, 1999). The similarity between the faunas of the Baltic and Moscow palaeobasins continued until the Idavere Stage, suggesting their inclusion in a single Baltic faunal province. The typical elements of the new brachiopod fauna are *Eorhipidomella* (Hints 1971) and *Multicostella*?, which are represented by abundant specimens crowding some bedding planes of the post-Kukruse argillaceous limestone. The disappearance of the Baltic type fauna roughly coincides with the beginning of the Mid Ordovician in the Moscow Palaeobasin. Up until then the genus *Eorhipidomella* occurs only the Mediterranean Province.

The development of faunas during most of the Viru Series (stages from the Aseri to Keila) has a distinct continuity, reaching peak diversity in the middle of the series, within the Kukruse Stage (Fig. 3). The coexistence of several first and last occurrences, and species restricted to the Kukruse Stage, enhances the diversity peak, especially in the lower half of the stage (see Rõõmusoks 1970, tab. 10). The environmental conditions during the first half of the Kukruse Stage favoured the rapid development of the cyanobacterium *Cloeocapsomorpha prisca* forming the kukersite kerogen in the Baltic oil shales; this process may have promoted radiation amongst a range of different faunal groups.

Relatively rapid changes in environments caused by a sea-level fall (Nestor & Einasto 1997, fig. 140) at the end of the Kukruse Stage led to the disappearance of most species and some genera (*Glossorthis*, *Leptoplium*, *Leptestia* and *Tetraodontella*) (low A/D ratio on Fig. 3). The faunal change at the Kukruse-Haljala boundary is most spectacular in northern Estonia, but this effect may have been exaggerated by a gap at the boundary in the order of 2–3 chitinozoan zones in the northern East Baltic (Hints, Meidla & Nõlvak 1994). Nevertheless the lower boundary of the

Fig. 6. Correlation of sections and the vertical distribution of selected brachiopods in the onshore (Kõrgessaare and Rapla) offshore (Ikla and Engure) profiles. For the lithological legend see Fig. 5; vertical lines mark the red colour of the rocks. BB - Kinnekulle K-bentonite.

Haljala Stage is one of the few biostratigraphical levels well constrained by chitinozoan zones in Sweden and East Baltic including NW Russia (Nölvak & Grahn 1993). The upper boundary of the Haljala Stage is traditionally marked by the lower boundary of the Kinnekulle K-bentonite bed (Fig. 2).

Within the Haljala brachiopod fauna, several species occur which are widely distributed in the upper ramp facies appearing in the lower unit of that stage and characterizing the younger, Jõhvi Substage (*Clitambonites schmidti epigonus* Öpik, *Cyrtonotella kuckersiana frechi* (Wysogorski), *Leptaena rugosoides* Oraspõld, *Platystrophia lynx lynx* (Eichwald), *Porambonites baueri* Noetling and others, see Rõõmusoks 1970, table 12). A similar brachiopod fauna is distributed over most parts of NW Russia (Alikhova 1969), but the correlation of sections between NW Russia and Estonia is difficult, due to differences in facies, strata thickness and possible temporal and spatial

shifts of some of the characteristic species within the macrofauna. Sections in the profile Kõrgessaare-Engure (Fig. 6) show that the northern-type brachiopod faunas are distributed through the Keila Stage up to the Pärnu. Southwards, in the biotrital grainstones of the Kukruse and Haljala stages, the brachiopod fauna is of the Scandinavian type, comprising taxa known from Sweden (*Leptellina*, *Bimuria* and *Skenidioides*).

Changes in climate as well as sea-level oscillations (Nestor & Einasto 1997), characteristic of post-Haljala time, initiated a sharp differentiation of the benthic fauna. The early Keila faunas, mainly holdovers, were replaced in the later Keila by a short-lived association of large strophomenids [*Longvillia*, *Strophomena* (*Keilamena*)] and dalmanellids (*Horderleyella kegelensis*, *Sowerbyella* and the last representatives of the endemic genus *Estlandia* together with several species, which first appeared during the

early Haljala. Many brachiopods characteristic of the Keila Stage in outcrop are also represented in drill-core sections (Fig. 6). For example, *H. kegelensis*, which is considered diagnostic for the Keila Stage, appears 5–8 m above the Kinnekulle Bed. Studies of sections in NW Russia confirm a similar pattern, with *H. kegelensis* appearing also somewhat higher above the K-bentonite that possibly corresponds to the Kinnekulle Bed in Estonia.

Alikhova (1960, 1969) identified the Keila Stage in NW Russia and in the Moscow Palaeobasin as the *Horderleyella* (ascribed to *Dalmanella* by Alikhova) *kegelensis* Zone. The different interpretation of the boundaries of the Keila Stage between the Estonian and Russian researchers is because of the lack of, or difficulties with the identification of, K-bentonites in NW Russia and the recognition of the lower boundary of the stage by the appearance of *H. kegelensis*. It is interesting to note that *Clinambon anomalus* occurs often in life position in northern Estonia, and this species is one of the few upper ramp brachiopods distributed close to the Livonian Tongue.

The Keila-Oandu faunal crisis

The discernible changes of facies and faunas at the Keila-Oandu transition (Põlma, Sarv & Hints 1988; Nestor & Einasto 1997) coincide roughly with the faunal changes known from other regions at the boundary between the early and later Caradoc (Williams 1973; Hurst 1979a, b). The upper ramp (northern Estonian) Keila and Oandu brachiopod faunas are analysed in several publications and the remarkable differences in their composition need not be reiterated here (see Rõõmusoks 1970; Põlma *et al.* 1988; Hints 1975, 1997; Meidla, Ainsaar, Hints, L., Hints, O., Martma & Nõlvak 1999). The late Keila brachiopod fauna, including the last *Clinambon* (with the exception of one species possibly in the Oandu Vasalemma mud mounds) and *Estlandia*, together with the large-shelled strophomenids *Strophomena (Keilamena)* and *Longvillia*, the dalmanellid *Horderleyella* and species of *Sowerbyella*, is replaced in the Oandu Stage by the *Howellites-Sowerbyella* fauna. Nevertheless, brachiopods from the Baltic included in the genus *Howellites* (*Dalmanella* of Alikhova 1960) have an external sculpture with primary costae on the pedicle valve (Kemezys 1968), but the representatives of the genus from Avalonia, at least part of them, have an isorthid type of ribbing (one medial primary costae). The diagnostic value of ribbing types is in need of further study; pending further investigations these brachiopod species remain within the genus *Howellites*. Some taxa from the north Estonian brachiopod fauna [for

example, *Strophomena (Keilamena)* and *Platystrophia rava*] are distributed up into the Pärnu and Ikla, close to the Livonian Tongue (Figs 6 and 7). Southwards, the Keila and Oandu brachiopods are divided between different associations; their temporal and spatial relationships with each other and the upper ramp faunas are not clear.

In the Livonian Tongue, the sequence of the argillaceous limestones and marls between the black shales of the Mossen Formation (*sensu stricto* = the Plunge Member of Ainsaar & Meidla 2001) and the K-bentonite, is characterized in its lower half by an association of brachiopods, dominantly of small size (*Onniella*, *Septorthis*, *Skenidioides* and *Sampo?* together with sowerbyellids) (Fig. 6, Engure section). In some sections large strophomenids supposedly belonging to the genus *Gunnarella*, an immigrant from Scandinavia (Spjeldnæs 1957), also appear in this part. The preliminary Keila age for this, the more carbonate-rich part with several K-bentonites, was based mainly on the occurrence of *Asaphus (Neoasaphus) ludibundus* Törnquist (Männil 1966, fig. 12, 13 and his unpublished data). The upper, marly part of the interval (the Blidene Formation; see Ainsaar & Meidla 2001) differs from the lower part by the frequent occurrence of *Onniella bancrofti* Lindström and *Leptellina cf. indentata* (Spjeldnæs) together with new trilobites (*Dindymene*, *Estoniops* and others). In some publications the latter beds are included within the Keila (Ainsaar *et al.* 1999; Nõlvak & Grahn 1993), while in others these beds are placed within the Oandu Stage (Männil 1966; Hints 1975). The ranges of the trilobite *Asaphus (Neoasaphus) ludibundus* and some brachiopods (*Howellites*, *Skenidioides*, *Laticrura*, *Taphrothis* and *Leptellina cf. indentata*) in southern Estonia are similar to those in Sweden, in the Fjäckå section from the Skagen to Moldå limestones (see Jaanusson 1982).

Correlation with both the Keila and Oandu stages is also proposed for the Mossen Formation (*sensu stricto* = Plunge Member of Ainsaar & Meidla 2001); its black shales comprise, besides a diverse association of phosphatic brachiopods, only two rhynchonelliform taxa, *Chonetoides* (= *Sericoides*) and *Onniella*; both are common in shale facies of different ages. Jaanusson (1984) suggested an ecological succession of articulated brachiopods along a gradient from coarse-grained rocks to shales; sowerbyelline-strophomenid-dalmanellid associations characterized shallow-water environments whereas the *Chonetoides* (= *Sericoides*) association typified deep-water shale facies. This succession apparently cannot be applied directly in the East Baltic for stratigraphical reasons [see Ainsaar & Meidla (2001)]. The facies and faunal differentiation during the Keila-Oandu interval was caused by bathymetric differentiation across the pal-

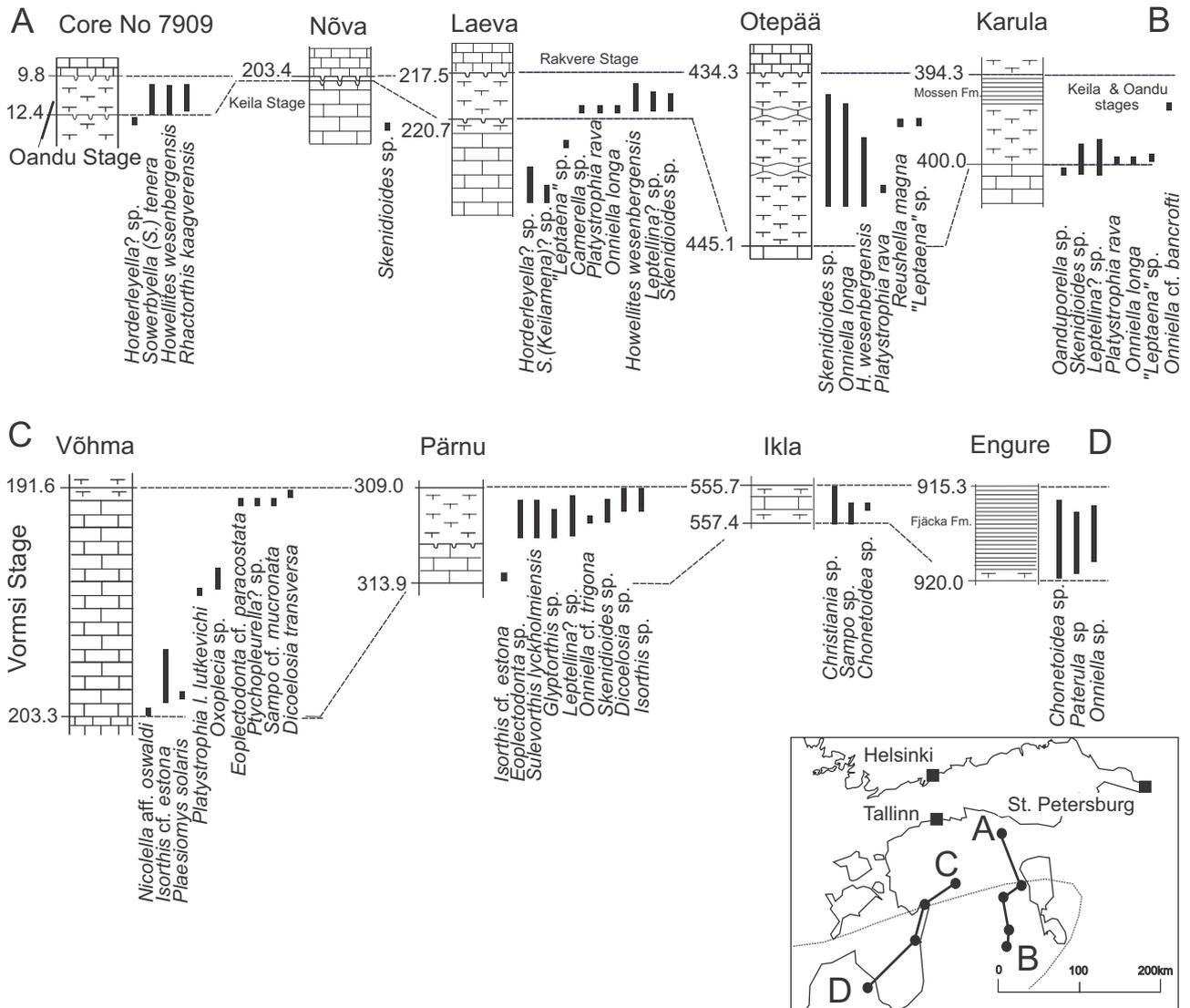


Fig. 7. The correlation of the Oandu and Vormsi stages across the onshore-offshore profiles A – B and C – D and the vertical distribution of selected brachiopods. For the lithological legend see Fig. 5.

aeobasin, the occurrence of gaps, and possibly the patchy or partly disjunct distributions of faunas.

The brachiopod fauna of the carbonate marls, within the Keila-Oandu interval, occurs landward of the area of black shale deposition within the Mossen Formation. This fauna consists of *Howellites* accompanied by *Reuschella*, *Laticrura*, *Skenidioides*, *Leptellina*, and its distribution in southern Estonia is restricted to a narrow belt (Fig. 7, Otepää section). In the southern East Baltic, within the Lithuanian facies belt, a diverse brachiopod fauna comprising the genera noted above has a wide distribution where the *Howellites wesenbergensis* – *Geniculina* (= *Rafinesquina*) *subaequiclina* – *Reuschella magna* community is distinguished (Paškevičius 2000). This association is supposedly missing in the Scandinavian part of palaeo-

basin, at least the characteristic Avalonian harknessellid *Reuschella* has not been reported.

A brachiopod association comprising *Rhynchotrema*, *Dactylogonia* and *Anazyga* in the mud mounds (carbonate buildups) and their lateral facies in NW Estonia together with a low diversity shelly fauna with *Rhynchotrema?* in the supposedly lagoonal sandy dolomites of NW Russia show an increase in biofacies differentiation across the Baltic palaeobasin during the Keila and Oandu stages. Many of the new taxa have Laurentian origins.

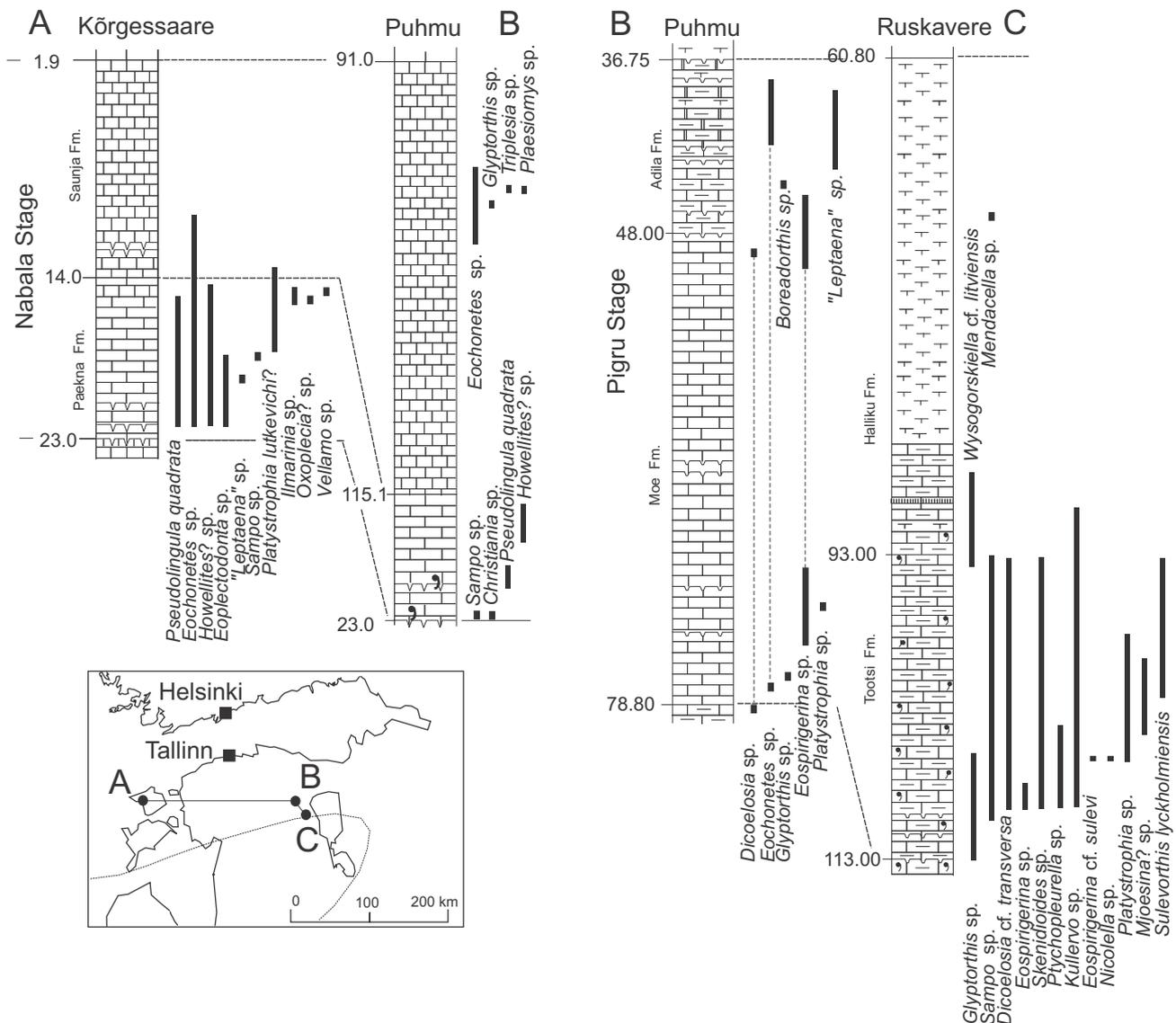


Fig. 8. The correlation of the Nabala and Pigu stages on profiles A – B and B – C and the vertical distribution of selected brachiopods. For the lithological legend see Fig. 5.

The Harju (Late Ordovician) brachiopod faunas

The Late Ordovician, essentially the interval from the Rakvere to Porkuni stages, consists in general of pure micritic limestones intercalated with more-or-less argillaceous limestones in the upper ramp facies (Hints, Meilda, Nõlvak & Sarv 1989). The argillaceous parts comprise a more diverse fauna than that in the pure, commonly, algal limestones. Most of the brachiopod data from northern Estonia are presented in monographic studies and overviews of the stratigraphical distribution of brachiopods (Rõõmusoks 1967a, b; Hints & Rõõmusoks 1997, and others).

The brachiopod fauna of the Rakvere Stage is less diverse (less than 20 genera) than the older, Oandu

and younger Nabala faunas. Rakvere brachiopods are represented by several taxa in common with those of the Oandu Stage [*Boreadorthis*, *Howellites*, *Sowerbyella* (*Sowerbyella*), *Microtrypa*, *Holtedahlina*, *Geniculina* and others]; *Triplesia* is a Lazarus taxon in the Rakvere Stage and *Sampo* is supposedly an immigrant from the deeper part of the palaeobasin. Brachiopods are relatively sparse in carbonate muddy environments where they, especially *Sowerbyella*, acted as opportunistic, appearing abundantly during intervals of increased terrigenous influx. These shell concentrations may also have been modified by storm activity.

The remaining part of the Upper Ordovician up to the base of the Porkuni Stage in northern Estonia has, in spite of facies differences, quite similar brachiopod faunas across the upper ramp. The *Nicolella*-*Boreador-*

this fauna (Harper & Hints 2001) occurs through the Nabala, Vormsi and Pirgu stages and consists mainly of large brachiopods, such as *Porambonites* (*Equirostra*), *Platystrophia*, *Plaesiomys*, *Leptaena* and *Geniculina*. The Nabala Stage contains a diverse brachiopod association in the lower more argillaceous part, confirmed by drill-core data (Fig. 8). Among the endemics, only a few taxa (*Apatorthis*, *Vellamo* and *Ilmarinia*) survived into the latest Late Ordovician; here the brachiopod fauna is represented mainly by the pandemic taxa noted above.

In Lithuania, from the Rakvere to Pirgu stages, the brachiopods have much in common with those from northern Estonia (Paškevičius 1998). Moreover, Paškevičius (2000) has identified a succession of brachiopod associations within the Lithuanian sections; however several of the nominal species apparently had a much wider stratigraphical distribution in the Estonian sections.

Eospirigerina and *Holorhynchus* are widely distributed in many Ordovician palaeobasins, appearing in the Baltic Palaeobasin at the beginning and at the end of the Pirgu Stage, respectively. *Eospirigerina* occurs in a range of different facies belts; its first appearance marks a more or less contemporaneous level in the lower part of the biodetrital limestones in the upper ramp facies (in the Moe Formation) and in the lower part of the red-coloured argillaceous limestones (the Jonstorp Formation) in the lower ramp facies. In Estonia *Holorhynchus* has been identified only in a very restricted area (Hiiumaa Island), but in the southern East Baltic it has wider spatial distribution (the Taučionis Formation: Kaljo & Hints 1997).

In the Livonian Tongue, the development of faunas is determined by marked and relatively rapid changes in environment. For example, the black shales (the Mossen and Fjäckå formations) with low-diversity associations, noted above, occur at two stratigraphical levels (Figs 2 and 7) and separate the distinctive brachiopod faunas distributed in argillaceous limestones and marls, below and above.

The brachiopod successions of the Vormsi Stage, along an onshore-offshore facies transect, show continuous changes of brachiopod composition from the relatively diverse association in the upper ramp carbonate sections to the low-diversity association in the black shales of the Fjäckå Formation (Fig. 7).

Brachiopod associations, quite different from the contemporaneous faunas occur within the lowermost Pirgu Tootsi Member (Fig. 8). Argillaceous limestones, with some glauconite grains, include *Glyporthis*, *Sampo*, *Dicoelosia*, *Eospirigerina*, *Kullervo*, *Sulevorthis* and some others. This association of brachiopods has similarities with the relatively deep-water *Dicoelosia-Skenidioides* Community (Boucot 1975; Sheehan 1987).

The red-coloured limestone, widely distributed in the Central East Baltic, contains a sparse brachiopod fauna [including *Sowerbyella* (*Rugosowerbyella*) *rosettana* and *Sampo* sp.]. By contrast with the Early and early Mid Ordovician red-coloured strata, the Upper Ordovician equivalents include only a few trilobites.

The Porkuni (Hirnantian) brachiopod faunas

The environmental conditions of the latest Ordovician varies from shoal facies, with the formation of oolitic limestones, to reef facies and supposedly exhumed areas at the end of period in the northern part

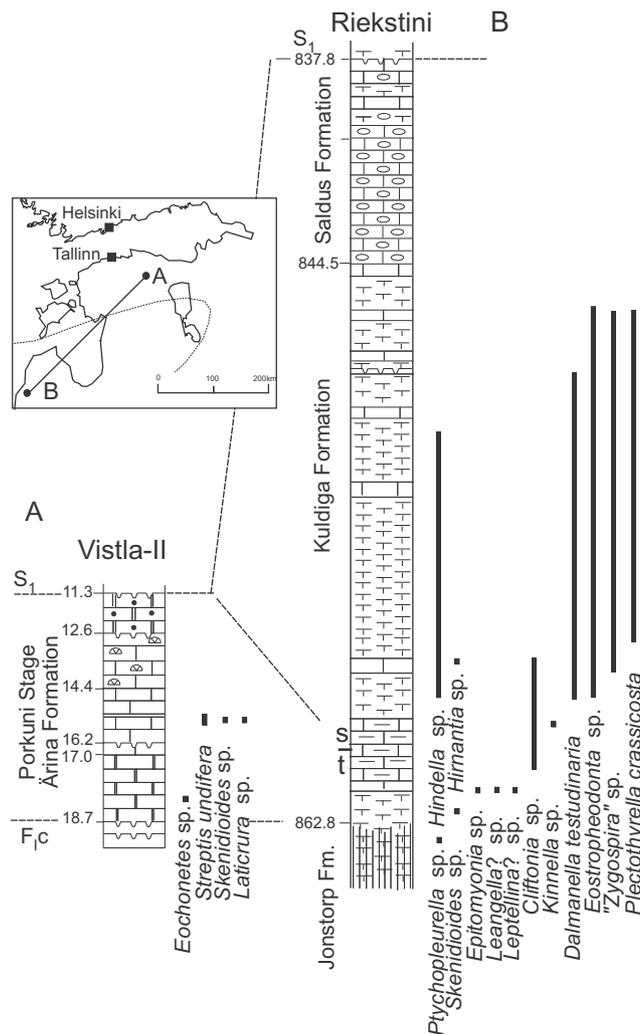


Fig. 9. The correlation of the Porkuni Stage on profile A – B and the vertical distribution of selected brachiopods. For the lithological legend see Fig. 5. Vertical lines on the log mark red-coloured rocks. The boundary between the chitinozoan *taugourdeaui* (t) and *scabra* (s) zones (data from J. Nölvak) is marked on the left side of the Riekstini core.

of the East Baltic. In Estonia, two early Porkuni brachiopod associations, the *Elsaella* and *Streptis* associations have been identified (Kaljo & Hints 1997). The first is characterized by *Elsaella bekkeri* (Rosenstein) and *Sowerbyella* (*Eochonetes*) sp., which are the commonest brachiopods in drill-core sections. The associated brachiopods (Rõõmusoks 1991) are known mainly from exposed outcrops. The sections with reported brachiopods in northern Estonia are correlated with the lower part of the argillaceous limestones and silty marls comprising the *Hirnantia* brachiopod fauna (*Hirnantia*, *Eostropheodonta*, *Hindella*, *Cliftonia* and others) in the Livonian Tongue.

The brachiopods appear gradually (Fig. 9) and typical Hirnantian brachiopods such as *Hirnantia sagittifera* (McCoy), *Cliftonia oxoplecoides* Wright and *Plectothyrella crassica* (Dalman) appear somewhat higher above the lower boundary of the Porkuni Stage (above the top of the red-coloured strata of the Jonstorp Formation). Brachiopod distribution indicates a continuous shallowing of the palaeobasin. The most diverse brachiopod fauna occurs in the lower half of the stage, at about the level of the most dramatic shift in the carbon isotopic values (Kaljo, Hints, Martma & Nõlvak 2001). Upwards brachiopods become less frequent and less diverse. *Trematis*, the eponymous taxon of the shallowest-water association in the central Oslo Region (Brenchley and Cocks 1982) occurs in some sections high within the Porkuni Stage.

During the Late Ordovician, the interval from the later Keila to Porkuni stages is marked by at least two important events. These two, the Keila-Oandu and Porkuni-Hirnantian events are both distinguished by the remarkable extinction of faunas, the appearance of new immigrants together with entire new faunal associations, litho- and biofacies differentiation and development of mudmounds and reefs; the events are also indicated by changes in stable isotopic compositions. Contrasts between the two events, such as the different origin of immigrants (Avalonia and Mediterranean), the various effects of extinction across the facies belts and differences in the carbon isotope shifts, do not exclude the possibility that both the Keila-Oandu and the Porkuni-Hirnantian events were both associated with sea-level fall.

Conclusions

The Ordovician rhynchonelliformean brachiopods in the East Baltic development of the Baltic Province occur within two different, upper ramp and lower ramp, magnafacies, with contrasting compositions at both the species and genus level. Brachiopods from

the epicontinental Moscow Palaeobasin are common within the upper ramp facies in the northern East Baltic during the early and mid Ordovician. The changes in brachiopod composition appear related mainly to transgressive-regressive events. Within the shallower parts of the palaeobasin (North Estonian facies belt) there are relatively continuous changes in taxonomic composition together with the evolution of endemics and the establishment of relatively persistent associations, especially during the later Ordovician. In the deeper parts of the palaeobasin (Central Baltoscandian confacies belt including the Livonian Tongue), changes in the brachiopod faunas are clearly determined by environmental fluctuations, and several different types of faunas are obvious: relatively low diversity associations in red-coloured sediments, a well-defined assemblage associated with black shales and more diverse associations in argillaceous carbonates. The appearance and distribution of some short-lived associations including immigrants to the Baltic (e.g., *Dactylogonia* and *Rhynchotrema* during the Keila-Oandu event, the *Holorhynchus* association during the mid-Ashgill and the *Hirnantia* fauna during the late Ashgill) are probably associated with more major climatic and sea-level changes in the palaeobasin (Bruton & Harper 1988).

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