Over 300 species of rhyonchonelliformean 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 Palaeobas-
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 Baltoscandinian 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

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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 (DIII) between the Keila and Rakevere stages is not shown in the table.
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 (biodetritus) 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.
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 rhyonchelliformean 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 (BIII) (end of the regional Oeland Series; middle of the Middle Ordovician). After a fall in diversity during the Aseri Stage (CIIa), diversity again climbs to reach a peak in the Uhaku (CIIc) and Kukruse (CII) stages at the Middle-Upper Ordovician transition. In Lithuania, high brachiopod diversities characterize the higher stratigraphical levels, particularly the Haljala (CIII-D) and Keila (DII) stages, which consist of argillaceous limestones and marls. In the northern East Baltic the third diversity peak occurs within the Pirgu Stage (FIc) (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 (BIII, CIc, FIc) (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) (Fig. 3). Values of the A/D ratio over unity in northern Estonia show that appearances prevail over disappearances in the Billingen (Bb), Lasnamägi (Ci) and Nabala stages (FIIIa) (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...
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 Volkov 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 Opik 1933; Rubel 1961). The presence of Angusticardinia in the lowermost Volkov 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 Volkov 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 Tetragnostus phylograptoides (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. phylograptoides 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? suecica* Tjernvik and *Nanorthis? billingensis* Tjernvik (Tjernvik 1956; Löfgren 1994, fig. 2), but the oldest brachiopods (*Archaeorthis christianeae 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 Volkov Stage in Lithuania recorded by Paškevičius (2000). In Poland, close to the Lithuanian border, *Plectella* is noted from the pre-Volkov rocks (Modlinski 1973). The age of the *Ranorthis carinata-Plectella uncinita* 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 drillcore 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 Volkov or both the Volkov 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 Volkov Stage, but unfortunately the distribution ranges of these species do not correspond to the whole stage (see Rubel 1961).

The most complete Volkov–Kunda transition is represented in NW Russia. In one section on the Lyna 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 Volkov Stage is *Paralenorthis orbicularis* (Pander) which occurs in 34 of the 44 samples collected from the 3.15 m thick uppermost Volkov Stage. *Paralenorthis* (see Jaanusson & Bassett 1993) occurs together with the plectambonitoids *Ingrina* and *Ahtiella*, which are also common in Avalonia faunas. In the Lyna section both plectambonitoids occur at the same stratigraphical interval (commonly in the same samples) together with the endemic brachiopod genera *Antigonambonites, Gonambonites* and *Ladogella*.

Within Lithuania, the *Paralenorthis orbicularis-Or-thambonites majuscula-Lycophoria nucella* association was established for the Kunda Stage (Paškevičius 2000). The bizarre genus *Lycophoria* appears in the middle of the Volkov 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, Nicoleta, Cyrtonentella, Platys-trophia* 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 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 Baltic-scaniadia 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 ascendentens (Pander) and Glossorthis verneulii (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 Sj pooled 1957).

Several early Viru (late Mid and early Late Ordovician) brachiopods, e.g. Hesperorthis, Crennorrhis, Vellamo, Sowerbyella, Leptelloidea, Bekkerina (=Oepikina), Kiaraomena (=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 sub-stage of the Lasnamägi Stage, as defined by Rõõmusoks (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. Apatorhistris jugata Öpik, Hesperorthis inostranzséf inostranzséf (Wysogorski), Parornibonites lati caudatus Bekker, Sowerbyella (Sowerbyella) (=Viruella) orvikui and Vellamo aff. ultima Opik] 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.) orchovenensis Nikanorova and some others] are restricted to that palaeobasin (Alikhova 1969; Dimitrovskaja 1991). To these species can also be added new species of Platystropheus 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 Clococapsomorpha prisa 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 Tetradontella) (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
Haljala Stage is one of the few biostratigraphical levels well constrained by chitinozoan zones in Sweden and East Baltic including NW Russia (Nõlvak & 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 schmidtii epigonus Öpik, Cyrtotellina kuckersiana frechi (Wysogorski), Leptaena rugosoides Oraspöld, 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 biodetrital 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 drillcore 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 anomalous 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 discernable 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 Västlima mud mounds) and Estlandia, together with the large-shelled strophomenids Strophomena (Keilamen) 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 isorhynch 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 (Keilamen) and Platystrophia rara) 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 strophomenides 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 (Neosaphus) ludibundus Törnquist (Männil 1966, fig. 12, 13 and his unpublished data). The upper, marly part of the interval (the Bieldene 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 (Neosaphus) ludibundus and some brachiopods (Howellites, Skenidioides, Laticurra, Taphrothris and Leptellina cf. indentata) in southern Estonia are similar to those in Sweden, in the Fjäcka section from the Skagen to Moldtå limestone (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 rhynchonelliformean taxa, Chonetoidea (=Sericoida) and Omniella; 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 Chonetoidea (=Sericoida) 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-
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*) *subaequiculina* – *Reuschella magna* community is distinguished (Paškevičius 2000). This association is supposedly missing in the Scandinavian part of palaeobasin, at least the characteristic Avalonian harknessellid *Reuschella* has not been reported.

A brachiopod association comprising *Rhynchootrema*, *Dactylogonia* and *Anazyga* in the mud mounds (carbonate buildups) and their lateral facies in NW Estonia together with a low diversity shelly fauna with *Rhynchootrema*? 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. 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.
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, Holtedahlinia, 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 opportunistics, 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* (*Equirosutra*), *Platystromphya*, *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 Tauionis 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 Fjäcka 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 Fjäcka 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 of Estonia. The Porkuni (Hirnantian) brachiopod faunas are determined by marked and relatively rapid changes in environment. For example, the black shales (the Mossen and Fjäcka 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.

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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 bekeri* (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* (M'Coy), *Cliftonia oxoplecoides* Wright and *Plectothyrella crassiscosta* (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 occurs 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 facies 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., *Dactyllogonia* and *Rhynchothrema*) during the Keila-Oandu event, the *Holohynchus* 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 (Brunton & Harper 1988).

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References


Hurst, J.M. 1979a: The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop. Bulletin of the British Museum of Natural History (Geology) 32, 183–304.


Rubel, M. 1963: O gonambonitakh (Clitambonitacea, Brach.)


