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Development of faunal diversity during the late Llandovery–early Wenlock in the easternmost part of the Baltic Palaeobasin – implications for the Ireviken Event

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Abstract. The composition, diversity and distribution of various groups of organisms in the late Llandovery (Telychian) and early Wenlockian (Sheinwoodian) interval of the Pahapilli 675 and Kõrkküla 863 sections (western Estonia) were studied. Due to the small size, fragmentation and disarticulation of the specimens, the studied paleontological material could, in the major part, be tentatively considered as "biodetritus" or "bioclast material" occurring in the carbonate and siliciclastic lithologies. The recognized conodont biozonation provides a detailed stratigraphic framework for this study. The brachiopod fauna is represented by two different *Dicoelosia–Skenidioides* communities, comprising diverse associations of non-brachiopod fauna, whose composition changes over time. Successive associations of trilobites are based on dominating taxa among odontopleurids, encrinurids, calymenids and aulacopleurids. The distribution and taxonomic composition of Silurian echinoderms (cyclocystoids, bothriocidarid echinoids, pisocrinid crinoids) in the East Baltic area are documented for the first time. New data on bryozoans, corals, sponges and other fossils are provided, improving the knowledge of the whole biota of the open shelf and transition to basinal environments. The distribution of faunas is affected by different changes in the ecosystem. The highest diversity was recorded in the Upper *Pterospathodus a. amorphognathoides* Conodont Zone, before the main faunal turnover caused by the Ireviken Event, which was associated with rapid sea-level fall and climate changes. The faunal recovery started at the early Wenlockian in the second half of the Ireviken Event, above the base of the Lower *Kockelella ranuliformis* Conodont Zone.

Keywords: Telychian, Sheinwoodian, offshore shelly faunas, bioclasts, Ireviken Event, Estonia.

INTRODUCTION

The early Palaeozoic shelly faunas of the East Baltic region have a long history of research. The monographic works on different groups of fossils since the 19th century have played an important role in the stratigraphy of Ordovician and Silurian strata. An overview of the fossil record in Estonia with references to previous studies is presented in the book *Geology and Mineral Resources of Estonia* (Raukas and Teedumäe 1997). This publication also summarizes data on the evolution of the Baltic Palaeobasin, including facies and faunal differentiation (Kaljo 1970). Earlier paleontological research in Estonia is largely based on materials from the shallow shelf outcrop areas. Rapid development of drilling activities in the East Baltic region in the second half of the 20th century opened opportunities for the study of the deeper shelf and basinal facies and faunas. Recently, important data on conodonts, chitinozoans and scolecodonts, together with different geochemical characteristics, have been presented for the late Llandovery–early Wenlock interval (Hints et al. 2006; Rubel et al. 2007; Munnecke and Männik 2009; Männik et al. 2014). That is the interval our study focuses on – the Velise Formation (Fm.) of the upper part of the Adavere Regional Stage (RS) and the lowermost Jaani Fm. of the Jaani RS.

The current paper is a continuation and updating of previous studies on biofacies differentiation, summarized for brachiopods, trilobites and tabulate corals on the transect shallow shelf–deeper basin by Kaljo and Klaamann (1982; Nestor and Einasto 1997). By involving practically all the remains of carbonate fossils found in the soft, more or less carbonate deposits of two sections (Pahapilli 675 and Kõrkküla 863, for brevity, hereinafter referred to as Pahapilli and Kõrkküla) on the island of Saaremaa (Fig. 1), we can provide as detailed an insight as possible into late Llandovery and early Wenlock biota of the easternmost part of the Baltic Palaeobasin. The occurrence of different shelly fossils in the composition of rocks has been mentioned or listed as "biodetritus" or "bioclast" material in earlier papers on microfossils (Hints et al. 2006; Rubel et al. 2007; Männik et al. 2014). However, a detailed faunal overview is not available.

The evolution and biofacies differentiation of the Llandovery–Wenlock interval was affected by extensive flooding of the Baltic Palaeobasin, which was the most extensive during the Silurian (Nestor and Einasto 1997). Over the last decades, much attention has been paid to different bio- and geo-events (Ireviken and Valgu events, Jeppsson 1998; Munnecke and Männik 2009), changes in sea level (Watkins et al. 2000; Kiipli et al. 2010b) and climate (Munnecke et al. 2003; Trotter et al. 2016), which creates an image of complicated patterns of the ecosystem in the basin.

Our aim is to improve the understanding of the late Llandovery–early Wenlock biotas in the eastern part of the Baltic Palaeobasin by studying the taxonomic composition and distribution of calcareous shelly fossils such as brachiopods, trilobites, echinoderms, corals and other less numerous groups. The trends in faunal changes are compared with the bioevents recognized in the conodont succession and with events in the evolution of the basin (e.g. Jeppsson and Männik 1993). The biodiversity in every conodont zone and the influence of the Ireviken Event on different faunas are analysed.

GEOLOGICAL BACKGROUND AND COMMENTS ON STRATIGRAPHY

In the East Baltic, the Telychian–Sheinwoodian deposits accumulated in the carbonate platform and transition to the deeper basin (Kaljo and Jürgenson 1977; Nestor and Einasto 1997). The prevailing humid climate (H-period, Munnecke et al. 2003) during the late Llandovery favoured the deposition of marlstones in the shelf and basinal facies (Nestor and Einasto 1997; Kiipli et al. 2010b) until the climate became arider (A-period) at the beginning of the Wenlock with an increase in carbonates in sediments. Both the Pahapilli and Kõrkküla sections are represented mainly by greenish-grey more or less calcareous marlstones with nodules and nodular inter-beds of the argillaceous limestone (more common and thicker in Pahapilli than in Kõrkküla). The higher content of carbonate rocks in the uppermost part of the sections has limited the quantity of fossils available by the methods used.

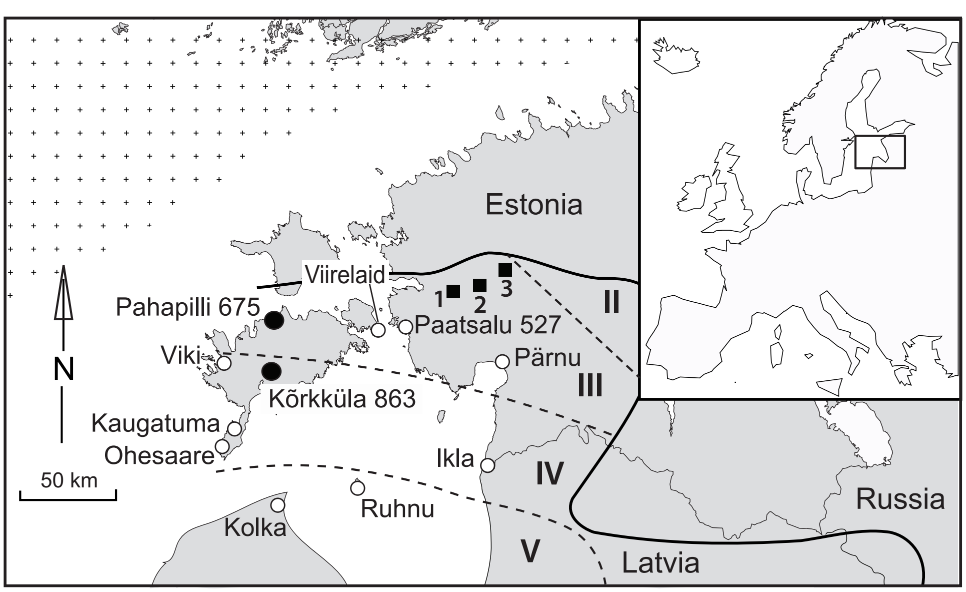

Fig. 1. Sketch map showing the facies zones of the Adavere Regional Stage (RS) (modified from Kaljo and Rubel 1982), location of the Pahapilli 675 and Kõrkküla 863 drillings, sections mentioned in the text and outcrops with the Adavere brachiopods: Lätiküla (1), Valgu (2), Võiva at Velise (3) (Rubel 2011). Legend: outer limit of the Adavere RS (solid line), boundaries between facies zones (dashed line) (according to Kaljo and Rubel 1982; Nestor and Rubel 1997) – shoals (II) and open shelf (III), transitional facies to deeper basin (IV), deep basin (V).

The deposits and faunas of the late Llandovery–early Wenlock have evolved in the process of changing environmental conditions. According to Kiipli et al. (2010b), the high sea level continued up to the *P. eopennatus* Zone with some lowering, possibly related to the Valgu Event (Munnecke and Männik 2009). The following part of the Telychian is characterized by the trend in the shallowing of the basin with smaller shallow-deeper oscillations up to the Llandovery–Wenlock transition with a notable drop in sea level, well-known for conodont succession and isotopic composition as the Ireviken Event. However, several authors have shown more remarkable sea-level oscillation (e.g. Johnson et al. 1991; Loydell 1998; Johnson 2006). The important changes in climate are detected by the changes in the isotopic composition of the rocks (Kiipli et al. 2010b) and fossils (Lehnert et al. 2010; Vandenbroucke et al. 2013; Trotter et al. 2016). The isotope data on conodont apatite ($\delta^{18}O_{phos}$) from the Kõrkküla section (Trotter et al. 2016) highlight the climate turnover from a relatively stable period up to the lowermost Upper *Pterospathodus a. amorphognathoides* Zone, which follows the cooling trend into the Wenlock (Fig. 2).

The Pahapilli and Kõrkküla sections on the island of Saaremaa provide an opportunity for the study of fossils in a much thicker section than in several neighbouring sections in the east. The thickness of the Velise Fm. in both studied sections is over 50 m. In several sections from eastern neighbouring areas, the thickness of Velise Fm. is less than 20 m (in Paatsalu about 12 m, in Viirelaid 14.4 m, in Suigu 8.9 m). The thick Velise Fm. (62.4 m) is described in the Viki section with a total thickness of 69.9 m in the Adavere Stage (Männik 2010).

The content of siliciclastic material in the Velise Fm. increases from 25% in northern Saaremaa to 75% in southern Saaremaa in the Adavere RS and from 25% to 50% in the Jaani RS (Jürgenson 1966; Hints et al. 2006). In the Kõrkküla core, the lowermost (unstudied here) rocks of the Velise Fm. (below a depth of 186 m) are predominantly red in colour, which is characteristic of deposits of the distal shelf environments (Nestor and Einasto 1997). The red interval thins out towards the proximal shelf and is replaced by greenish-grey rocks. In the Pahapilli section, only a few thin reddish-grey intervals occur in the lowermost Velise Fm., at the level below a depth of 63 m corresponding to the *Pterospathodus eopennatus* ssp. n. 2 Conodont Zone. Rare white and grey ooids are found in the Kõrkküla section in two samples (C95-255, C95-304). The upper-most finds occur below the Datum plane 1 at the top of CZ6b. The ooids occur at the same stratigraphic level in the neighbouring Viirelaid and Paatsalu sections, where most parts of the Ireviken Event are missing, suggesting non-deposition or very shallow active water environments (Männik et al. 2014). The exact position of ooids in the lower sample is unclear for conodont zones. They occur about 2 m above the reddish interlayer at the bottom of the studied interval, in the strata which could be correlated with the latest part of the Valgu Event (Munnecke and Männik 2009).

Both sections contain several volcanic ash beds such as Llandovery–Wenlock sections in the East Baltic (Kiipli and Kallaste 2002; Kallaste and Kiipli 2006; Kiipli et al. 2010a). However, the volcanic ash beds in the Pahapilli and Kõrkküla (corresponding to Tehumardi in Kiipli and Kallaste 2002) sections differ in the composition of magmatic K–Na sanidine, while having coeval beds in some other sections of the region (e.g. Viki, Kaugatuma). Only one volcanic ash bed in the Pahapilli core at a depth of 20.85 m has a geochemically proven (Kiipli et al. 2010a) analogue in the Ohesaare section where the boundary between the Adavere and Jaani regional stages is defined (see below). The 2 cm thick bentonite layer at 137.2 m in the Kõrkküla core is pinkish, visually similar to the Ireviken Bentonite in its nominal locality but it has not been tested here yet. Although positioned in the lowermost CZ7b, it is a potentially promising tool for further correlation.

In this study, the stratigraphic framework, dating and correlation of the sections are based on conodonts (Fig. 2). A high-resolution conodont zonation has been established for Telychian and Sheinwoodian strata (Jeppsson 1997a; Männik 2007a, 2007b). The subzones of the *Pt. eopennatus* ssp. n. 2, *Pt. am. angulatus* and *Pt. am. amorphognathoides* conodont zones as indicated by Männik (2007a) are considered here as zones. In Fig. 2 only the key taxa denoting zonal boundaries are indicated. For simplicity, the boundaries of the zones are drawn at the sample's lower or upper contacts with the nominal taxon of the zone.

The boundary between the Lower and Upper *Pt. am. angulatus* zones corresponds to the appearance level of *Ozarkodina* aff. *gulletensis*, and the boundary of the Lower and Upper *Pt. am. amorphognathoides* zones is drawn right above the sample yielding the uppermost specimens of *Aspelundia*? sp. n. In the upper part of the studied interval, starting from the lower boundary of the Lower *Ps. bicornis* Zone, zonal boundaries correspond to the Datum planes (D1–D8) of the Ireviken Event (Jeppsson 1997b) and, hence, are drawn at the upper contacts of samples yielding the uppermost specimen(s) of taxa whose disappearance defines a certain datum. However, in reality, a zonal boundary might be at any level between the sample yielding the first (or last) specimens of a nominal taxon. A detailed analysis of conodont distribution and assemblages will be the topic of another paper.

The samples studied from the Pahapilli core originate from the interval 18.2–76.2 m corresponding in the

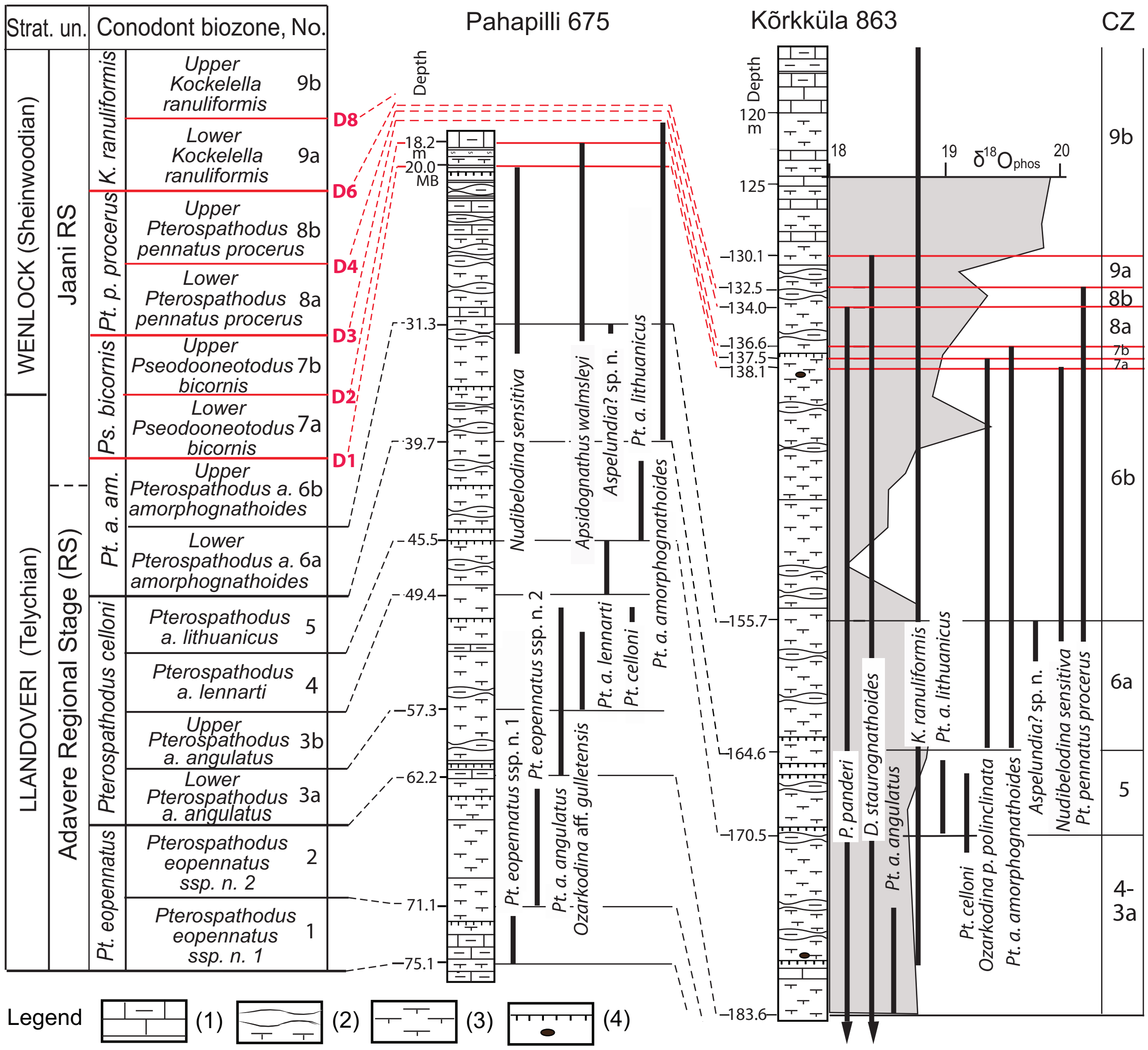

Fig. 2. Stratigraphical scheme, conodont biozonation (with numbers referred to in the text) of the late Llandovery and early Wenlock, as well as correlation of the Pahapilli 675 and Kõrkküla 863 sections with diagnostic species of the conodont biozones. D1–D8: Datum planes of the Ireviken Event marking step by step extinctions among conodonts. The contact of the grey-white area on the right-hand side of the Kõrkküla log marks the trend in general climate change by changes in $\delta^{18}O_{phos}$ values (from 18 to 20‰) (Trotter et al. 2016). Legend for the general lithology in Figs 2–8: (1) – argillaceous limestone (upper) and limestone (lower), (2) – nodular argillaceous limestone with marl interlayers, (3) – marl, (4) – volcanic ash bed (upper) and ooids (lower). Conodonts*: P. panderi – Panderodus panderi, D. staurognathoides – Distomodus staurognathoides.*

conodont succession to the *Pt. eopennatus* ssp. n. 1 Conodont Zone (CZ) from below up to the Lower *Pseudooneotodus bicornis* Zone above and belonging to the upper Velise Fm. of the Adavere RS. However, due to ecologically restricted distribution of several conodont taxa (e.g. Männik 1998, 2007b), the Lower and Upper *Pt. am. angulatus* and *Pt. am. lennarti* zones are not separable in the Kõrkküla section and are thus indicated as a single unit in Fig. 2. The studied interval in this section (114.65–194.1 m) correlates with conodont zones from the Lower *Pt. am. angulatus* Zone below up to the Upper *Kockelella ranuliformis* Zone above (both zones included).

The Llandovery–Wenlock boundary (as defined in its type section at Leasows, Welsh Borderland, UK) corresponds to a level close to Datum plane 2 of the Ireviken Event, near the boundary between the Lower and

Upper *Ps. bicornis* zones (Jeppsson 1997b; Männik 2007b).

The boundary between the Adavere and Jaani regional stages, originally established at 345.8 m in the Ohesaare (Loydell et al. 1998) section and believed to be coeval with the Llandovery–Wenlock boundary (Nestor and Einasto 1997) is biostratigraphically poorly constrained and cannot be precisely dated in the conodont succession. However, based on available data (Männik et al. 2014), the stage boundary evidently lies in the upper(most) part of the Upper *Pt. am. amorphognathoides* Zone, not far below the lower limit (D1) of the Ireviken Event. In the Ohesaare core, the boundary is marked by a K-bentonite (ID210) which, according to Kiipli and Kallaste (2002), probably correlates with a K-bentonite at 20.85 m, with a level of 0.85 m below the lower boundary of the Lower *Ps. bicornis* Zone in the Pahapilli core (Fig. 2).

MATERIAL AND METHODS

The studied material was obtained from residues of unlithified (strongly argillaceous marlstone and clay) samples collected from the Pahapilli 675 and Kõrkküla 863 (also known as Korkküla 863 and Tehumardi 863) core sections on the island of Saaremaa, western Estonia (Fig. 1). The samples were processed for conodonts in the mid-1990s by P. Männik. The remains of shelly fossils were studied in 161 samples, 57 from the Pahapilli and 104 from the Kõrkküla sections. The 10–15 cm thick samples were collected at 40–90 cm intervals. The remains of calcareous fossils originate from samples which were disintegrated in water, without using any acid. Some samples of calcareous rocks above 129.25 m in the Kõrkküla and at 30 m in the Pahapilli cores were still dissolved with acetic acid, resulting in few and poorly preserved calcareous fossils found in these samples.

The residues were picked and sorted for different fossil groups by L. Hints. The estimated number of fossils is several thousand specimens, whereas over one thousand trilobite remains of different preservation stages were counted. The fossils were identified by L. Hints (brachiopods and some general data on the occurrences of bryozoans, corals, crinoid ossicles, sponges), H. Pärnaste (trilobites), M. Reich (cylocystoids, echinoids, holothurians, some fossils of the group "Varia") and S. Rozhnov (pisocrinids). All fossils and their remains are small, usually less than 10 mm in size. Fossils have suffered from mechanical crushing and bioerosion, therefore cracks and borings in them are common. All this complicates their species-level identification.

The studied palaeontological collections (collection numbers GIT 798, GIT 799), and additional paleontological material referred to or shown in figures, are housed at the Department of Geology, Tallinn University of Technology. Data on the palaeontological collections and samples studied for conodonts can be found in the database of the Geoscience Collections of Estonia. The studied material comprises many potential new taxa, therefore the list of taxa will be specified in future paleontological studies. All technical data on drilling and photographs of drill cores are available at the Geoportal of the Estonian Land Board (https://geoportaal.maaamet.ee as MA ID 28253 and 28289). The drilling material is stored at the Geological Survey of Estonia.

DISTRIBUTION OF FOSSILS

The shelly faunas established in the Pahapilli and Kõrkküla sections are represented by relatively deep-water inhabitants in association with those presumably transported from neighbouring shelf areas. The occurrence and stratigraphic distribution of fossils are illustrated in Figs 3–8. For brevity, in the text below the conodont zones (CZ in Figs 1–8) are marked by numbers instead of the names of zonal conodonts.

RHYNCHONELLIFORMEAN BRACHIOPODS

The brachiopod species of the genus *Dicoelosia* (Dalmanelloidea) and taxa of the genus *Skenidioides* (Protorthida) range through the most part of the Velise Fm. of the Adavere RS and the lowermost Jaani RS in the Pahapilli and Kõrkküla sections. The frequency of these brachiopods varies between the sections and stratigraphical levels (Fig. 3). The approximate abundance of *Dicoelosia* per sample was calculated on the basis of the number of complete shells (33% of all finds), valves (24%) and lobes of valves (45%). Using these data, 10–50 specimens of *Dicoelosia* supposedly occurred in the samples of CZ6b in the Kõrkküla section, while the number of *Skenidioides* specimens did not exceed 35 (Fig. 3). Such a large number of disarticulated and broken shells of *Dicoelosia* refers to water movement having destructive influence on delicate brachiopods. The brachiopods of these two genera are associated with other small-sized brachiopods (*Leangella, Jonesina*, *Visbyella*, dalmanellids) and fragments of large brachiopods (*Cyrtia*, *Eostropheodonta*, *Leptaena, Katastrophomena*), whose poor preservation allows to suppose some transportation of them and/or crushing effects of wave activity (Figs 4 and 5). These remains are often represented by a thick umbonal part of the shell or valve. Characteristic Silurian brachiopods *Atrypa*, *Atrypoidea*, *Alispira*, *Hesperorthis* and others are rare in our collection (Figs 4 and 5). *Leangella segmentum*, a characteristic species of the

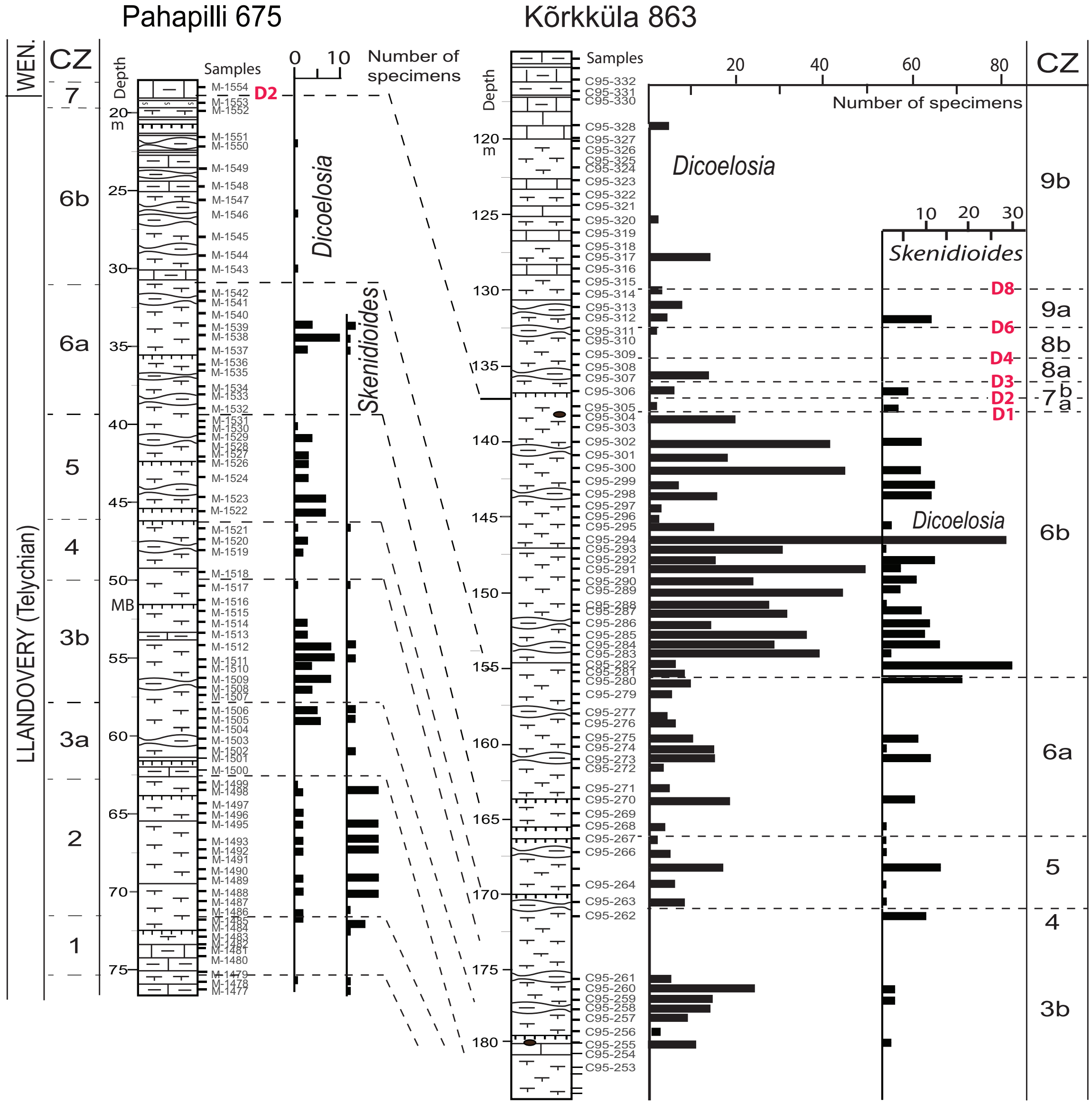

Fig. 3. Distribution and number of specimens of brachiopods *Dicoeloidea* and *Skenidioides* in the Pahapilli 675 and Kõrkküla 863 sections. For the legend and explanation of indexes, see Figs 1 and 2. To the right of the logs are the primary sample numbers by P. Männik (samples from the Pahapilli section are marked with "M", samples from Kõrkküla with "C95"). WEN. – Wenlock; CZ – Conodont biozones; D1–D8 – Datum planes of the Ireviken Event.

Benthic Assemblage BA5 of Boucot (1975), is missing in the Pahapilli section, probably due to somewhat shallower water environments there than in the Kõrkküla section.

The species of the genera *Dicoelosia*, *Skenidioides*, *Eoplectodonta*, *Jonesea* and *Visbyella* are common in the lower half of the Pahapilli section and in the lowermost part of the Kõrkküla section, in the range of CZ1–CZ4. The listed brachiopods, together with *Leangella* in the Kõrkküla section, belong to the *Dicoelosia–Skenidioides* community group of the deep-water Benthic Assemblages BA4–5 of Boucot (1975; Hurst 1975; Watkins et al. 2000). The study of Lithuanian brachiopods (Musteikis and Cocks 2004) highlights the extensive (from Newfoundland to Urals) distribution of plectambonitoid brachiopods *Eoplectodonta*, *Leangella* and *Jonesea* belonging to the *Dicoelosia–Skenidioides* communities of BA4– 5.

The lower part of the Pahapilli and Kõrkküla sections (CZ3a–4; Figs 4 and 5) contains strongly eroded fragments of ventral valves supposedly belonging to *Pentlandella*?. They are more common in the Kõrkküla section occurring in nine successive samples in the strata

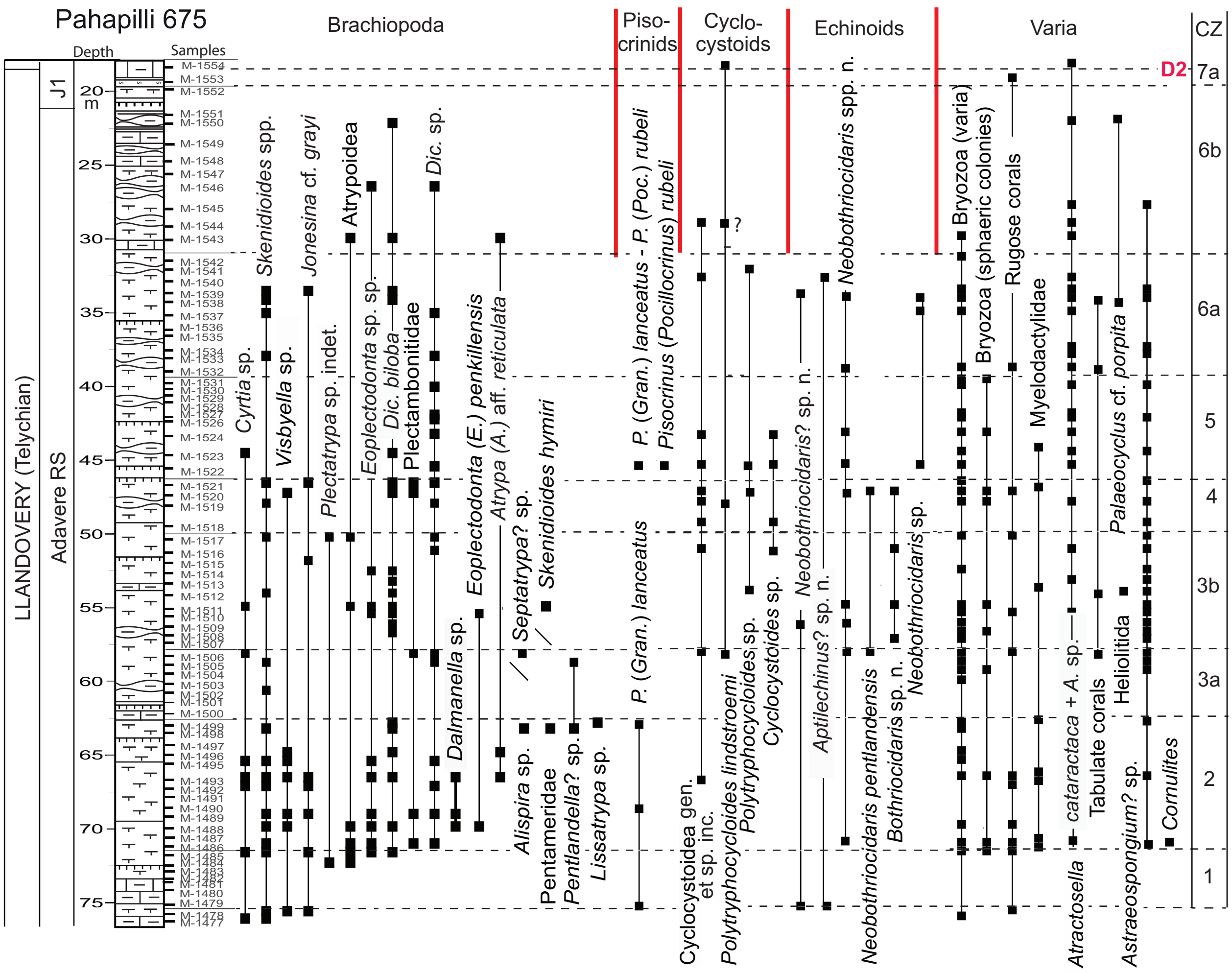

Fig. 4. Distribution of shelly fossils in the Pahapilli 675 section. For the legend and explanation of indexes, see Figs 2 and 3. J1– Jaani Regional Stage.

corresponding to the same conodont zone (Fig. 4). The co-occurrence of *Pentlandella* fragments with *Leangella segmentum* and *Jonesea grayi* in Kõrkküla supposedly refers to its accidental occurrence in the deep-water environments. The species *Pentlandella tenuistriata* is described (Rubel 1970b) from three outcrops, each about 3 metres high (Valgu, Võiva at Velise, and Lätiküla) on the mainland of western Estonia (Fig. 1). The strata in the Valgu localities comprise two different faunas. The lower part (Rumba Fm.) (Männik 2008) comprises the shallow-water *Pentamerus* community BA2–3 (Kaljo and Rubel 1982), the upper part of the section belongs to the Velise Fm. (Männik 2008) with deeper-water faunas (Klaamann 1982) such as brachiopods *Dicoelosia* and *Eoplectodonta.* The shift of deeper-water facies and faunas in onshore direction on the westernmost mainland of Estonia was caused by sea-level rise during the transgressive phase in the development of the basin (Nestor and Einasto 1979).

The Lätiküla section stands out as a locality where brachiopods of the genera *Visbyella* and *Resserella* occur. The latter is not represented in the studied sections in the Adavere RS. *Resserella*, appearing in the latter stage, is more common in the Wenlockian Jaani and Jaagarahu stages (Rubel 2011). Brachiopods of both genera are inhabitants of soft-bottom and quiet-water environments (Hurst 1975) and possibly a future detailed study of the Lätiküla section enables to highlight some facies differences of the strata with *Visbyella* or *Resserella*.

The differences in the stratigraphic ranges of the brachiopods *Pentlandella* and *Visbyella* could refer to some trend in environmental changes. The *Pentlandella* and *Visbyella* occur in the Valgu section that belongs to CZ1 (Männik 2008). The former occurs in the Pahapilli section in CZ2–3a and in Kõrkküla in CZ3a–b. The brachiopods of the genus *Visbyella* in CZ1–4 of the Pahapilli section are shifted to CZ5–6b in the Kõrkküla section.

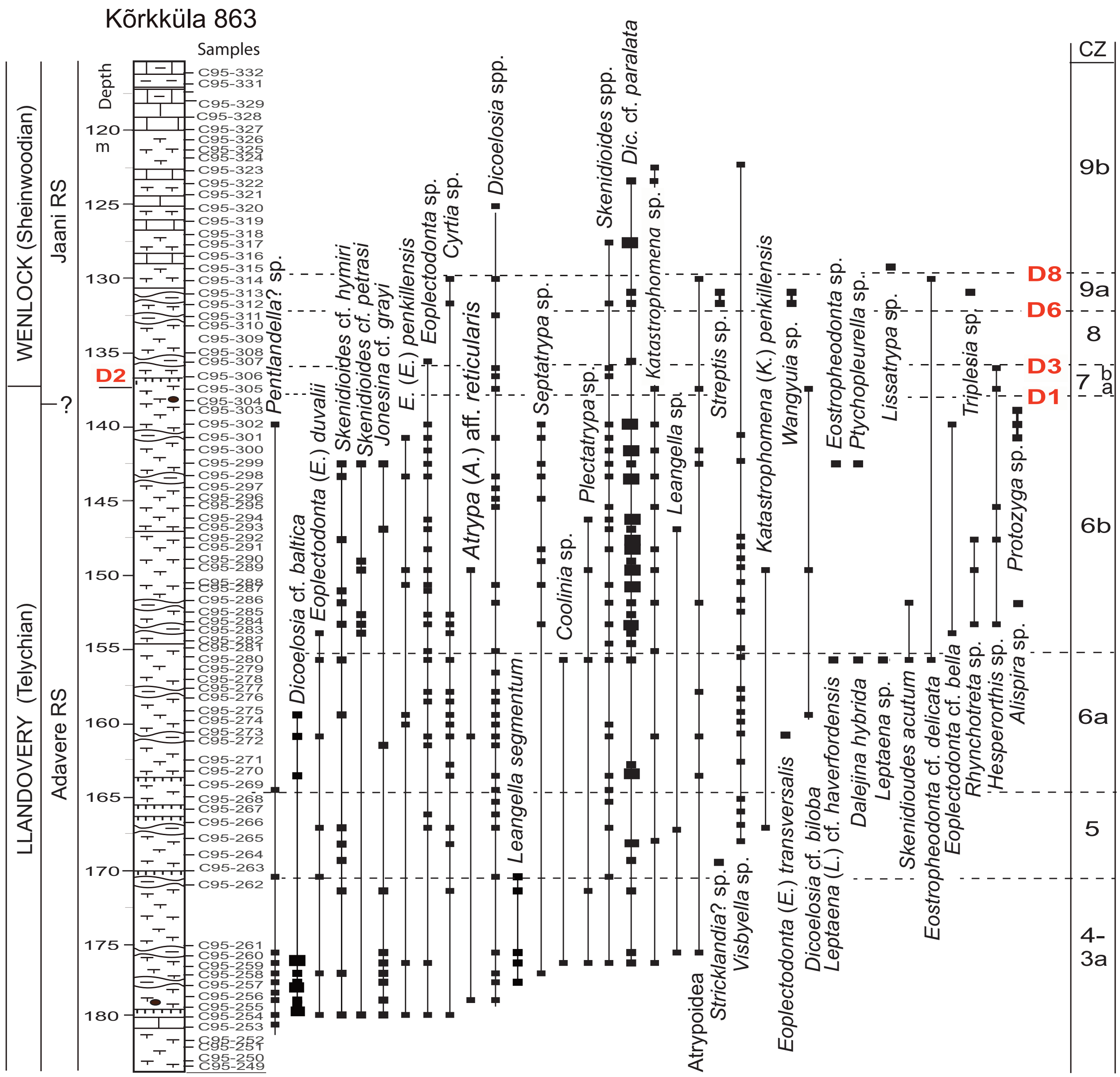

Fig. 5. Distribution of brachiopods in the Kõrkküla 863 section. For the legend and explanation of indexes, see Figs 2 and 3. Larger rectangles mark more than one specimen in sample.

The differences between the brachiopod fauna of the Pahapilli and Kõrkküla sections are particularly distinct in CZ5 and CZ6a. In the Pahapilli section, brachiopods of the genera *Skenidioides* and *Dicoelosia* are practically the only brachiopods identified. The rarity of fossils in this section is partly due to their more onshore location (about 35 km) of Kõrkküla and due to the destruction of carbonate fossils by acid used in the processing of several uppermost samples. In the Kõrkküla section, however, the brachiopod fauna is diverse in CZ5 and CZ6a (Fig. 5). It differs from the older fauna by the absence or rare occurrence of *Jonesea* and *Leangella*, and by frequent and almost continuous occurrence of incomplete specimens of *Visbyella* (up to the upper part of CZ6b) and *Cyrtia* (up to the lower part of CZ6b) in numerous successive samples.

Several new brachiopods (*Leptaena*, *Hesperorthis*, *Eostropheodonta*, *Protozyga*) appear in the Kõrkküla section in CZ6b together with transitional brachiopods from older strata, including the wide-lobed species of *Dicoelosia* cf. *paralata.* The latter brachiopod is abundant in this zone. In Lithuania, *Dicoelosia (Dic.) paralata* is a nominal species of two communities in the siliciclastic facies of BA4 in the uppermost Llandovery (Musteikis 1991a). It is also a dominant species in the latest Llandovery *Dicoelosia paralata–Skenidioides lewisii–Glassia* (=*Lissatrypa*) *obovata* community (Musteikis 1989). The detailed studies of brachiopod communities in Lithuania (Musteikis 1989, 1991a, 1991b, 1993; Musteikis and Kaminskas 1996) and comparison of their distribution on the facies transect allowed to assume that *Dic. paralata* could even belong to BA3, not to BA4–5. The same was presumed in Arctic Canada, where Chen et al. (2012) have tied *Dic. paralata* to BA3. They were based on a comparative study of the shell outline and environments: the brachiopods with wide-lobed shells such as *Dic. paralata* lived in somewhat shallower-water environments than those with divergent long-lobed shells such as *Dic*. *biloba* (Rubel 1971, 2011). In the Kõrkküla section, the numerous occurrences of the Llandovery age *Dic*. cf. *paralata* immediately precede the Ireviken Event. The diversity of brachiopods and high frequency of *Dicoelosia–Skenidioides* brachiopods in CZ6b is possibly related to some lowering of sea level or influenced by the cooling of climate and changes in food supply.

The brachiopod diversity decreases upwards from CZ6b. The sharp decline in the frequency of *Dicoelosia* and *Skenidioides* coincides with changes in the conodont fauna at Datum plane 1 of the Ireviken Event, at the boundary between the Upper *Pt. am. amorphognathoides* and Lower *Ps. bicornis* zones. The interval of the Ireviken Event contains few brachiopods but shows some recovery near its top, above the lower boundary of the Lower *Kockelella ranuliformis* Zone (CZ9) where brachiopods of the genera *Streptis*, *Triplesia*, *Wangyuia* and *Lissatrypa* appear (Fig. 5). The first three genera appearing in the Upper Ordovician are relatively rare in the Silurian and their occurrence in the studied sections could be random, or they preferred more carbonate environments, which are inherent to the latest part of the Ireviken Event (Rubel 1970a, 2011). The occurrence of brachiopod *Lissatrypa* could be related to the *Dicoelosia–Atrypa hedei–Glassia* community, identified by Kaljo and Rubel (1982) in the Adavere RS. This community is replaced towards the deeper environments by the *Dicoelosia–Skenidioides* community, common in the Adavere RS and the Jaani RS in the easternmost East Baltic.

Summarizing the data on the Late Llandovery and early Wenlockian brachiopod faunas in the two sections on the island of Saaremaa, two communities can be distinguished. The most typical deep-water *Dicoelosia–Skenidioides* community with *Jonesea* cf. *grayi*, *Leangella segmentum* and *Eoplectodonta* sp. (Watkins et al. 2000) belongs to CZ2–4. The rarity of *Cyrtia*, disappearance of *Visbyella* at the top of CZ4 in the Pahapilli section as well as the frequent occurrence of *Jonesea* cf. *grayi* and *Leangella segmentum* up to the top of CZ4 in the Kõrkküla section refer to differences in the communities of *Dicoelosia–Skenidioides* and *Dicoelosia–Skenidioides* cf. *paralata*. The occurrence of *Pentlandella*? sp. in the studied section and in the composition of the Llandoverian *Skenidioides lewisii–Pentlandella tenuistriata–Dicoelosia paralata* community in Lithuania with a high frequency of *Pentlandella* (28.8% of brachiopod specimens) seems to be controversial. However, the Estonian *Pentlandella* belongs to another, supposedly somewhat deeper-water *Dicoelosia–Skenidioides* association, where *Skenidioides* cf. *paralata* is missing.

The replacement of the *Dicoelosia–Skenidioides* community with the following *Dicoelosia* cf. *paralata–Skenidioides* community is transitional. The high number of specimens of *Dic*. cf. *paralata* together with other related species per sample characterizes CZ6 (Fig. 3). *Visbyella* sp., *Eoplectodonta* sp., *E*. cf. *bella*, *Septatrypa* sp., *Hesperorthis* sp., the uppermost few *Leangella* and *Jonesea* cf. *grayi* are the associated taxa in the community. The interval of the Ireviken Event and the overlying Wenlockian strata presumably represent a continuation of the *Dicoelosia* cf. *paralata–Skenidioides* community as it is known from Lithuania.

Several authors have assigned a broader meaning to the *Dicoelosia–Skenidioides* group communities by incorporating other brachiopods and fossils of different groups: trilobites (Doyle et al. 1990; Watkins and Coorough 1997; Watkins et al. 2000), bryozoans, echinoderms (including pisocrinids) (Watkins 1996), sponges (Watkins and Kuglitsch 1997), crinoids and trilobites (Watkins et al. 2000). A relevant overview of the dynamics of brachiopod and non-brachiopod faunas in the Upper Silurian of the Anglo-Welsh basin is available in Cherns (1988). The present study provides analogous data for the Llandovery and the transition to the Wenlock in the Baltic region.

TRILOBITES

This is the first high-resolution study of mid-Telychian–early Sheinwoodian trilobites through the continuous open-shelf succession of the Baltic Palaeobasin. The Wenlock timeframe was earlier investigated by Reet Männil, who established trilobite associations and communities from the nearshore to offshore environments covered by drill cores in Estonia and Latvia (Männil 1977a, 1982, 1986). Trilobite distribution in the coeval strata on Gotland, Sweden, was studied by Ramsköld (1985a). The overview of trilobites given below is based on two characteristics: the number of specimens in a sample and the number of species in a sample or in some interval.

Trilobites are frequent in marly lithologies of the Kõrkküla section and relatively rare in more carbonate-rich deposits of the Pahapilli section. Only 17 of the 57 samples studied from the latter drill core contain trilobites, and only two of those reach ten or more specimens (M-1485, CZ1; M-1511, CZ3b; Fig. 6). However, nearly all samples comprise three to four species and every conodont zone contains five trilobite taxa except CZ2b with three species. A too small sample outcome in the Pahapilli section provides inadequate diversity data and enables poor comparison with the Kõrkküla section. In Kõrkküla, the information is considerably prolific with 50 samples containing altogether over a thousand specimens. The richest samples come from CZ3b and CZ4 (C95-262 with 59 specimens), while in CZ5 and CZ6a rich samples are altered by sparse ones with only ten (twenty) specimens. In CZ6a, the largest sample (C95-270) contains trilobite fragments differing in colour (from light grey to dark brown) and preservation (cracks), suggesting some transportation, bioturbation or influence of volcanic ash beds. The frequency of trilobites above, in CZ6b, is more even, pending between twenty and thirty-five

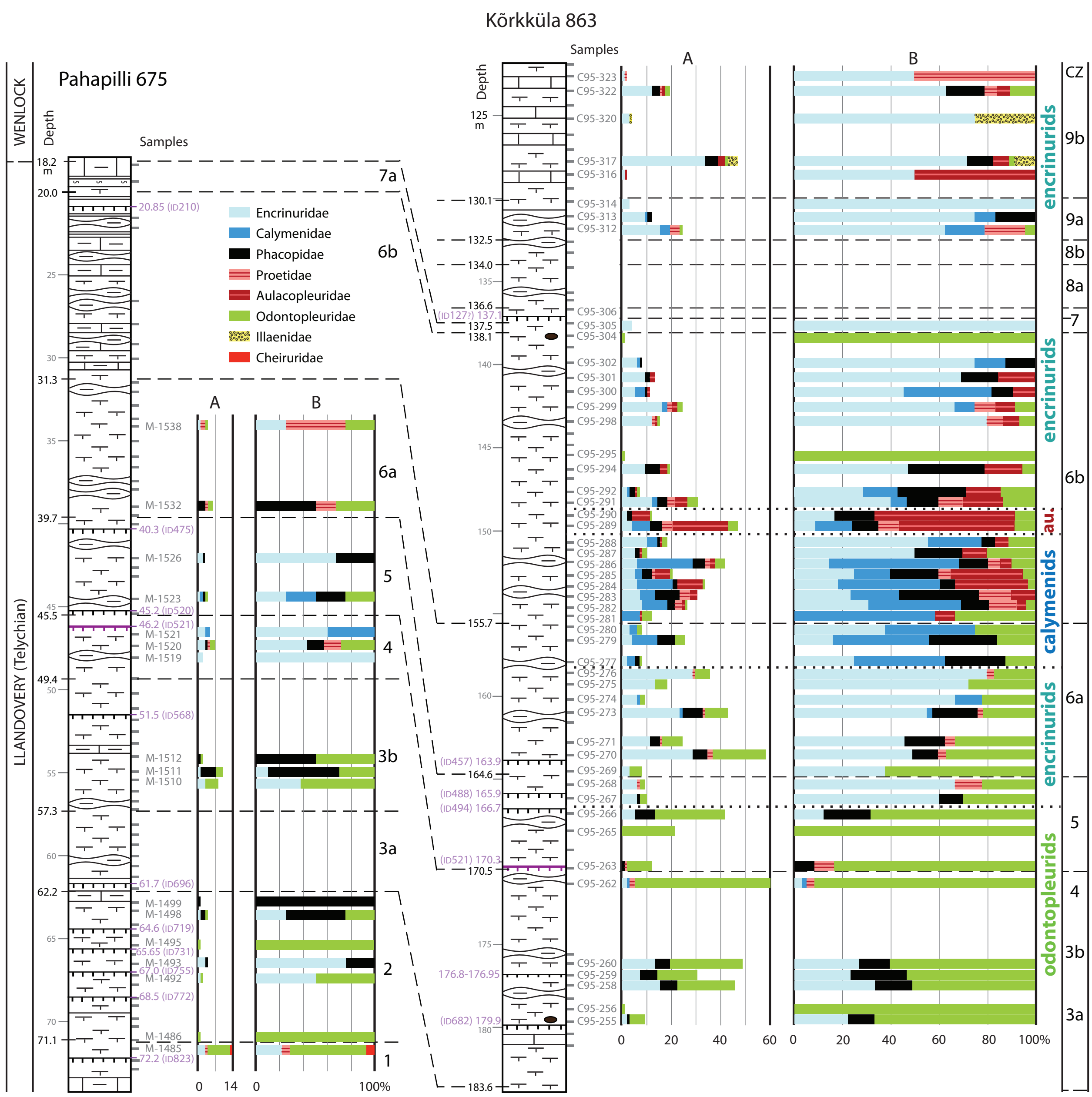

Fig. 6. Trilobite associations in the Pahapilli 675 and Kõrkküla 863 sections. Number of specimens by samples (A), and composition of trilobite fauna in samples by the percentage of different trilobite families (B). ID numbers next to the logs mark the volcanic ash beds (see Kallaste and Kiipli 2006). For the legend and explanation of indexes, see Figs 2 and 3.

specimens in its lower half. An exception is the sample C95-289 enriched in the aulacopleurid trilobite *Harpidella*. Co-occurrence of 21 fragile juvenile free cheeks of similar size and all the left ones suggest some minimal sorting by water flow rather than a coincidence. However, as the samples are 10–15 cm thick, they most probably cumulate multiple events. Trilobites become fewer and are practically missing in CZ7 and CZ8 at the beginning of the Ireviken Event because the samples collected from there were treated with acetic acid and part of carbonate fossils are destroyed. Only one marly sample from the lower CZ9b is again rich in trilobites, marking the faunal renovation shortly after the Ireviken Event.

The diversity of trilobite fauna in CZ6b with eight, in CZ6a with seven species as a maximum per sample, and four to five species in other intervals is relatively low, especially in comparison with data from Gotland (Bruton et al. 1979; Ramsköld 1985a).

In general, the lower parts of the sections are enriched in the odontopleurid genera *Anacaenaspis*, *Kettneraspis*, *Exallaspis* and *Ceratocephala*, which reach over 50% per sample until the middle of CZ5 (Figs 6 and 7). They decrease drastically, and the encrinurids begin to dominate right above the volcanic ash bed at a depth of 166.7 m (bed ID494; see Kallaste and Kiipli 2006). Exceptionally at one more level (sample C95-270), near the base of CZ6a, the odontopleurids are abundant again. The odontopleurids are associated with the phacopid *Acernaspis* and the encrinurids *Encrinurus* and *Wallacia*. The latter genus appears in CZ4 in both drill cores. At the boundary of the odontopleurid/encrinurid trilobite associations, also a change in the morphology of *Kettneraspis reetae* takes place, and a new variety *K.* aff. *reetae* appears. In the Pahapilli section, the change from the odontopleurid association to the encrinurid association probably occurs earlier, in CZ4.

Encrinurids prevail in samples C95-267 to C95-276, where *K.* aff. *reetae* vanishes. Odontopleurids still comprise from one third to one fifth of the association, while *Acernaspis* together with *Cyphoproetus* and some rare occurrences of *Calymene* in the upper part remain in minority. The species *Wallacia jaanussoni*, which characterizes CZ5, is replaced by *W. triangula* above the boundary with CZ6a. The latter species is known from the Kaugatuma, Ohesaare, Ruhnu and Kolka (in Latvia) cores (Männil 1977b; Ramsköld and Edgecombe 1994), but never from nearshore localities. This species may reflect the deepening of the basin at the base of CZ6a and CZ6b or the influx of fauna from the more offshore shelf. Männil (1986) concluded from her study on trilobites of the Baltic shelf that relatively wider pygidia are common to the outer shelf and vice versa. Accordingly, the appearance of *Encrinurus* aff. *schisticola*, which is much wider than *Encrinurus punctatus*, may mark a relative sea-level rise in CZ6a but also below, in CZ3a–3b. However, two reasons could be proposed to explain why pygidia became wider: (a) to cover the larger gills developed due to the deficiency of oxygen, or (b) to increase buoyancy because of softer bottom conditions.

Starting from sample C95-277 in the uppermost part of CZ6a, the frequency of calymenids rises to half (or a quarter) of all specimens per sample, mainly on account of encrinurids. This association with calymenids is of low diversity with only 3–4 species per sample, but diversity doubles above the lower boundary of CZ6b. First, an aulacopleurid genus *Harpidella* appears at the base of CZ6b and is well represented throughout the zone. *Wallacia masterleei* is replacing *W. triangula* near the base of the zone, and slightly above it is a maximum abundance of calymenids, in sample C95-286. It also happens to be the sample where the oxygen isotope $\delta^{18}O_{phos}$ is determined from conodont apatite, showing the lowest value (18.19) and marking thus a small-scale warming cycle (Trotter et al. 2016). The rise in trilobite diversity may be related to that.

A sudden short-term increase in aulacopleurids (samples C95-289 and C95-290) is marked here as the nominal association due to a decrease in calymenids. The latter become a minor component in the upper parts of CZ6b and CZ9a and are missing above; however, encrinurids soon become dominant at higher levels. A similar association with the prevalence of *Harpidella* has been identified in the marl from the Lower Visby Beds in the Rönnklint-1 section as the richest (16 species per sample) Silurian trilobite community on Gotland, 9.5–9.75 m below the level of the disappearance of at least half of these taxa (Ramsköld 1985a). This extinction plane coincides with the conodont extinction D2 (Jeppsson 1987, 1997a, 1997b). In the Kõrkküla section, the *Harpidella* level is 11.55–12.55 m below D2, and unlike on Gotland, it is less diverse (7 species per sample). No taxonomic changes are observed in this interval and boundary beds.

The following part of the section, starting from sample C95-291, is again dominated by encrinurids. The species content changes in the upper part of CZ6b, where *Wallacia masterleei* is first outnumbered by the narrow-tailed long-spined *W. jaanussoni*, but both species become extinct somewhere near the top of the zone as do the phacopids *Acernaspis quadrilineata* and *A. sororia.* New short-time arrivals are the odontopleurids *Dudleyaspis* and *Ceratocephala*, an encrinurid *Distyrax* and a proetid possibly related to *Proetus verrucosus* and its successor *Proetus osiliensis* that traditionally marks the Jaani RS (Männil 1990).

All trilobite genera occurring above the gap in trilobite data (sampling bias C95-306-311) and the boundary between the Llandovery and Wenlock are transitional to the Jaani RS. A new association recovering within the

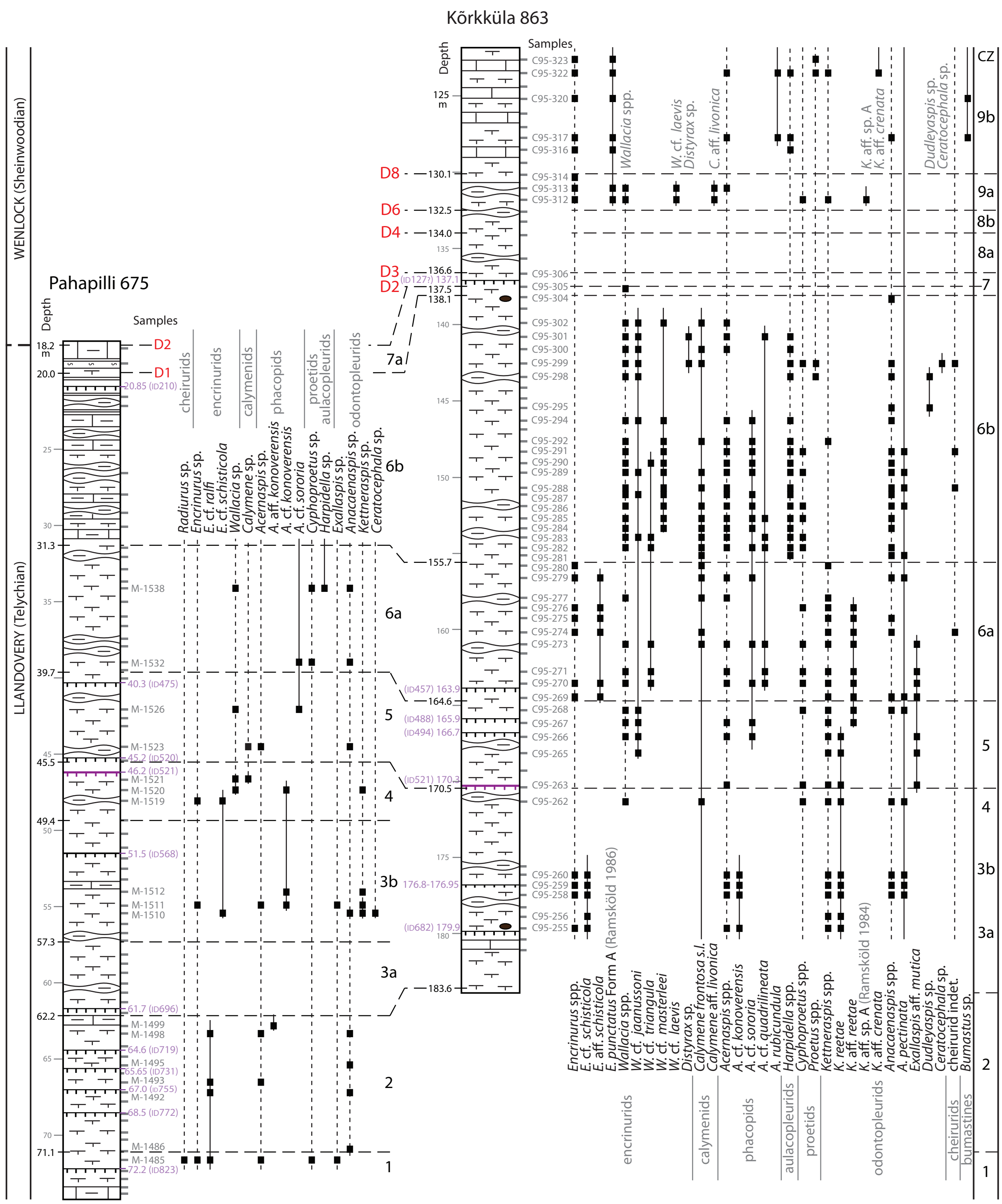

Fig. 7. Distribution of trilobites in the Pahapilli 675 and Kõrkküla 863 sections. ID numbers next to the logs mark the volcanic ash beds (see Kallaste and Kiipli 2006). For the legend and explanation of indexes, see Figs 2 and 3.

Ireviken Event is represented by new species such as *Wallacia laevis*, *Kettneraspis* aff. sp. A (Ramsköld 1984), *Encrinurus punctatus* Form A (Ramsköld 1986) and *Calymene* aff. *livonica* in CZ9a. All except the last one are also known from the Upper Visby Beds on Gotland. The *Acernaspis rubicundula* that appears here in CZ9b is also common in the Högklint Beds of Gotland. However, *Wallacia* becomes extinct without reaching CZ9b, and *Acernaspis* is last spotted in the Högklint Beds (Ramsköld 1985b), corresponding to CZ9b. *Bumastus* is a new element of the reefal association (Fig. 7) that on Gotland appears in the Upper Visby Beds (Bruton et al. 1979), thus before the end of the Ireviken Event.

ECHINOIDS AND CYCLOCYSTOIDS

Skeletal parts of echinoderms (dissociated ossicles, thecal plates, spines), along with fragments of bryozoans, dominate the bioclastic material. Within the disarticulated echinoderm material, the marginal ossicles of cyclocystoids and the ambulacral plates of bothriocidarid echinoids are easily recognizable and also the most interesting, as available data from this time period within the Baltic area remain understudied (e.g. Männil 1983; Figs 3, 5). Aside from that, the Ordovician–Silurian transition is associated and characterized by a faunal turnover and extinction of a number of echinoderm groups (e.g. Lefebvre et al. 2013; Thompson et al. 2022). Due to this, better knowledge of the distribution and stratigraphic range, e.g. of echinoids and cyclocystoids, is necessary for a more detailed understanding of this time interval of the Earth's history.

Echinoids are a diverse and widespread group of echinoderms, at least since the Mesozoic (e.g. Smith 2004). Although already known since the Middle Ordovician, the Early Palaeozoic fossil record of sea urchins is poor (e.g. Lefebvre et al. 2013; Thompson et al. 2022), especially from Silurian strata. Even from Estonia there are only two preliminary mentions of Silurian echinoids available (Männil 1983; Männil and Hints 1986). Several hundred skeletal elements and ossicles (mostly ambulacral and interambulacral plates) of echinoids were isolated from both the Kõrkküla and Pahapilli sections. The majority of the detected taxa belong to *Neobothriocidaris* and *Aptilechinus*, including new species known from Gotland, Sweden (unpublished data by Kutscher and Reich). An apparently new species of *Bothriocidaris* (Adavere RS) as well as ambulacral plates which can probably be assigned to the Lepidocentridae and Lepidesthidae? (Jaani RS) were found. For a long time, all *Bothriocidaris* species were considered as typical representatives of Ordovician strata (e.g. Schallreuter 1989). However, a few preliminary studies also show several different species from the Silurian (from Telychian to Ludlowian strata) of Gotland (Kutscher and Reich 2001, 2004; Kutscher 2010) and thus, a higher ('hidden') diversity from Baltica was to be expected, to which our new finding from Estonia contributes well. All the recorded echinoids were epibenthic scooping detritus feeders, probably on reef debris or secondary hardgrounds on soft bottoms.

Cyclocystoids are a rare extinct group of small, circular to pentagonal flattened, disc-shaped echinoderms (Smith and Paul 1982), ranging from Middle Ordovician to Early Carboniferous strata (Reich et al. 2018, fig. 5). Around 125 marginal plates and a few radial plates were studied from samples of both sections (Adavere and Jaani regional stages) and determined as taxa of *Polytryphocycloides*, *Cyclocystoides* and *Zygocycloides*?. *Polytryphocycloides lindstroemi*, also known from the Visby and Högklint formations of Gotland (e.g. Franzén 1979; Reich and Kutscher 2010), is the most common species in our material. The other taxa cannot currently be precisely determined down to species level, since only a handful of articulated cyclocystoid specimens from this time interval are known worldwide (Ewin et al. 2019). The life orientation of cyclocystoids is still under debate (Sprinkle et al. 2015; Ewin et al. 2019); however, they are very likely vagile surface feeders.

The stratigraphic significance of both echinoderm groups, echinoids and cyclocystoids, is not clear. However, some of them deserve attention as taxa occurring in strata corresponding to the Ireviken Event. Still, they will remain minor, but in terms of diversity, important components of Silurian marine benthic communities.

PISOCRINIDS

The Baltic Silurian pisocrinids of the order Disparida (Echinodermata) are known by four species from the Jaani and Jaagarahu regional stages, the lower and middle Wenlock. According to Rozhnov et al. (1989), these pisocrinids were adapted to shallow-water environments. However, the investigated pisocrinids from the older Adavere Stage occur in association with deeper-water *Dicoelosia–Skenidioides* brachiopods. The studied samples contain four (or five) pisocrinid species. All belong to the genus *Pisocrinus* and are distributed among its three subgenera: (1) rare *Pisocrinus (Pisocrinus) pilula*, (2) common *Pisocrinus* (*Granulosocrinus*) *lanceatus*, (3) the most common *Pisocrinus* (*Pocillocrinus*) *rubeli* (Rozhnov et al. 1989). In addition, an intermediate form often occurs between *Pisocrinus* (*Pocillocrinus*) *rubeli* and *Pisocrinus* (*Granulosocrinus*) *lanceatus*, which can be considered as a separate new species. This form has the following morphological features: the calyx is conical with moderately convex radial plates, hence almost spherical; the facets are spear-shaped, pointed, but only slightly tapering towards the base, being moderately lanceolate; the stem facet is slightly deepened, as if outlined by the protruding edges of the basal plates. It differs from *P.* (*G.*) *lanceatus* in a conical calyx shape, has only a slightly deepened stem facet, less lanceolate outgrowths and wider facets for arm attachment. It differs from *P.* (*Poc.*) *rubeli* in having a rounded-conical rather than a conical or bell-shaped calyx, a deepened stem facet and less lanceolate outgrowths.

Three samples from the uppermost CZ6b (C95-283, C95-299, C95-300) yielded specimens with an unusual barrel-shaped calyx with very narrow facets for the attachment of arms, separated by low and wide processes. This is obviously a new species, which should apparently be attributed to the subgenus *Granulosocrinus* as *Pisocrinus* (*Granulosocrinus*) sp. n. It is characterized by the following features: very narrow facets for the attachment of arms; wide and very low processes of the radial plates between them; the calyx is barrel-shaped and thin-walled.

All five species lived near the place of their burial and experienced only limited post-mortem transport. This is evidenced by their good preservation, including the well-preserved proximal processes of the radial calyx plates, which easily break off upon significant transportation. All species are similar to each other, which indicates their evolutionary radiation in this basin. They are of small size in comparison with typical representatives of pisocrinids. This complex of pisocrinids is close to the Silurian pisocrinids previously identified from Estonia (Rozhnov et al. 1989). Similarly to them, the pisocrinids described here were confined to the deeper zone of the benthic complex, an intermediate area between the carbonate shelf and graptolite facies.

SELECTED SHELLY FOSSILS

Corals. Small, 2–10 mm long, horn-shaped **solitary rugose corals** were found in many samples, whereas some of them contained up to 10 specimens (e.g. samples C95-285 and C95-286) (Fig. 8). However, special taxonomic study is needed to identify these specimens and to establish their probable connections with earlier known Telychian–early Sheinwoodian rugose taxa. On Gotland, a large, horn-shaped coral *Phaulactis* is very common in a short interval and plays an important role in the identification of the boundary between the Lower and Upper Visby beds (Munnecke et al. 2003; Adomat et al. 2016). *Phaulactis* is missing in the studied sections but has been reported from the Pärnu 1 drill core, where it occurs in a 5–12 m interval above the probable lower boundary of the Jaani RS at a depth of 94.1 m (collection GIT 397, Geoscience Collections of Estonia).

Many samples contain the horn-shaped rugose corals and small tubular fossils which, judging from the occurrence of short septa inside the tubes, could belong to rugosans.

The globally widely distributed button-shaped rugose coral *Palaeocyclus porpita* (Scrutton 1996) is represented by small (1.2–4 mm in diameter) specimens in both the Kõrkküla and Pahapilli sections in the upper part of the Upper *Pt. am. amorphognathoides* Zone (Figs 4, 8). One specimen in the Kõrkküla section reaches CZ7 of the lowermost Wenlock. On Gotland, this species has been reported from the basal beds of the Vattenfallet section, mainly from the topmost Lower Visby Beds and rarely in the Upper Visby Marl, which belongs to the lowermost Wenlockian (Jaanusson 1979; Neuman and Hanken 1979,). The Wenlockian age of the uppermost finds of *P. porpita* is supported by the associated conodont *Pt. pennatus procerus* of CZ8 (Jeppsson and Männik 1993). In the mainland of Estonia *P. porpita* is known from the upper Adavere RS (Kaljo 1970). The total range interval of *P. porpita* in the Baltic region crosses the series boundary and extends from the upper(most) Llandovery to the lowermost Wenlock.

Small, poorly preserved rare fragments of **tabulate corals**, probably transported from the shelf area to the deeper facies, are found in both sections. However, in the more onshore Pahapilli section, these occur already in CZ3b, but are much higher in the offshore Kõrkküla section, in CS6b.

A group of corals that has received little attention in palaeontology (Fernández-Martínez et al. 2019) and was previously not known from Estonia includes fleshy soft corals belonging to Octocorallia (Alcyonacea: Alcyoniina) (Bengtson 1981a, 1981b). Isolated sclerites or semi-articulated specimens (*Atractosella cataractaca*), first misinterpreted as sponge spicules (Hinde 1888; Bengtson 1979), echinoid spines (Regnéll 1956) or chordates (Lamont 1978), are probably widespread in the Silurian strata of Gotland (Bengtson 1981a, 1981b) and the Baltic region (Reich 2002). Similarly to modern soft corals, the Palaeozoic representatives also needed hard substrate for settlement, either on the reef slope or reef overhangs. Our numerous specimens from the Kõrkküla and Pahapilli sections in western Estonia belong to the same genus and mostly the same species as described from the Visby and Högklint formations, Gotland, Sweden.

Bryozoans are represented by small (less than 10 mm) hemispherical colonies and small fragments (less than 10 mm) of branching colonies (Figs 4, 8), dominating among carbonate fossil remains at some levels in the Kõrkküla section. A holdfast-type attachment base is often preserved in some branching colonies. Part of the bryozoans have an attachment scar or are attached to the fragments of some other carbonate fossils. The frequency of bryozoan remains in the studied residues is lower in the deeper-

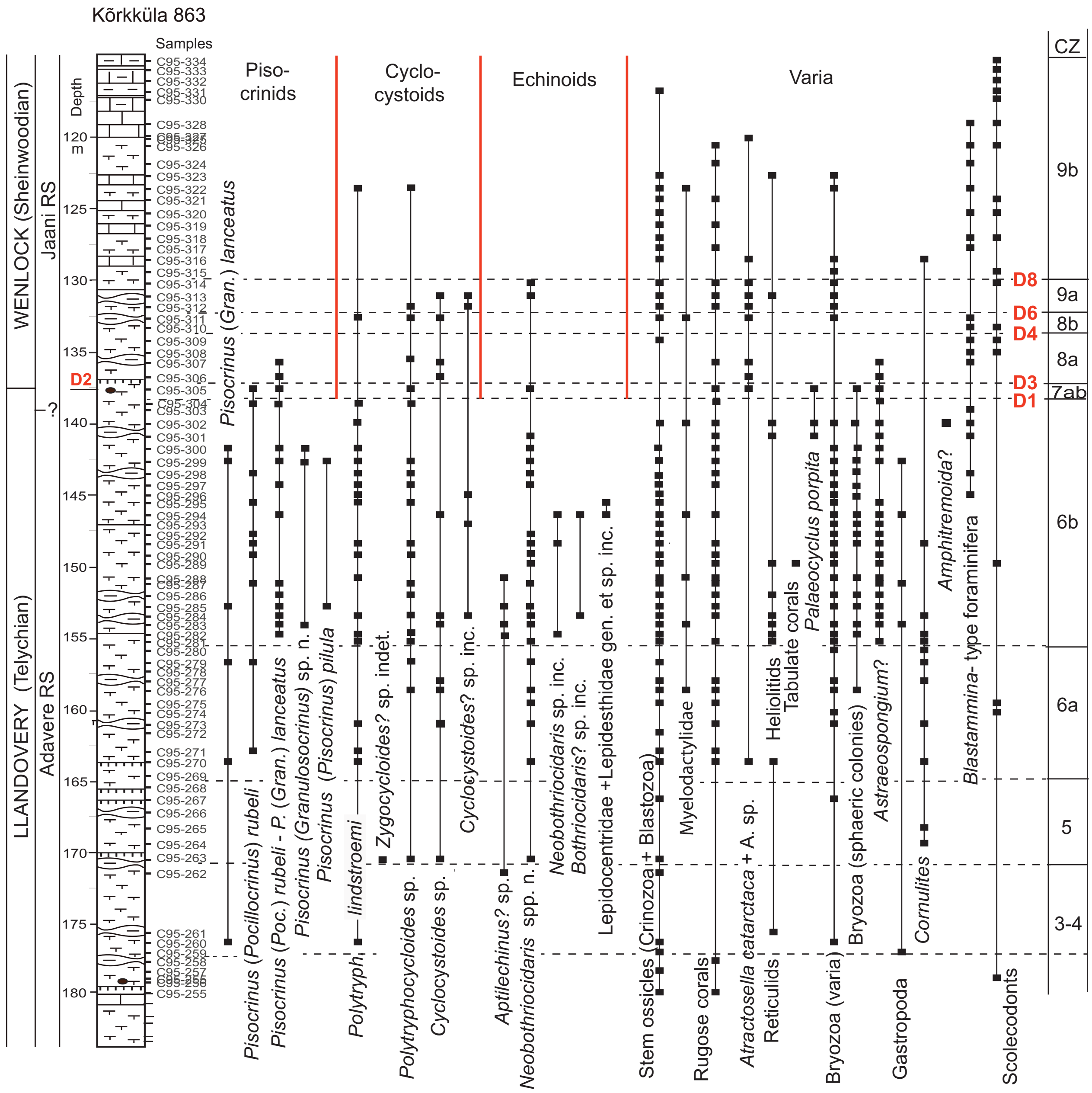

Fig. 8. Distribution of echinoderms and selected fossils ("Varia") identified at different taxonomic levels in the Kõrkküla 863 section. For the legend and explanation of indexes, see Figs 2 and 3.

water deposits of the Kõrkküla section than in the shallower, open-shelf facies in the Pahapilli section.

Sponges are represented in the geological record as preserved body fossils or as disaggregated structural elements of their skeletons – spicules or scleres (e.g. Donovan 2000). The skeleton of sponges disintegrates easily during the depositional and burial processes and, as a rule, isolated spicules are often the only remains of a sponge preserved. Complete Silurian sponges and their spicules have been well studied on Gotland, Sweden (Bengtson 1979; Rhebergen and Botting 2014), and in Herefordshire, UK (Nadhira et al. 2019).

The octactine-type spicules without axial rays found in the Pahapilli and Kõrkküla sections resemble those of *Astraeospongium* (Rhebergen 2005) and may be conspecific with *Astraeospongium patina* from Gotland (Bengtson 1979). Some spicules having a blunt or stump perpendicular ray may belong to other sponges. Sponge spicules occur in both sections in numerous successive samples from CZ2 up to CZ7. Their occurrence together with the *Dicoelosia–Skenidioides* brachiopods community and rapid disappearance at the beginning of the Ireviken Event (Datum plane 3) emphasize the adaptation of sponges to deep-water environments with a soft bottom. On Gotland sponges occur from the upper Llandovery up to the Ludlow, having a wide amplitude of ecological niches from oncoid-rich deposits to deep-water deposits in the basin (Rhebergen 2005). An example of sponge-rich deep-water fauna has been described from North America by Watkins and Coorough (1997), where the Silurian (Wenlockian) fauna of Benthic Assemblage 5 represents the equivalent of the *Clorinda* community (Ziegler 1965).

Graptolites are very rare in the studied sections. Few fragments of retiolitids were found in only two samples (C95-261 and C95-270) in CZ4 and CZ6 of the Kõrkküla section (Fig. 8). In the Latvian Kolka-54 drilling, retiolitid graptolites are present up to the level corresponding to CZ6 (Loydell et al. 2010).

Foraminifera are poorly known microfossils in the Baltic sections, although often occuring together with other micro- and macro-fossils. The brown proteinaceous *Blastammina*-type foraminifera have been identified also in the Kõrkküla section from the uppermost CZ6b through the Ireviken Event up to CZ9b.

Another, probably agglutinated type of foraminifera represents the genus *Amphitremoida* Eisenack (family Hippocrepinellidae) (Nestell et al. 2009). They resemble sponge spicules in size and lenticular outline, and occur mostly in the Pahapilli core. The *Amphitremoida*-type foraminifera have a long stratigraphic range from the Lower Ordovician (Nestell and Tolmacheva 2004) up to the Lower Mississippian (Kaminski et al. 2008).

Small conical specimens in the samples represent tubicolous annelids **cornulitids**, whose total stratigraphic range extends from the Ordovician up to the end of the Carboniferous (Ippolitov et al. 2014). In Estonia, cornulitids are known from the Ordovician Lasnamägi RS to the latest Silurian Ohesaare RS included (Geoscience Collections of Estonia).

CONCLUSIONS

1. Our investigation of shelly fossils in two borehole sections, Pahapilli 675 and Kõrkküla 863 on the island of Saaremaa, provides the first comprehensive insight into the late Llandovery and earliest Wenlock biota of the open shelf and transition to deeper basinal environments within the Baltic Basin (Nestor and Einasto 1997). For the first time, data on the rich and diverse association of brachiopod and non-brachiopod fossils are presented. Data on the distribution of different groups of echinoderms revealed the occurrence of several potential new species that are related to the Gotland species. Species composition of cyclocystoids indicates the importance of the Baltic Basin as a place for their evolutionary radiation. The rich trilobite fauna is represented by small-sized individuals whose dominant taxa change over time. For the first time, the occurrence of bryozoans, corals, different stem ossicles, spicules of sponges and some other fossils identified on different taxonomic levels is represented sample by sample.
2. The identified *Dicoelosia–Skenidioides* group communities tie the studied Baltic faunas to their globally distributed analogues distributed mainly in fine siliciclastic deposits with low carbonate content deposited in the conditions of humid climate (Watkins et al. 2000; Munnecke et al. 2003). According to this, the Baltic region represents a part of the Earth with unique long-lasting Early Palaeozoic *Dicoelosia–Skenidioides* group communities (Boucot 1975, 1992, 1999) of the Benthic Assemblages BA4–5, which have been recognized in the upper Llandovery and Wenlock strata on Avalonia, Laurentia and in northern China (Watkins et al. 2000; Bassett and Rong 2002; Cocks and Rong 2019). Two communities with *Dicoelosia* and *Skenidioides* are identified. The lower *Dicoelosia–Skenidioides* community in CZ1–4 with *Jonesea grayi* and *Leangella segmentum* represents the characteristic deep-water community of the Benthic Assemblages 4–5. The *Dicoelosia–Skenidioides* cf. *paralata* association, possibly belonging to BA3–4 is transitional into the Wenlock. The data set presented in Figs 3–8 shows the main trend in faunal dynamics by certain stratigraphic intervals – conodont biozones. It should be noted that the number of the taxa (species, genera) reported is likely underestimated (due to numerous species, which are shown under the open nomenclature and could represent new taxa) up to the level of the Ireviken Event. However, the faunal extinction rates during the Ireviken Event are overestimated because part of the samples were dissolved in acid, and especially calcareous fossils were lost.
3. Brachiopods represent a common group of shelly fossils in almost all conodont biozones, with an increase in the number of taxa from 17 in CZ2 of the Pahapilli section up to 28 in CZ6b of the Kõrkküla section. The diversity of trilobites, and probably of echinoderms represented by several potential new taxa, shows a stepwise increasing trend up to CZ6b. The number of the taxa of trilobites increases from 12 in CZ5 up to 18 in CZ6b. The statistical analyses of trilobite fauna have enabled to identify a succession of associations with dominants of different taxa. The frequency of stem ossicles of Crinozoa and Blastozoa together with different bryozoans increases upwards up to CZ6b.

4. The high number of specimens of the brachiopods *Dicoelosia* and *Skenidioides*, as well as the diversity of trilobites and echinoderms in CZ6b, is undoubtedly remarkable in the Upper *Pterospathodus a. amorphognathoides* Zone (CZ6b). Initially, many more than 50 taxa can be considered to occur in CZ6b of the Kõrkküla section. This zone can possibly be delimited by the frequent occurrence of *Skenidioides* cf. *paralata*, the presence of *Wallacia* cf. *masterleei* and the abundance of *Harpidella* sp. A probable new pisocrinid species (transitional varieties *P*. (*G*.) *lanceolatus*–*P*. (*Poc.*) *rubeli*, *Pisocrinus* (*P*.) *pilula*) appears at the lower boundary of CZ6b, and the sponge spicules become frequent. Some decrease in faunal diversity is notable in the uppermost CZ6b, where the boundary supposedly lies between the Adavere and Jaani stages. The fast increase in faunal richness in the lower part of CZ6 seems to roughly coincide with the short warming event, which is followed by a cooling trend with some warming episodes up to the earliest Wenlock.
5. The *Dicoelosia*–*Skenidioides* communities, together with associated non-brachiopod faunas, represent a case of long-lasting Palaeozoic evolutionary fauna adapted to offshore environments. However, while maintaining a largely similar ecotype, the taxonomic composition and associated non-brachiopod fauna have changed through time. Our Baltic data have the potential, when examining a larger stratigraphic interval, to reveal disturbances of these communities caused by various geological events in the basin.
6. The Ireviken Event within the Llandovery–Wenlock transition (Jeppsson 1998; Munnecke et al. 2003; Männik et al. 2014; Trotter et al. 2016) is stratigraphically quite complete in the Kõrkküla section, covering all steps (Datum planes D1–8) in the development of conodont fauna. However, notable gaps of different duration occur in this interval in several sections of the neighbouring areas (Suigu S-3, Paatsalu, Viirelaid) (Männik et al. 2014). Besides a few brachiopods (*Dicoelosia* cf. *paralata*, *Skenidioides* sp. *Hesperorthis* sp.) transitional from the Llandovery, some echinoderms among pisocrinids and cyclocystoids reach different levels of the Ireviken Event. Despite the trilobite data within the range of the abovementioned datum planes being scarce in the lower part, the same genera that are common below such as *Wallacia*, *Acernaspis*, *Kettneraspis*, *Anacaenaspis, Encrinurus, Calymene, Harpidella* and *Proetus* continue their existence with the evolving of new species; however, some of them (*Wallacia*, *Acernaspis*) become extinct somewhere near the end of the Event or soon after that (top of the Högklint Beds on Gotland). A remarkable part of the Ireviken fauna belongs to the group "Varia". The rugose corals that occur frequently starting from CZ6a are common fossils together with crinozoans (stem ossicles) and bryozoans in the interval of the Ireviken Event. In addition to the shelly fossils, some microfossils, foraminifera and scolecodonts occurring in the strata of the Ireviken Event deserve attention, although based on random collections.
7. Our data are insufficient to tie some faunal changes in the *Pt. eopennatus* ssp. 1 and *Pt. eopennatus* ssp. 2 conodont zones (CZ1–CZ2) to the Valgu Event, which is defined in the Viki drill core (western part of the island of Saaremaa, Männik 2007) in the conodont and carbon isotope succession and described later in Sweden and other parts of the world (Munnecke and Männik 2009; Waid and Cramer 2017; Hammarlund et al. 2019). The Pahapilli section comprises a few fossils from the beginning of the Valgu Event (CZ1). The diverse association of brachiopods in CZ2 is related to their favourable environments rather than to the stressing conditions of the Valgu Event. Possibly the strata with the peak values of the Valgu Event in the Viki core are partly missing in the Pahapilli section.
8. The conodont zonation is a useful tool for assessing the biostratigraphic value of shelly fossils. However, different taxa have a varying importance biostratigraphically due to dissimilarities in the life strategy of organisms and adaptation to different environments on the facies transect. The shelly fauna of the Pahapilli core, in CZ5, comprises relatively few brachiopods, trilobites, echinoderms, but numerous bryozoans and remains of soft corals, which are rarer in the deeper-water Kõrkküla section, where trilobites show an increase in diversity. The brachiopod *Jonesea* cf. *grayi* in CZ1 is a species that indicates deeper-water environments and is rather unsuitable as a biostratigraphic marker. Its total stratigraphic range comprises the Raikküla RS and the Adavere RS, and the thickness of the rocks containing *Jonesea grayi* reaches over 80 m (on Ruhnu 79.2 m, on Ohesaare 81.6 m; Rubel 2011). There are a few species whose appearance or changes in abundance are inextricably linked to the boundaries of the conodont biozone. The total stratigraphic range of several species is much longer than in the studied sections and does not coincide with the zone boundaries in our sections. The brachiopod *Leangella segmentum* seems to be restricted only to CZ3 and CZ4, although its total range extends to the Jaani RS. In the Kõrkküla section, the earliest specimens of the brachiopod *Visbyella* were identified in samples from CZ5. In contrast, in the Pahapilli section, this species occurs in older strata (mainly in CZ1 and CZ2) and indicates its shift into the younger strata.

9. The whole association of fossils occurring in the studied sections is represented by small individuals, which are common in siliciclastic deposits of the deeper part of the basin (Chen et al. 2012). The disarticulation and damaged specimens imply some transport and/or destructive activity of water movement. The influence of climatic change is not clear, but a possible turning point towards a cooler climate at the beginning of CZ6b has a greater influence than the sea level change. Here the faunal change seems to precede the climate change. The studied material shows differences between the sections in different locations on the offshore-onshore transect; however, the identification of the width of zones with similar faunas and transition to shallow shelf requires further studies and comparison of data from different sections.

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Fauna mitmekesisuse kujunemine hilis-Llandoveris ja vara-Wenlockis Balti paleobasseini idaosas ning selle tähendus Irevikeni sündmusele

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Käesolevas töös on uuritud erinevate fossiilirühmade taksonoomilist koosseisu ja levikut hilis-Llandoveris ning Irevikeni sündmuse intervallis Balti paleobasseinis. Uuritud materjal kahest Saaremaa puursüdamikust (Pahapilli 675 ja Kõrkküla 863) on valdavalt pärit savikatest kivimitest, mille desintegreerimine vees võimaldas koguda hulgaliselt erinevaid fossiile (brahhiopoode, trilobiite, okasnahksete toese elemente, sammalloomi, koralle jt). Rikkalik detriidina säilinud paleontoloogiline materjal esindab mitmekesist ja arvukat elustikku sügavamaveelistes tingimustes paleokeskkonnas.

Esmakordselt on kajastatud ülevaade praktiliselt kogu elustikust paleobasseini avašelfil, mis on esindatud valdavalt väikesemõõduliste eksemplaridega (alla 10 mm) või suuremate vormide fragmentide näol. Proovid olid algselt kogutud ja töödeldud konodontide uurimiseks, kus nende biotsonaalne skaala on antud töös läbilõigete korrelatsiooni aluseks. Uuringus on esitatud kõigi fossiilide levik proovide kaupa. Brahhiopoodide hulgas domineerivad taksonid, mis viitavad suhteliselt sügavaveelistele keskkonnatingimustele. Nende tüüpilised esindajad on perekondadest *Dicoelosia* ja *Skenidioides*, mis iseloomustavad vara-Paleosoikumi unikaalset ja pikaajalist faunakooslust erinevates regioonides. Trilobiidifauna muutused ajas ilmnevad teatud taksonite (odontopleuriidid, encrinuriidid, calymeniidid ja aulacoporiidid) domineerimises. Esmakordselt on statistiliselt uuritud trilobiidikoosluste ajalisi muutusi. Rikkalik okasnahksete fauna (pisocriniidid, cyclocystoidid, echinoidid, crinoidid) sisaldab rea Eestis vähetuntud ja seni tundmata liike ning perekondi, mille täpsem taksonoomiline uurimine vajab täiendavat tööd. „Varia“ grupi all käsitletud fossiilid (sammalloomad, korallid, käsnad jt) rikastavad oluliselt andmeid basseini elustiku kohta.

Konodontide biotsonaalne skaala tagab läbilõigete suure täpsusega korrelatsiooni ja võimaldab võrrelda puuraukude faunasid ajaliste üksuste, konodonditsoonide kaupa, selgitada liikide leviku erinevusi läbilõigetes ning tuvastada stratigraafiliselt olulisi liike. Analüüsitud on fauna muutuse seost keskkonnatingimustega, sh kliima ja meretaseme kõikumistega.