

## Ordovician conodont diversity in the northern Baltic

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**Abstract.** The diversity data presented in this paper are based on recently revised collections of conodonts from outcrops (northern Estonia) and core sections of Estonia and western and northern Latvia. Based on variations in the abundance of taxa, four intervals with different general trends in diversity changes can be recognized in the Ordovician part of the succession: (1) the *proavus*–*crassus* zones and (2) *crassus*–*anserinus* zones, both intervals forming quite distinct diversity cycles; (3) the *variabilis*–*ventilatus* zones, characterized in general by stable diversity values, and (4) the *ventilatus* Zone—the topmost Ordovician, with a steady increase in diversity up to the *ordovicicus* Zone, followed by a decline during the End-Ordovician Extinction Event. Diversity was lowest in the earliest and latest Ordovician but reached maximum values at the end of the Early Ordovician radiation of conodonts, in the middle and upper Darriwilian, and just before the start of the End-Ordovician Extinction Event. Four supersequences (transgressive–regressive cycles) are proposed here for the northern Baltic Ordovician succession. The diversity changes recognized in the conodont succession demonstrate general correlation with these supersequences: boundaries between supersequences are characterized by low diversity values; diversity increases more or less rapidly in the lower, transgressive parts of the supersequences and decreases in their upper parts.

**Key words:** Ordovician, northern Baltic, biodiversity, conodonts.

### INTRODUCTION

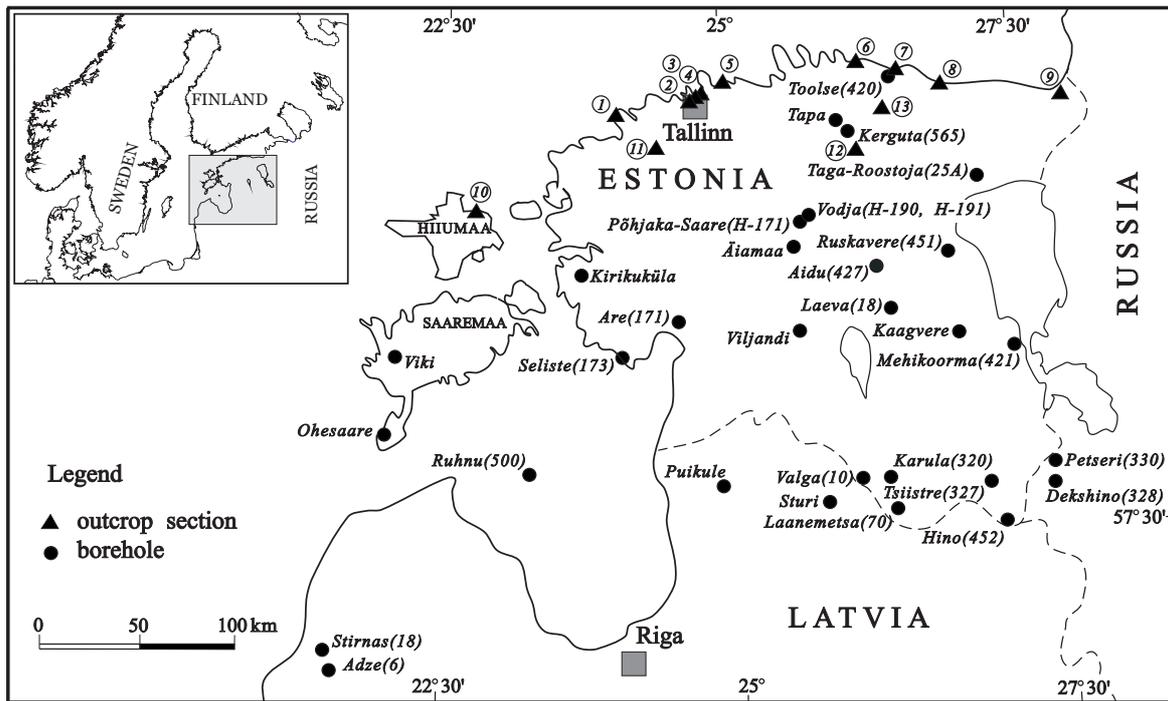
Ordovician conodonts from Estonia have been known since the discovery of the fossils by C. H. Pander more than 150 years ago. Systematic studies of Ordovician conodonts in the northern Baltic started in the middle of the last century (Viira 1966, 1967, 1974). Since then, large collections of conodonts from all stratigraphic intervals represented in the region, and from all facies available for study, have been collected. The abundance of specimens and richness of taxa are highly variable in time and space. Several radiation and extinction events have been recognized in the succession of Ordovician conodont faunas in Estonia (Männik 2006). Recently, some general analyses of variations in the biodiversity in Ordovician faunas, including conodonts, have been published (Hammer 2003; Albanesi & Bergström 2004; Wu et al. 2010a, 2010b; Goldman et al. 2011; Sheets et al. 2011). The aim of the present paper is to give a brief overview of the diversity changes recognized in the Ordovician conodont succession in the northern Baltic (in Estonia and Latvia).

### MATERIAL AND METHODS

This study is based on material from 31 drill core sections (25 from Estonia, 4 from Latvia and 2 from westernmost

Russia; Fig. 1). Additionally, the distribution of conodonts in 12 outcrop sections exposing Lower to Middle Ordovician strata and 4 exposing Upper Ordovician strata were analysed. Both published and unpublished data were used. In several earlier publications (Viira 1966, 1967, 1974) conodont identifications were based on form taxonomy. Before using these data the collections were restudied to update the taxonomy. Other older identifications were checked as well.

The oldest conodonts in Estonia come from the upper Cambrian, from sandstones and shales of the lower Pakerort Stage exposed in North Estonia (Heinsalu et al. 1987, 1991, 2003; Viira et al. 1987; Kaljo et al. 1988; Mens et al. 1989, 1996). Conodonts from the clays of the Varangu Stage (middle Tremadocian) were studied by Viira (1970) and Viira et al. (1970). Data on conodonts in the Hunneberg and Billingen stages (late Tremadocian–Floian) come mainly from the Pakri (in western North Estonia) and Saka (in eastern North Estonia) outcrop sections (Löfgren et al. 2005; Viira et al. 2006b; Fig. 1). Detailed data on conodont faunas in the upper Tremadocian to the upper Darriwilian interval were obtained from the Mäekalda sections located close to Tallinn (Viira et al. 2001; Fig. 1). Only a small part of conodont data from the Upper Ordovician outcrops in Estonia is published (Hints et al. 2004, 2005). The information on Ordovician conodonts in drill cores was obtained mainly from recent publications



**Fig. 1.** Location of the studied sections (only those exposing Ordovician strata are indicated). Numbers in circles: 1, Pakri (I) and Pakri (II); 2, Mäekalda (I) and Mäekalda (II); 3, Tõnismägi; 4, Suhkrumägi; 5, Ülgase; 6, Vihula; 7, Varangu; 8, Saka (I) and Saka (II); 9, Orasoja; 10, Paluküla; 11, Vasalemma; 12, Porkuni; 13, Ussimägi.

(Taga-Roostoja (25A): Viira & Männik 1999; Valga (10), Ruhnu (500), Viki: Männik 2001, 2003, 2010; Mehikoorma (421): Männik & Viira 2005; Kerguta (565): Viira et al. 2006a; Stirnas (18): Hints et al. 2010). Additionally, unpublished material from several core sections (Fig. 1) was used. Although the current paper deals mainly with Ordovician faunas, data from the lowermost Silurian were included to highlight the faunal changes caused by the End-Ordovician Event.

In this paper the focus of the diversity study is on taxonomic richness as adequate abundance data of the taxa are not available at the moment (specimens are not counted). The total numbers of species and genera, and the numbers of the appearing and disappearing species were counted per stratigraphical unit recognized (Fig. 2). To subdivide the succession, the smallest available, and recognizable all over the studied region, conodont-based biostratigraphical units (zone, subzone or an informal unit: e.g. ‘Uppermost *Baltoniodus* range’, ‘*Noixodontus* fauna’; Männik 2007) were applied. In some intervals application of stage slices *sensu* Bergström et al. (2009) in addition to the conodont-based units allowed a more detailed subdivision of the strata (e.g. in the *ordovicicus* Zone). Data for the uppermost Ordovician, for the interval above the ‘*Noixodontus* fauna’ come from drill cores from southern Estonia and western Latvia

(Männik 2001, 2003; Hints et al. 2010). In northern Estonia this interval corresponds to a gap. In the Stirnas (18) core section (Hints et al. 2010), the taxa occurring in this interval but represented by redeposited specimens were not counted. The stratigraphical chart used in this study is based on Nõlvak et al. (2006). For general correlation time slices *sensu* Webby et al. (2004) were also included in the figure. However, as the location of the time slice boundaries in a particular section is often problematic, these units were not used as a basic stratigraphical framework in our study.

The diversity measures used in this paper follow Cooper (2004). Total diversity is the number of species occurring in a stratigraphical unit recognized. Normalized diversity is the sum of species that range from the interval below to the interval above, plus half the number of species that originate and/or become extinct within the interval, plus half of those that are confined to the interval itself. The origination and extinction ‘rates’ are calculated for each interval by dividing the number of species appearing or disappearing in the interval with the total number of them recorded in the unit. We did not apply any method which requires geochronological dating of strata, as such datings of finer units are still too speculative.

## TRENDS IN THE FAUNAL CHANGES

In total, the Ordovician conodont fauna in the northern Baltic comprises, as presently known, 177 species belonging to 64 genera (Fig. 2). The distribution of taxa in the stratigraphic succession is variable, in abundance of specimens as well as in the number of taxa. Diversity is lowest in the lowermost and topmost Ordovician (Fig. 3). The total diversity of species reaches maximum values at the end of the Early Ordovician radiation of conodonts (in the *evae* Zone), in the *suecicus* Zone and just before the start of the End-Ordovician Extinction Event (in the *ordovicicus* Zone). Diversity is lower between these three levels, lowest in the lower Darriwilian (in the *crassus* Zone) and somewhat higher and slowly but continuously increasing in the main part of the Upper Ordovician (from the *variabilis* Zone below up to the *ordovicicus* Zone above). Changes in species and genus diversity follow similar trends, although the variations in species diversity are more distinct. Tentatively, four intervals with different general trends in diversity changes can be recognized in the studied succession: (1) the *proavus*–*crassus* zones forming a distinct diversity cycle, (2) the *crassus*–*anserinus* zones, also forming a diversity cycle (which is particularly distinct in the normalized diversity curve; Fig. 3), (3) the *variabilis*–*ventilatus* zones, characterized by quite stable diversity values and (4) the *ventilatus* Zone–the topmost Ordovician, with gradual increase in diversity up to the lower *ordovicicus* Zone, followed by its decline during the End-Ordovician Extinction Event. Below, the changes in the diversity trends will be discussed in more detail.

### The *proavus*–*crassus* zones

This interval corresponds to the Lower Ordovician and the lower part of the Middle Ordovician. In sense of regional stratigraphy, the Pakerort, Varangu, Hunneberg, Billingen and Vokhov stages, and the lower part of the Kunda Stage form these strata. Starting from the topmost Cambrian and through the Tremadocian up to the upper Floian, in the *proavus*–*evae* zones, conodont diversity increased continuously. Both the total species and genus diversities reached their highest values in the *evae* Zone, with species diversity having a distinct peak in the upper part of the zone (Fig. 3). Normalized species and genus diversity reached their maximums higher in the succession, in the middle Dapingian *originalis* Zone. Both curves have minor peaks also in the lower *evae* Zone and decreased values in the *triangularis*–*navis* interval.

The *proavus*–*evae* time was characterized by highly variable simple-cone conodonts (*Paroistodus*, *Paltodus*,

*Acodus*, *Drepanodus*, *Drepanoistodus*, *Oistodus*, *Scolopodus*) and by the appearance of new, more complicated types of apparatus in which elements have denticulated processes (*Prioniodus*, *Oepikodus*, *Periodon*, *Trapezognathus*) (Fig. 2). Also *Baltoniodus* that appears higher in the section, in the *triangularis*–*navis* Zone, represents this type of apparatus. At the end of the Early Ordovician radiation, after its maximum in *originalis* time, normalized species diversity decreased rapidly and reached a minimum for this interval in the *crassus* Zone (Fig. 3). At the same time, decline in normalized genus diversity was minor. Total species and genus diversities started to decrease earlier, after their maximums in the upper *evae* Zone, and reached minimum values, respectively, in the *crassus* Zone and in the *antivariabilis*–*variabilis* interval. This is the largest decline in conodont species diversity recorded in the conodont succession between the Tremadocian and the Katian in the northern Baltic. Many taxa with simple-cone apparatuses (e.g. *Oistodus*, *Scolopodus*, *Paroistodus*) became extinct in the *navis*–*crassus* zones. However, during this general decline in conodont diversity in the *antivariabilis*–*variabilis* Zone, the first taxa with platform elements in their apparatuses (e.g. *Lenodus*) appeared in the studied region. In the lower half of the *proavus*–*crassus* zones interval, up to the *elegans* Zone, species origination clearly dominates over extinction. In the upper half of the interval, in the *evae* to *crassus* zones, the origination and extinction rates are more variable.

### The *crassus*–*anserinus* zones

This interval corresponds to the middle and upper parts of the Middle Ordovician and, in the studied region, includes the upper Kunda, Aseri, Lasnamägi, Uhaku and the lowermost Kukruse stages. Characteristic of these strata are two highs in the species total diversity curve: the most distinct one in the *suecicus* Zone, the other one more like a plateau in the *reclinatus*–*lindstroemi* interval.

Starting from the *crassus* Zone, total species diversity increased rapidly up to the *suecicus* Zone. A number of new taxa, apparatuses with denticulated processes, such as *Yangtzeplacognathus* and *Eoplacognathus*, and several simple-cone conodonts (*Dapsilodus*, *Panderodus*, *Oslodus*, *Costiconus*, *Walliserodus*) appeared in this interval (Fig. 2). Above the maximum in the *suecicus* Zone, total species diversity decreased rapidly up to the *foliaceus* Zone, increased again higher in the succession, and a plateau-like maximum (upper *reclinatus*–lower *lindstroemi* zones) followed.

Normalized species diversity increases almost continuously from a minimum in the *crassus* Zone up to



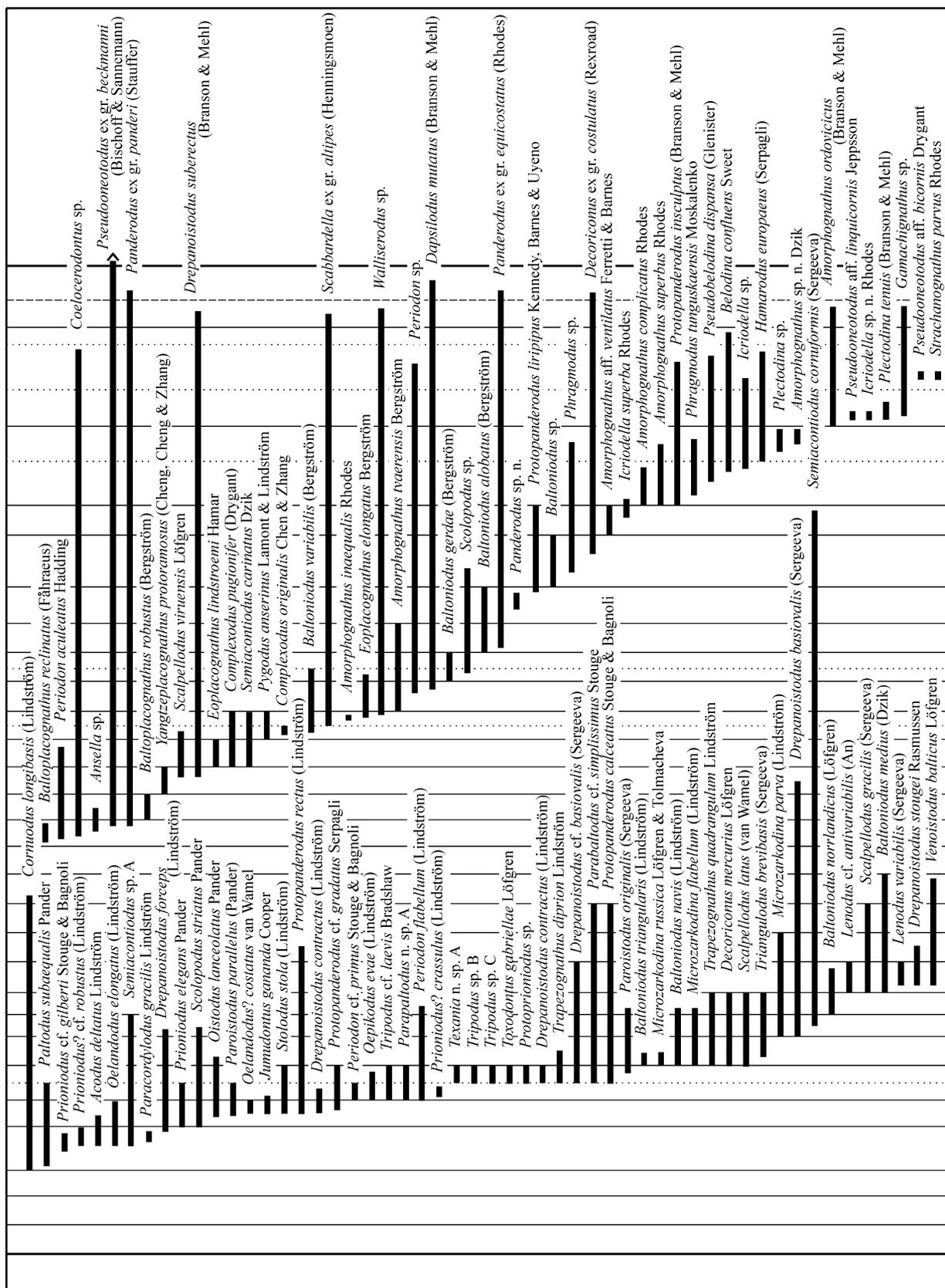


Fig. 2. Continued.





its maximum in the *robustus* Zone above. Higher in the succession, normalized species diversity decreases (quite slowly in the upper *robustus*–lower *lindstroemi* interval, but more rapidly starting from the upper *lindstroemi* Zone) and has minimum values in the upper *anserinus*–lower *variabilis* interval (Fig. 3). Total species diversity has a minimum in the *variabilis* Zone. Changes in normalized genus diversity have an almost identical trend to that in species diversity, but total diversity seems to be more variable and has three highs instead of two. The uppermost of them lies in the upper *anserinus* Zone. From the *pseudoplanus* Zone to the *reclinatus* Zone, the origination of taxa dominated over their extinction. Higher in the succession extinction is dominating.

### The *variabilis*–*ventilatus* zones

This interval corresponds to the lower Upper Ordovician, to the main part of the Kukruse Stage, and the Haljala, Keila and lower Oandu stages. In the faunal succession, after considerable decline in conodont species diversity in the *anserinus*–*variabilis* zones, and a total diversity minimum in the *variabilis* Zone, the diversity stayed relatively stable up to the *ventilatus* Zone. This interval is characterized by gradual increase in total species diversity in its lower part (up to the ‘Uppermost *alobatus* range’) and decrease in the upper part (Fig. 3). Normalized species and genus diversities are even more stable. *Amorphognathus* and *Baltoniodus* dominate the faunas in the lower part of this interval, but *Amorphognathus* is missing and *Baltoniodus* becomes rare in its upper part. The ‘Uppermost *Baltoniodus* range’ is dominated by several simple-cone taxa (e.g. *Decoriconus*, *Drepanoistodus*, *Panderodus*; Männik 2004). *Amorphognathus* reappears in the *ventilatus* Zone.

### The *ventilatus* Zone–topmost Ordovician

This interval corresponds to the upper part of the Upper Ordovician, to the upper Oandu, Rakvere, Nabala, Vormsi, Pirgu and Porkuni stages. In this interval,

starting from the low in the *ventilatus* Zone, diversity starts to increase and reaches its maximum in the *ordovicicus* Zone: normalized species and genus diversities in the lower *ordovicicus* Zone (in the Vormsi Stage) and total species diversity in the middle *ordovicicus* Zone (in the Pirgu stage) (Fig. 3). Several new genera (e.g. *Belodina*, *Hamarodus*, *Pseudobelodina*) and a number of new species appear in this interval in the northern Baltic but, again, the most common constituent of the faunas is *Amorphognathus* (Fig. 2). Higher, in the lowermost Porkuni Stage, conodont diversity drops rapidly and reaches its minimum (in both the number of species and genera) in the uppermost Ordovician (Fig. 3; Kaljo et al. 2011).

The early Silurian (Rhuddanian and early Aeronian; Juuru and lower Raikküla stages in Estonia, respectively) was a time of rapid radiation and almost complete turnover of conodont faunas. Only some, mainly simple-cone lineages survived the End-Ordovician Event (Männik 2001, 2003, 2010; Hints et al. 2010).

## DISCUSSION

### Conodont diversity

Several authors have carried out generalized analyses of Ordovician conodont diversity in greater or lesser detail and published various diversity curves (Sweet 1985; Hammer 2003; Albanesi & Bergström 2004; Sheets et al. 2011). Sweet (1985) and Albanesi & Bergström (2004) included in their discussions information available all over the world at the time of their studies, whereas Hammer (2003) and Sheets et al. (2011) analysed data from the Baltic Palaeobasin.

The greatest diversity radiation in conodont history occurred in the earliest Ordovician (Tremadocian). Shortly after their appearance in the Late Cambrian, euconodonts (‘true’ conodonts) spread widely, differentiated rapidly in terms of both single-element and apparatus morphology and reached a peak in diversity in the early Arenig (= Floian according to modern nomenclature; Sweet 1985). However, based on earlier publications, the authors have

**Fig. 3.** Diversity dynamics of Ordovician–lowermost Silurian conodonts, events and sequences of different magnitudes recognized in the northern Baltic region. The stratigraphic chart, including time slices of Webby et al. (2004), is given in accordance with Nölvak et al. (2006). Stage slices after Bergström et al. (2009). Roman numbers to the right of the diversity curve of genera: characteristic intervals of diversity changes discussed in the text. Basal Tremadoc, Basal Arenig, Basal Llanvirn and Basal Caradoc events after Barnes et al. (1996); Mid-Caradoc Event after Männik (2004); End-Ordovician Event after Kaljo et al. (2011) (the Upper Asgill event *sensu* Barnes et al. (1996) corresponds to its upper part); Sandvika Event after Aldridge et al. (1993). Black arrows to the right of the supersequences indicate the sequence boundaries (vertical ruling) corresponding to regional gaps and characterized, as a rule, by increased input of terrigenous material into the basin. Supersequences: O s-sq. 1 = Varangu–Volkhov; O s-sq. 2 = Kunda–Kukruse; O s-sq. 3 = Haljala–Oandu; O s-sq. 4 = Oandu–Porkuni.  $E_{Di}$  = extinction rate,  $O_{Di}$  = origination rate.

different ideas about the timing of the Early Ordovician diversity peak in the conodont succession. According to Albanesi & Bergström (2004), global conodont species total diversity in the Lower Ordovician exhibits its first peak in the *communis–elegans* interval (in the *elegans* Zone) and reaches a maximum in the *spinuosa–suecicus* interval (in the *suecicus* Zone). A small drop in total species diversity occurs in the uppermost Lower Ordovician, in the *andinus–evae* interval (in the *evae* Zone). Generic total diversity follows a similar trend. Sheets et al. (2011) suggested an almost identical diversity pattern when analysing conodont data from Baltoscandia. In addition to the data (some of it) used by us in this study, Sheets et al. (2011) included information from outcrop sections from southern Sweden, Norway and westernmost Russia.

The total species diversity trend in the *manitouensis–deltifer* to *andinus–evae* interval (in the *deltifer–evae* zones) as indicated by Albanesi & Bergström (2004) fits quite well with our data. Also in the northern Baltic region total species diversity increases almost continuously up to the *evae* Zone (Fig. 3). However, higher in the section our data suggest a different pattern of conodont diversification. According to Albanesi & Bergström (2004), after a small decline in the *evae* Zone species diversity continues to increase rapidly and reaches a maximum in the lower Darriwilian (in the *crassus–suecicus* zones). Sheets et al. (2011) state that these peak values of conodont diversity were reached somewhat earlier, in the lowermost Darriwilian. Higher in the succession, conodont diversity decreases gradually up to the top of the Ordovician. Our data indicate that after a maximum in the *evae* Zone, total species diversity in the northern Baltic region dropped rapidly in the *triangularis–navis* zones, continued to decrease higher in the succession and reached a minimum in the *crassus* Zone. This level of low diversity values in our curve almost correlates with the level of maximum values indicated by Albanesi & Bergström (2004) and Sheets et al. (2011). The data from the northern Baltic suggest that in the *norrlandicus–crassus* zones the disappearance (extinction) of taxa dominated.

Our results fit better with the diversity trends described by Sweet (1985), based on data all over the world. According to him, after a peak in the early Arenig (= Floian) which ‘...was not to be rivalled or exceeded at any subsequent stage in their history...’ (Sweet 1985, p. 488) the species-level diversity of conodonts decreased up to the end of the Whiterockian, i.e. up to the early Sandbian (= Kukruse time). Moreover, the decline in diversity detected by Sweet (1985) was not continuous but his diversity curve demonstrates a distinct increase in the Llanvirn–Llandeilo interval (in the Darriwilian

according to modern terminology), following a minimum in the topmost Arenig (in the upper Dapingian–lowermost Darriwilian). Both of these trends can be established on the basis of our data. The late Dapingian–early Darriwilian diversity minimum recognized by Sweet (1985) evidently corresponds to the upper Volkhov–lower Kunda low-diversity interval in the northern Baltic and the Darriwilian increase to the high-diversity interval in the upper Kunda to Uhaku stages (Fig. 3). Additionally, Sweet (1985) results indicate a similar gradual increase in conodont diversity starting from the Sandbian (from the lower Caradoc *sensu* Sweet) up to the beginning of the End-Ordovician Extinction Event, as do our data.

More generalized data from the Baltic basin (Hammer 2003) fit well with the results of Albanesi & Bergström (2004) in the Lower and Middle Ordovician interval but are similar to ours in the Upper Ordovician. According to Hammer (2003), the maximum of the mean standing conodont species diversity occurred near the Arenigian–Llanvirnian boundary, in the lower Darriwilian according to modern terminology (Hammer 2003, fig. 3D). This is higher in the succession than the maximum diversity values recognized in the northern Baltic and correlates with the low-diversity interval in the *variabilis–anti-variabilis* and *crassus* zones but seems to fit with the maximum in the *spinuosa–suecicus* interval *sensu* Albanesi & Bergström (2004).

Recently, data about Lower to Middle Ordovician (Tremadocian to Darriwilian) conodont diversity from the southeastern margin of the Yangtze Platform (China) were published (Wu et al. 2010a, 2010b). The diversity trends of conodonts discussed by these authors are very similar to those recognized by us in the same stratigraphic interval in the northern Baltic. In both regions the diversity increases continuously from the *deltifer* Zone below, reaches its maximum in the *evae* Zone and decreases rapidly above this level. However, in Central China the diversity minimum which follows its maximum in the *evae* Zone seems to occur somewhat earlier than in our region: in the *norrlandicus* Zone (Wu et al. 2010b). In both regions the interval above this minimum up to the *anserinus* Zone is characterized by higher conodont diversity, which is more variable in Central China than in the northern Baltic. However, also in this interval the peaks occur at different levels in these two regions.

The differences between the diversity trends based on our data and those published earlier may have several explanations. Differences between diversity trends based on our data and those by Albanesi & Bergström (2004) may result from the stratigraphic framework (the units for which the ranges of taxa were generalized) used. Our stratigraphic framework is of higher resolution than

that used by Albanesi & Bergström (2004). This is particularly evident in the Middle Ordovician where two intervals used by Albanesi & Bergström (2004) correspond to seven units in our data base. The lower Middle Ordovician is also the interval where the diversity trends recognized have the greatest differences. Also, Albanesi & Bergström (2004) analysed data available from all over the world, covering, in that way, a considerably wider range of environments than we did. Hammer (2003) as well as Sheets et al. (2011) analyses are based on data from Baltoscandia in general. The material used by these authors also cover wider areas than ours, hence, a wider range of environments and potentially more different faunas are included. Our data come from the same basin, but only from its northern part. Including data from a wider variety of environments adds to the number of taxa and, accordingly, also to diversity (e.g. Wall et al. 2009). However, the results of Sweet (1985) analysis, based on global data, i.e. on data from even a wider range of environments, fit much better with our results than with those by Hammer (2003) and Sheets et al. (2011), based on the information from the Baltic Palaeobasin only. Also, some special studies indicate that sampling proxy and diversity are in good correlation, i.e. the more samples from an interval are available for study, the more taxa you will find (Lloyd et al. 2011). The number of samples used by us is indicated in Fig. 3. Unfortunately, no such data are available in earlier publications.

All the biases listed above may have had affected the results of our diversity studies but we think that, before assessing the effect of any of them, one serious problem related to (all) published earlier diversity analyses should be resolved: reliability of the data used. It is well known that there is much subjectivity in taxonomy, and identifications made by different authors (but also by the same author at different times), as a rule, are not directly comparable without restudying collections. For that reason analyses based on lists of taxa may provide problematic results. Detailed analyses require very careful checking of basic data: at least one specialist should restudy all collections to be used and check and update (if needed) the identifications of taxa to guarantee taxonomic consistency in the data to be analysed. Considering the data from the northern Baltic used in the papers referred to above, we see that this work has not been done.

### Changes in conodont diversity and sedimentary succession

An interesting question is how, if at all, the diversity trends recognized in the conodont succession in the

northern Baltic are related to the changes in the sedimentary succession and basin evolution in that region. Might the variations recognized in conodont diversity be controlled by sea level changes? Four transgressive–regressive macrocycles (= sequences) have been described for the northern Baltic Ordovician succession (Nestor & Einasto 1997). All of these sequences are bounded by major gaps in deposition in the proximal part of the basin and, evidently, are of eustatic origin. During sea level lowstands, marking the sequence boundaries, input of terrigenous material into the basin increased, forming interbeds rich in quartz silt and/or fine-grained sand. Duration of these sequences is highly variable, from 4–5 Ma to 8–11 Ma (according to the ICS website). As the ranking of sequences is highly subjective and depends on the architecture of a particular succession (e.g. Miall 2000), and considering the data by Harris et al. (2005), all these sequences (macrocycles *sensu* Nestor & Einasto 1997) are treated as supersequences in this paper. Stratigraphically, the supersequences are tentatively named as (from the oldest) the Varangu–Volkhov, Kunda–Kukruse, Haljala–Oandu and Oandu–Porkuni supersequences. In Fig. 3 they are indexed as (also from below) O s-sq. 1, O s-sq. 2, O s-sq. 3 and O s-sq. 4. However, to recognize systems tracts in these supersequences, further detailed sedimentological analysis of the Ordovician succession in the Baltic is needed.

More detailed sequences for the Ordovician of the northern Baltic were proposed by Dronov & Holmer (1999) (an updated version in Dronov et al. 2011), and for the upper part of the succession also by Harris et al. (2004). Dronov & Holmer (1999) distinguished ten sequences (14 in Dronov et al. 2011), considered to represent third-order cycles of relative sea-level change in the sense of Vail et al. (1977). Harris et al. (2004) analysed the upper Katian to Hirnantian (upper Nabala to Porkuni stages) interval and recognized eight sequences. The uppermost Ordovician sequence (O8; corresponds to the Saldus Formation) *sensu* Harris et al. (2004) was later reinterpreted as the lowstand systems tract of the lowermost Silurian sequence (S1 in Harris et al. 2005). Correlation between these different sets of sequences is indicated in Fig. 3.

Our studies demonstrate that a general correlation exists between diversity changes in the conodont succession and the main stages in basin evolution for the northern Baltic (Fig. 3). In relation to the supersequences, diversity changes recognized by us follow a pattern similar to that described, e.g., by Leckie & Olson (2003) and by Wakefield (2003). According to these authors, the diversity of fossils in general is lowest at the sequence boundary, increases during transgression (transgressive systems tract), reaches maximum values

at the maximum flooding surface and decreases gradually during the highstand systems tract. All boundaries (boundary intervals) between supersequences in our succession are characterized by low diversity values. Diversity increases more or less rapidly in the lower, transgressive parts of the supersequences and decreases again in their upper parts. Such changes are particularly distinct in the Varangu–Volkhov, Kunda–Kukruse and Oandu–Porkuni supersequences but also in the lowermost Silurian supersequence (in S1 *sensu* Harris et al. 2005). The Varangu–Volkhov supersequence in general corresponds to the interval studied by Wu et al. (2010a), who also noted a good correlation between variations in conodont diversity and sea level changes. The diversity acme in the *evae* Zone correlates with the ‘*evae* drowning event’ *sensu* Nielsen (2004). In the Haljala–Oandu supersequence changes in diversity are small, but still species diversity values are somewhat higher in the middle part of the sequence. From above it is evident that based on generalized distribution data and in comparison with large-scale sequences (cycles), Ordovician conodont faunas in the northern Baltic seem to respond to the depositional processes in the same way as faunas from younger strata (e.g. in the Mesozoic and Cenozoic: papers in Olson & Leckie 2003).

No specific correlation seems to exist between our generalized diversity data and sequences proposed by Dronov & Holmer (1999), Dronov et al. (2011) and Harris et al. (2004, 2005). The only exception is the Kegel sequence *sensu* Dronov & Holmer (1999), but this is understandable because it corresponds to our Haljala–Oandu supersequence.

As noted above, the boundaries of the Ordovician supersequences in the northern Baltic correspond to major gaps in the succession. In the conodont succession all these boundaries correspond to low-diversity intervals following a distinct diversity decline (extinction) of faunas (Fig. 3). Barnes et al. (1996) recognized five high-order global bioevents, namely the Basal Tremadoc, Basal Arenig, Basal Llanvirn, Basal Caradoc and Upper Ashgill bioevents. According to them, these events are related to significant eustatic sea level lowstands. All events are characterized by extinctions but some of them are overshadowed by a rapid innovation event with a radiation of a more diversified fauna. Most of the events described by Barnes et al. (1996) are easy to recognize in the northern Baltic. They lie close to the boundaries between our supersequences (Fig. 3). An exception is the Basal Arenig Bioevent. However, its reflection in our succession might be the small drop in total conodont species and genus diversity recognized in the *elegans* Zone. The Basal Tremadoc Bioevent *sensu* Barnes et al. (1996) is not well represented in

our data due to gap(s) in the Cambrian–Ordovician transition, and sporadic occurrence of strata of this age, in the northern Baltic. But several new apparatus types and conodont lineages appear in this interval also in the northern Baltic. The Basal Llanvirn, Basal Caradoc and Upper Ashgill bioevents *sensu* Barnes et al. (1996) all correlate with a level close to a supersequence boundary in our succession, indicating that at least these gaps resulted from global sea level lowstands. Additionally, a distinct extinction event in the conodont succession, the Mid-Caradoc Event, is recognized in the interval from the ‘Uppermost *alobatus* range’ to the *ventilatus* Zone (Männik 2004). This event was also directly followed by a sea level lowstand which resulted in a major gap in the succession (Fig. 3; Nestor & Einasto 1997).

## CONCLUSIONS

The diversity of Ordovician–lowermost Silurian conodont faunas in the northern Baltic is highly variable. Based on general trends in diversity changes, four intervals with characteristic features can be recognized: (1) the *proavus*–*crassus* zones and (2) the *crassus*–*anserinus* zones forming distinct diversity cycles, (3) the *variabilis*–*ventilatus* zones, characterized in general by low diversity values and (4) the *ventilatus* Zone–the topmost Ordovician, with quite stable increase in diversity up to the *ordovicicus* Zone, followed by its decline during the End-Ordovician Extinction Event.

Diversity was lowest in the earliest and latest Ordovician but reached maximum values at the end of the Early Ordovician radiation of conodonts, in the middle–upper Darriwilian, and just before the start of the End-Ordovician Extinction Event.

Four supersequences, separated by regional gaps, can be recognized in the northern Baltic Ordovician succession. Certain correlation between these supersequences and diversity variations exist in the conodont succession, suggesting that changes in sea level affected the composition of faunas in the basin in the same way: all boundaries between supersequences are characterized by low species diversity values, diversity increases more or less rapidly in the lower, transgressive parts of the supersequences and decreases again in their upper, regressive parts.

And, finally, we would like to stress that, although there occur many biases influencing the results of diversity analyses of faunas, the most important factor is the reliability of the data to be analysed. Comparison of lists of taxa instead of real faunas should be avoided.

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## Ordoviitsiumi konodontide mitmekesisus Põhja-Baltikumis

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Konodontide mitmekesisus läbilõikes on muutlik. Kuigi selgeid tendetse arvukuse muutustes ei ilmne, võib siiski eristada nelja iseloomulikku intervalli: (1) *proavus*'e–*crassus*'e tsoonid ja (2) *crassus*'e–*anserinus*'e tsoonid moodustavad kaks mitmekesisuse rütmi; (3) *variabilis*'e–*ventilatus*'e tsoonidele on iseloomulik üldiselt madal fauna mitmekesisus; (4) intervallile *ventilatus*'e tsoonist kuni Ordoviitsiumi lõpuni on iseloomulik mitmekesisuse pidev kasv intervalli alumises pooles ja langus selle ülemises pooles. Konodontide mitmekesisuse muutuste ja läbilõikes fikseeritud kõrgemat järku sedimentatsioonitsüklite vahel on märgatav teatud korrelatsioon: konodontide mitmekesisus kasvab tsüklite alumistes ning langeb nende ülemistes osades, madalaim on mitmekesisus tsüklitevaheliste piiride intervallides.