

CONVENTIONAL AND CONOP9 APPROACHES TO BIODIVERSITY OF BALTIC ORDOVICIAN CHITINOZOANS

O. Hints, J. Nölvak, L. Paluveer and M. Tammekänd

Institute of Geology at Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia.
Olle.Hints@gi.ee

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INTRODUCTION

Chitinozoans are organic-walled microfossils, probably eggs of cryptic marine metazoans that were common and diverse from the Early Ordovician through Devonian times (Grahn and Paris, 2011). Chitinozoans have proved to be among the most useful index fossils for this time span (e.g., Nölvak and Grahn, 1993; Webby et al., 2004) and their diversification history has been discussed by several authors (e.g., Paris and Nölvak, 1999; Paris et al., 2004; Grahn and Paris, 2011).

With respect to Ordovician chitinozoans, the Baltic region stands out with excellent preservation, good stratigraphical coverage and some of the largest collections in the world (Paris et al., 2004). The first diversity curves of Baltic Ordovician chitinozoans were published by Kaljo et al. (1996), studying material from a single drill core. Based on the entire Baltic collection, the diversity patterns of Ordovician chitinozoans were summarised by Nölvak in Paris et al. (2004). Using the latter Baltic curve, alongside with those from other regions, Achab and Paris (2007) argued about possible driving mechanisms behind the chitinozoan diversification, highlighting climatic, paleogeographic and paleo-oceanographic factors. More recently the diversity of Baltic Ordovician chitinozoans was discussed by Hints et al. (2010).

All these paleobiodiversity studies have been based on a temporal framework of regional stages, subdivisions thereof, or time slices such as those defined by Webby et al. (2004). Diversity curves using different time scales and data sets are often difficult to compare. A time scale that is too coarse, may also obscure the details of biodiversity patterns and the underlying environmental, climatic and paleogeographic signals.

In order to increase stratigraphical resolution of the hitherto available chitinozoan biodiversity curve and get more reliable estimation of the standing diversity in the Baltic Ordovician, we herein use quantitative stratigraphic approach based on CONOP9 software (Sadler and Cooper, 2003 and references therein). This tool has proved very efficient in reconstructing successions of biostratigraphical events for a large number of taxa and sections. The resulting best fit composite sequence can be used both as a time-scale, and as a basis for biodiversity curves. We aim to compare the CONOP9-derived results with those produced by a more conventional stage-based approach. As a lot of new material on Ordovician

chitinozoans has emerged from Estonia since the compilation of the data base for the IGCP410 compendium (Paris et al., 2004), we also aim to improve the previously published diversity curves.

MATERIALS AND METHODS

This study is based on collections of Mid to Late Ordovician chitinozoans from nine localities in Estonia (Fig. 1): the Kerguta, Männamaa, Mehikoorma, Ruhnu, Taga-Roostoja, Tartu, Valga and Viki drill cores (see Nõlvak 2010 and references therein), and the Uuga cliff section (see Tammekänd et al., 2010). These localities represent near-shore to deeper shelf carbonate facies of the eastern part of the Baltoscandian Palaeobasin (Fig. 1).

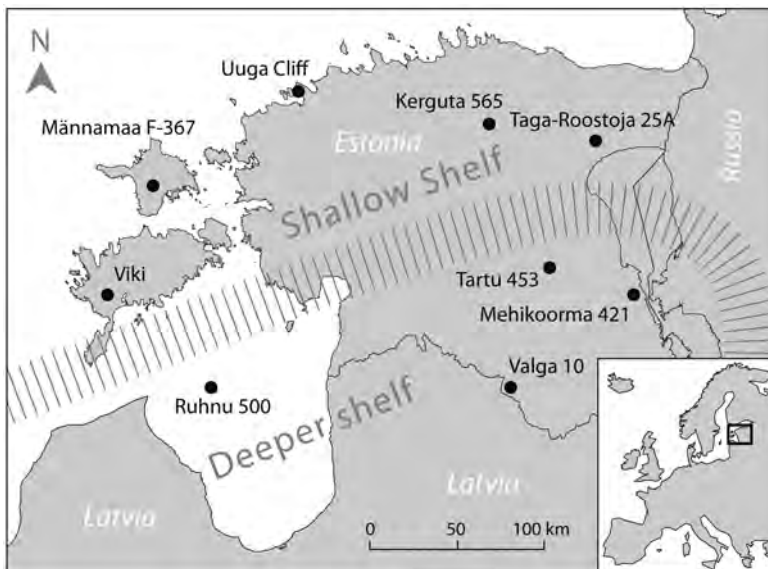


Figure 1. Locality map and broad scale facies patterns in the eastern Baltic.

The chitinozoans were extracted from limestone and marl samples, usually 100-500 g in size (depending on average yield), using digestion in acetic acid. Altogether, the data set consists of 1079 productive samples and 8565 occurrence records of 166 taxa, of which 145 species were included in the analysis (the other 21 being only genus-level or doubtful identifications). Species currently under open nomenclature were included in the data set. The vast majority of hitherto known Baltoscandian chitinozoan species were identified in the localities studied. Moreover, as the differences between chitinozoan faunas of Estonia, Latvia, Lithuania, Poland and Sweden are small, the current data set can be considered representative for the entire region. The Lower Ordovician, where the first chitinozoans are recorded, is not included in the current analysis, and lower Middle Ordovician and uppermost Ordovician are less completely covered, leaving possibilities for future improvement of the data set.

The general stratigraphical framework is based on Baltic regional stages (Nõlvak et al., 2006) with reference to time slices of Webby et al. (2004). Usage of diversity measures follows Cooper (2004). Total diversity (TD) is the number of species recorded from a time interval. Normalised diversity (ND) is the sum

of species that range from the interval below and above, plus half the number of species that appear and/or disappear within the time interval. Additionally the balanced total diversity (BTD) of Paris et al. (2004) is discussed, which is similar to ND, except that a full score is given to species that are confined to the time slice. All these measures are used to estimate the mean standing diversity (MSD).

For the CONOP9 analysis, as well as for the stage-based approach, all occurrences of all species were entered into Excel spreadsheets and then transferred to a custom-built SQL database. The database records were carefully checked for taxonomic inconsistencies and other potential errors. In order to enhance the CONOP9 composite sequence, the Kinnekulle K-bentonite at the base of the Keila Regional Stage was included where present. From the database, the data files in CONOP9 format were generated automatically, then sorted using the CONSORT utility and analysed with CONOP9 program (version 7.61 of July 5, 2009, courtesy of P. Sadler). Tests were run with different configuration options; rather consistent results were produced with 1500 steps and 500 trials using level penalty. The diversity curve is derived from the running FADs minus LADs along the composite sequence. For full explanation and examples of using CONOP9 software see Sadler and Cooper (2003).

RESULTS

Conventional approach

The results of the conventional stage-based approach to the diversity of Baltic Ordovician chitinozoans are illustrated in Fig. 2. The curves of TD and ND generally run parallel, the TD showing on average 7 more species per stage, and the BTD running in between. The highest diversity increase is observed in the Kunda and Aseri stages, lower to middle Darriwilian, where 31 and 36 species are recorded, respectively. It should be added, however, that the Volkhov Stage (most of the Dapingian) is poorly represented in the sections studied due to dolomitisation or redbeds and thus the increase from Volkhov to Kunda may, in fact, be more gradual. The increase continues in the Lasnamägi Stage, where the peak TD value of 41 and ND of 33.5 are recorded. Slightly lower diversity is observed in the Uhaku Stage, followed by a diversity peak in the lowermost Upper Ordovician Kukruse-Haljala interval, where a TD of 46 and a ND of 34 are recorded — the highest values for the Baltic Ordovician. It is worth noting that in this interval the discrepancy between TD, ND and BTD is the highest and TD shows increasing trend whilst ND and BTD reflect a slight diversity drop from Kukruse to Haljala. A significant decline begins in the Keila Stage, close to the Sandbian-Katian boundary, where 37 species are recorded (ND 27.5). A decreasing trend is characteristic of the rest of the Ordovician, with two minor positive shifts in the TD curve in the Nabala and Pirgu stages. The ND curve is slightly different with a low in the Oandu Stage and a minor peak in the Rakvere-Nabala interval (Fig. 2). The Hirnantian extinction is marked by the decrease of TD by 13 species, corresponding to 50% loss, from the Pirgu to Porkuni Stage. Only a low diversity assemblage crossed the Ordovician-Silurian boundary. Few data available from the lowermost Silurian reveal a very low diversity chitinozoan fauna, which is in agreement with Nestor (2009).

CONOP9 model

The diversity curve based on CONOP9 composite sequence has much higher resolving power and probably can be considered as the best achievable approximation of the standing diversity (SD), without

the usual binning problems of the conventional approach. It should also be noted that the CONOP9 curve is independent of the stage-based time scale and dating problems. This, in turn, means that the two curves presented on Fig. 2 cannot always be correlated precisely. With different model runs the maximum species richness estimate was between 35 and 37. Small fluctuations of 1-2 species, appearing at different levels, represent methodological uncertainty rather than true events.

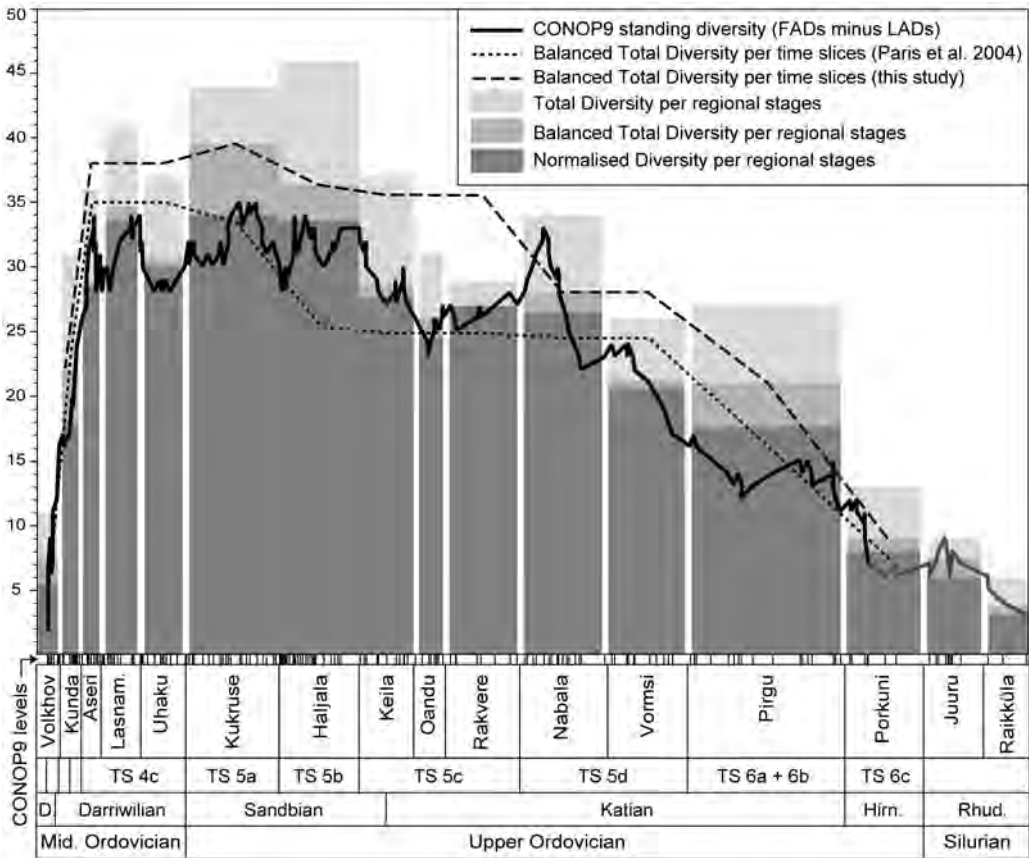


Figure 2. Diversity of Baltic Ordovician chitinozoans as revealed by the conventional stage-based approaches (TD, ND and BTS) and CONOP9 model. The CONOP9 composite sequence was fitted to regional time scale using ranges of selected chitinozoan species. White areas between the "stage bars" indicate that precise calibration of the CONOP9 composite against the stages was not possible. Two BTS curves based on the time slices of Webby (2004) are included: one using the current data set and the other redrawn from Nölvak in Paris et al. (2004). The horizontal scale corresponds to the average composite sequence of the CONOP9 model reflecting thickness rather than a regular time scale. Abbreviations: TS, time slice; D., Dapingian, Hirn., Hirnantian; Rhud., Rhuddanian.

A rapid diversity increase occurs in the Volkhov to Aseri stages, where the values reach to about 34 (Fig. 2). A slight decline is observed close to the Aseri-Lasnamägi boundary, possibly resulting from insufficient data. This is followed by a high diversity interval and another decline, both within the *Conochitina clavaherculi* range, which corresponds to the upper Lasnamägi and lower Uhaku strata. The Uhaku Stage is characterised by a relatively lower diversity, below 30 species, followed by an increasing

trend in the succeeding Kukruse Stage, where the maximum of about 35 species is met. In the upper Kukruse and lower Haljala strata another diversity low with less than 30 species is observed. However, the Haljala Stage, in general, has a rather high diversity. The lower boundary of the Keila Stage is precisely dated based on the widespread Kinnekulle K-bentonite. Starting from this level, the diversity starts to decline, and only about 25 co-existing species are recorded in the Oandu stage. The Rakvere Stage is characterised by a slightly increasing trend and a rather conspicuous diversity peak is recorded in the Nabala Stage, coinciding with the lower part of *Armoricochitina reticulifera* range. Subsequently further lowering of the diversity is observed, falling below 20 in the Vormsi, below 15 in the Pirgu, and below 10 in the Porkuni Stage. In the topmost Ordovician and lower Silurian the model is not well-constrained due to too few overlapping species and insufficient number of sections studied.

DISCUSSION AND CONCLUSIONS

The CONOP9 modeled diversity curve reflects the same general trends as the conventional stage-based approach (Fig. 2), but reveals also some differences and some features that were not evident in the latter.

From the methodological point of view it should be noted that the CONOP9 curve runs closest to the ND curve of the stage-based approach. The TD, on the other hand, clearly overestimates the MSD in most cases, as shown also by Cooper (2004). Similarly, the balanced total diversity (BTD) of Paris et al. (2004) tends to overestimate MSD, especially in longer time slices (Fig. 2).

A rapid diversification of chitinozoans from the Volkhov to Aseri stages is unveiled by both approaches. According to Achab and Paris (2007), a similar radiation event is recorded on other paleocontinents, probably driven by intrinsic factors, as suggested by the great number of morphological innovations that appeared during the Darriwilian.

The following biodiversity pattern appears slightly differently in conventional and CONOP9 curves. The stage-based approach suggests that the chitinozoan fauna reached the highest diversity during the Kukruse-Haljala interval. The CONOP9 curve, on the other hand, shows that rather similar maximum values were characteristic to the entire Aseri-Haljala interval. According to estimations by Kaljo et al. (1996) and Webby et al. (2004), the Aseri, Lasnamägi and Uhaku stages are notably shorter in duration than Kukruse and Haljala stages. Thus, the TD and ND peaks in the latter stages may merely represent "binning bias" and the CONOP9 curve likely provides more appropriate MSD estimation here. Several small scale diversity fluctuations revealed in the CONOP9 curve need further examination. However, the diversity low in the Uhaku Stage is documented also by the stage-based approach as well as by Kaljo et al. (1996).

A general diversity decline established by both approaches starts in the Keila Stage, at the Sandbian-Katian boundary. This interval coincides with the beginning of changes in regional environmental settings evidenced by first tropical carbonates and reefs, increased facies differentiation, increased variation in carbon isotope composition, and a general biotic change (Kaljo et al., 2011). The chitinozoan diversity was particularly low in the Oandu and Rakvere stages (the "Oandu crisis" according to Kaljo et al., 1996). Here it is important to stress good correspondence between the CONOP9-modeled and stage-based curves indicating that certain correlation problems have not affected per-stage calculations (but note that occurrences with ambiguous stratigraphy were omitted from the stage-based curves).

Following the Oandu crisis, a conspicuous peak in the CONOP9 curve, reaching 33 species in the lower Nabala Stage (Fig. 2), deserves further attention. In the binned TD curve this peak is less prominent, and entirely absent in the ND curve (Fig. 2). This short-lived diversity peak on the generally falling Katian trend

is probably related to temporarily improved environmental conditions for chitinozoans. Such interpretation is supported by the elevated concentration of phosphorus in the lower part of the Nabala Stage (Kiipli et al., 2010), which might have had positive effect on bioproduction and food supply for chitinozoans. The deeper shelf Mõntu Formation (lower Nabala Stage) is also rich in glauconite, which, together with elevated phosphorus concentration, may imply a regional upwelling event. An upwelling of presumably colder water masses might have had positive effect also through dropped water temperatures on the shelf – it has been shown by Vandenbroucke et al. (2010) that chitinozoans seem to thrive in high latitude (i.e. colder) regions.

Subsequently, the chitinozoan diversity continued to decline, with small positive peaks in the Vormsi and upper Pirgu stages revealed by the CONOP9 approach. By the Hirnantian (Porkuni Stage), the chitinozoan fauna was already strongly impoverished in Baltica and few species continued into the Silurian. According to Nestor (2009), the diversity of Silurian chitinozoans started to increase only in the late Aeronian.

The previous analyses of biodiversity of Baltic Ordovician chitinozoans are limited in number. As discussed above, the currently revealed trends fit well with those of Kaljo et al. (1996), even though the latter authors reported lower total numbers (maximum TD value of 29). The BTM data of Nõlvak in Paris et al. (2004; reproduced by Achab and Paris, 2007 and Hints et al., 2010), show a different pattern, which is partly due to the use of longer time bins. In order to facilitate comparison, the current data were also recalculated into time slices of Webby et al. (2004). The resulting curve (Fig. 2) still shows some differences from Nõlvak in Paris et al. (2004) curve, particularly in time slices 5b and 5c, where notably higher diversity is now recorded. To some extent this discrepancy could be explained by improved data and inclusion of open nomenclature species. Nonetheless, the diversity decline from the Kukruse (TS 5a) to Haljala (TS 5b) indicated by Nõlvak in Paris et al. (2004) seems to gain little support from the current data set – the new TS-based curve shows a major decrease in the Nabala Stage.

It should be stressed, however, that both curves based on time slices fail to resolve the Keila decline, the "Oandu crisis" and the peak in the Nabala Stage, which are prominent on the CONOP9 curve and evident on regional time scale. It follows that a global stratigraphic framework, such as that of Webby et al. (2004), is too generic to document at least regionally important bioevents. Although the new TS-based BTM curve is more accurate than the one discussed by previous authors (Paris et al. 2004, Achab and Paris 2007, Hints et al. 2010), higher temporal resolution is needed to reveal timing and driving factors of the diversification process.

In summary we conclude that the presented data set, albeit only from nine sections, is currently the best coherent data source for assessing biodiversity of Baltic late Mid to Late Ordovician chitinozoans. The CONOP9 model proved to fit well with the empirical data on chitinozoan distribution. The resulting composite sequence provides a valuable addition to the conventional paleobiodiversity approach and represents probably the best possible proxy for standing diversity.

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REFERENCES

- Achab, A. and Paris, F. 2007. The Ordovician chitinozoan biodiversification and its leading factors. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 245, 5-19.
- Cooper, R.A. 2004. Measures of Diversity. In B.D. Webby, M. Droser, F. Paris and I. Percival (eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 52-57.
- Grahn, Y. and Paris, F. 2011. Emergence, biodiversification and extinction of the chitinozoan group. *Geological Magazine*, 148, 226-236.
- Hints, O., Delabroye, A., Nölvak, J., Servais, T., Uutela, A. and Wallin, Å. 2010. Biodiversity patterns of Ordovician marine microphytoplankton from Baltica: Comparison with other fossil groups and sea-level changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 294, 161-173.
- Kaljo, D., Hints, L., Hints, O., Männik, P., Martma, T. and Nölvak, J. (2011, in press). Katian prelude to the Hirnantian (Late Ordovician) mass extinction: a Baltic perspective. *Geological Journal*, 46.
- Kaljo, D., Nölvak, J. and Uutela, A. 1996. More about Ordovician microfossil diversity patterns in the Rapla section, northern Estonia. *Proceedings of the Estonian Academy of Sciences*, 45, 131-148.
- Kiipli, E., Kiipli, T., Kallaste, T. and Ainsaar, L. 2010. Distribution of phosphorus in the Middle and Upper Ordovician Baltoscandian carbonate palaeobasin. *Estonian Journal of Earth Sciences*, 59, 247-255.
- Nestor, V. 2009. Chitinozoan diversity in the East Baltic Silurian. *Estonian Journal of Earth Sciences*, 58, 311-316.
- Nölvak, J. 2010. Distribution of Ordovician chitinozoans. In A. Pöldvere (ed.), *Viki drill core. Estonian Geological Sections Bulletin*, 10, 17-18.
- Nölvak, J. and Grahn, Y. 1993. Ordovician chitinozoan zones from Baltoscandia. *Review of Paleobotany and Palynology*, 73, 245-269.
- Nölvak, J., Hints, O. and Männik, P. 2006. Ordovician timescale in Estonia: recent developments. *Proceedings of the Estonian Academy of Sciences, Geology*, 55, 95-108.
- Paris, F., Achab, A., Asselin, E., Xiao-hong, C., Grahn, Y., Nölvak, J., Obut, O., Samuelsson, J., Sennikov, N., Vecoli, M., Verniers, J., Xiao-feng, W. and Seeto, T. W. 2004. Chitinozoans. In B.D. Webby, M. Droser, F. Paris and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 294-311.
- Paris, F. and Nölvak, J. 1999. Biological interpretation and paleobiodiversity of a cryptic fossil group: the "chitinozoan animal". *Geobios*, 32, 315-324.
- Sadler, P.M. and Cooper, R.A. 2003. Best-Fit Intervals and Consensus Sequences. In *High-Resolution Approaches to Stratigraphic Paleontology*. Kluwer Academic Publishers, Dordrecht, Boston, Paris, 49-94.
- Tammekänd, M., Hints, O. and Nölvak, J. 2010. Chitinozoan dynamics and biostratigraphy in the Vao Formation (Darriwilian) of the Uuga Cliff, Pakri Peninsula, NW Estonia. *Estonian Journal of Earth Sciences*, 59, 25-36.
- Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Paris, F., Sabbe, K., Zalasiewicz, J.A., Nölvak, J. and Verniers, J. 2010. Epipelagic chitinozoan biotopes map a steep latitudinal temperature gradient for earliest Late Ordovician seas: Implications for a cooling Late Ordovician climate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 294, 202-219.
- Webby, B.D., Cooper, R.A., Bergström, S.M. and Paris, F. 2004. Stratigraphic Framework and Time Slices. In B.D. Webby, M. Droser, F. Paris and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 41-47.