

Chitinozoan diversity in the East Baltic Silurian

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Abstract. Data on the diversity of the East Baltic Silurian chitinozoans have been compared to global chitinozoan biozones that are approximately correlated with the graptolite scale. The total diversity and balanced total diversity curves have three main positive peaks in the Wenlock and Ludlow and diversity lowstands in most of the Llandovery and Pridoli. The turnover ratio and species origination curves are lowest and species extinction is highest in the lower Wenlock, correlating partly with the Ireviken Event. Chitinozoan diversity is related to the transgression–regression phases of the Silurian Baltic basin, water chemistry and temperature, and evolutionary processes of the faunal group. At the level of the Silurian standard stages the trends in the East Baltic and Swedish chitinozoan diversity curves are in general outline similar to the global diversity curve.

Key words: Silurian, East Baltic, chitinozoans, diversity.

INTRODUCTION

The regional dataset, including species diversity, and origination and extinction events of the Ordovician chitinozoans, shows similar patterns in all palaeo-continental plates (Paris et al. 2004). The main feature of chitinozoan diversification is the radiation that began in the earliest Ordovician, developed rather regularly up to the latest mid-Ordovician, and decreased progressively during the Late Ordovician (Paris et al. 2004). A similar trend characterizes East Baltic chitinozoan diversity patterns throughout the Silurian (Fig. 1). The evaluation of physico-chemical factors affecting Ordovician chitinozoan diversity and comparison of the diversification patterns with other benthic and pelagic fossil groups are given by Ahab & Paris (2007).

Kaljo et al. (1995) have discussed the most important Silurian bio-events and compared diversity changes in different groups and regions. The first study of Silurian chitinozoan diversity dynamics in the East Baltic sections revealed considerable changes in diversity (Nestor 1992). In that paper an attempt was made to integrate chitinozoan zonation with the graptolite scale, using graptolite data from the Ohesaare and Ventspils cores (Kaljo 1970; Kaljo et al. 1984; Gailite et al. 1987). Later studies showed, however, that several graptolite biozones are probably missing due to stratigraphic gaps in the East Baltic Silurian sequence, and besides, the precise zonal boundaries are usually indistinct due to insufficient graptolite data (Loydell et al. 1998, 2003). In the present paper the Silurian East Baltic chitinozoan diversity diagram has been linked to the global chitinozoan bio-

zonal succession (Verniers et al. 1995) (Fig. 1), correlating approximately with the graptolite scale (Fig. 2).

DATABASE AND METHODOLOGY

In this review only published materials are used, with the exception of Pridolian species, which are presently under restudy, as preliminary unpublished identifications have already been made. A total of 120 species of 22 genera derived from 2546 samples from the East Baltic drill cores (see, e.g., Nestor 1994, 2003, 2005, 2007, 2009; H. Nestor & V. Nestor 2002; H. Nestor et al. 2003) will be discussed. Most taxa, published in open nomenclature, are excluded. For comparison, chitinozoan diversity data from Gotland (Laufeld 1974), Skåne (Grahn 1996), drill cores of Gotland (Grahn 1995) and mainland of Sweden (Grahn 1998) are considered below.

The diversity diagram (Fig. 1) has been compiled as in Paris et al. (2004). Besides total diversity of species, also balanced (or normalized) total diversity (BTD) is counted. Following Paris et al. (2004), a full score (equal to 1) is given to the species ranging through a whole time slice (biozone in this paper) or in case of short-ranging species to part of it. A half score (equal to 0.5) is given to species having their FAD or LAD within a time slice (biozone) and ranging into the succeeding or preceding time slice (biozone).

The turnover ratio has also been calculated according to Paris et al. (2004): the number of originations, minus the number of extinctions, divided by the BTD recorded in a zone. Extinction events have negative values, while

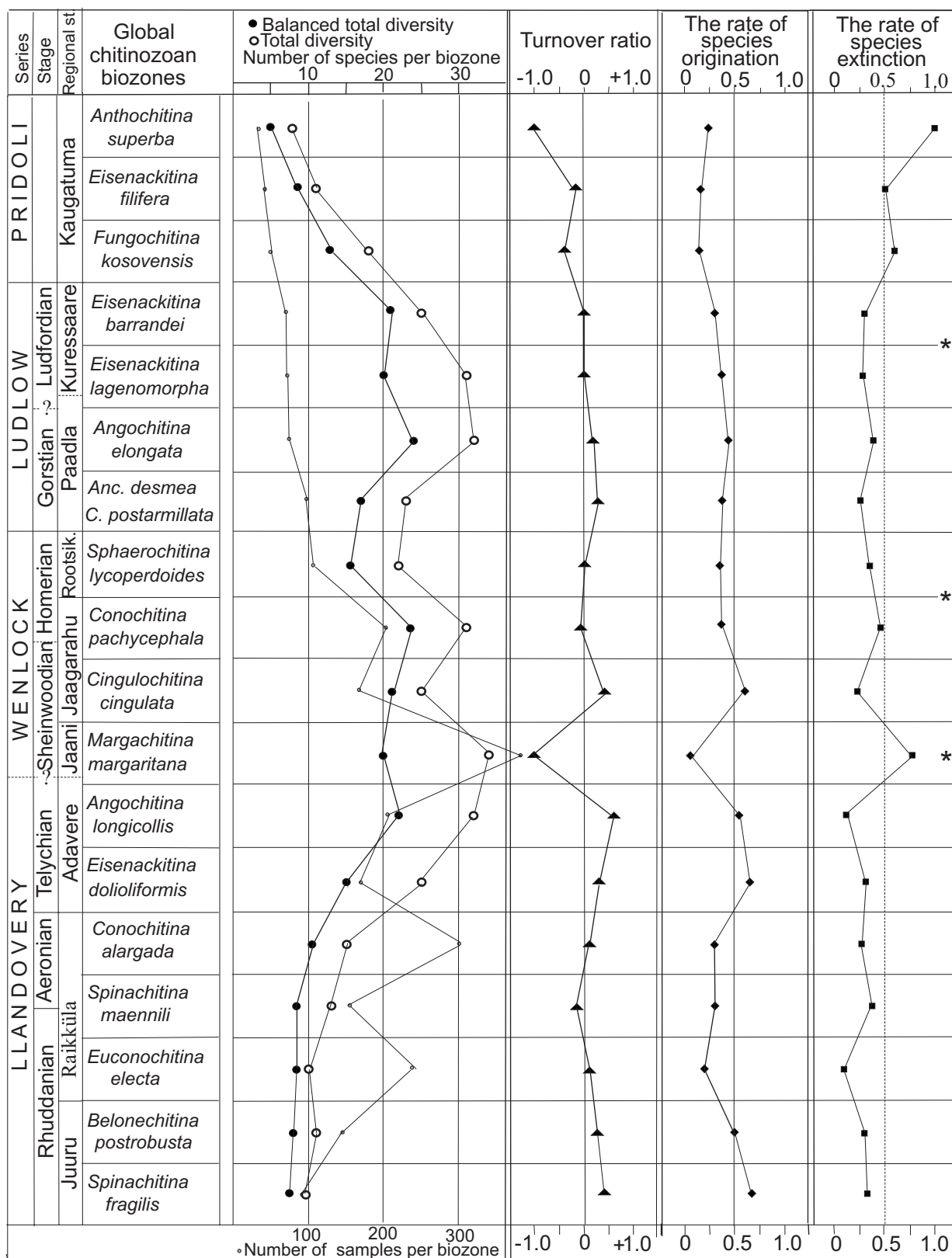


Fig. 1. Biodiversity of the East Baltic Silurian chitinozoans in the global biozones (Verniers et al. 1995). Asterisks show main chitinozoan extinction events. Rootsik., Rootsiküla.

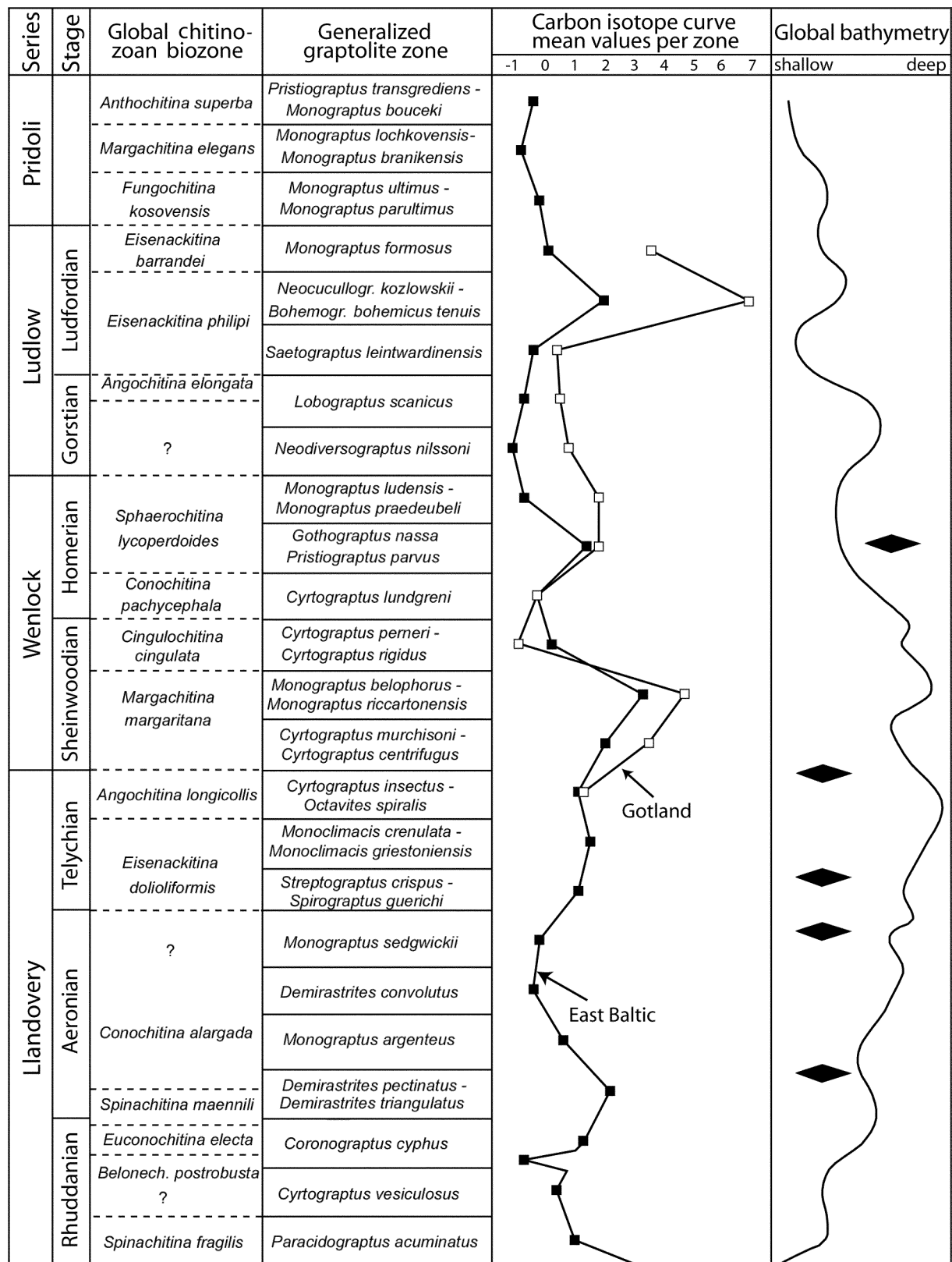


Fig. 2. Correlation of global chitinozoan biozones with generalized graptolite zones, carbon isotope mean values, and the sea-level eustatic curve (according to Kaljo et al. 1998). Black rhombs are Brazilian glaciations (after Grahn & Caputo 1992 and Johnson et al. 1991).

radiation events have positive values. The rates of species origination and extinction are calculated for each biozone by dividing the number of originations or extinctions by the total number of species recorded in the corresponding zone.

TAXONOMIC DIVERSITY AND TURNOVER

As the duration of global chitinozoan biozones, compared with the graptolite scale, is different (Fig. 2), and duration of global stages in millions of years (Fig. 3) is also different, we can speak only about general diversity trends in the chitinozoan succession of the East Baltic sections. The total diversity and BTD curves show a similar trend throughout the Silurian (Fig. 1). Both curves have three main positive peaks, in the *Angochitina longicollis*, *Conochitina pachycephala*, and *Angochitina elongata* biozones. The highest total diversity established in the *Margachitina margaritana* Biozone might be related to the high number of the studied samples (461), but in the other cases (for example *Euconochitina electa* and *Conochitina alargada* biozones) no such dependence of high diversity on the high number of samples was observed. Besides the diversity lowstands in the Rhuddanian and in the upper part of the Pridoli, the most significant fall of diversity is documented at the Wenlock–Ludlow boundary, in the global *Sphaerochitina lycoperdoides* and in the East Baltic *Ancyrochitina desmea* and *Conochitina postarmillata* biozones (Nestor 2007).

It is worth mentioning that the diversity curve of pelagic graptolites (Melchin et al. 1998) reveals a different pattern to that of chitinozoans. Intense radiation of graptolite taxa starts in the Rhuddanian, with a diversity peak in the early Aeronian, and is followed by an overall diversity decline from the early Telychian through the rest of the Silurian (Melchin et al. 1998, fig. 4). Contrary to graptolites, chitinozoan diversity increases from the early Telychian up to the late Homerian. Though, some increase in the diversity of both fossil groups is observed in the late Gorstian. The reason for the different patterns of chitinozoan and graptolite diversity trends is unclear, but the levels of large diversity drops (extinction events) are almost coincident, related to the Ireviken, Mulde, and Lau events (Fig. 1, see also V. Nestor et al. 2002; Nestor 2007, 2009).

The turnover ratio, species origination and extinction curves (Fig. 1) are more or less regular except the high peak in the *M. margaritana* Biozone (Fig. 1), correlating partly with the Ireviken Event level. On the contrary, the Mulde Event at the boundary of the *C. pachycephala* and *S. lycoperdoides* biozones (Nestor 2007) and the Lau Event at the boundary of the *E. lagenomorpha* and *E. barrandei* biozones (Nestor 2009) are not expressed in the diagram. The turnover ratio values close to 0 indicate that the numbers of originations and extinctions are more or less identical. The curve shows decline only in the upper part of the Silurian, in the Pridoli, related to the major extinction of chitinozoan species.

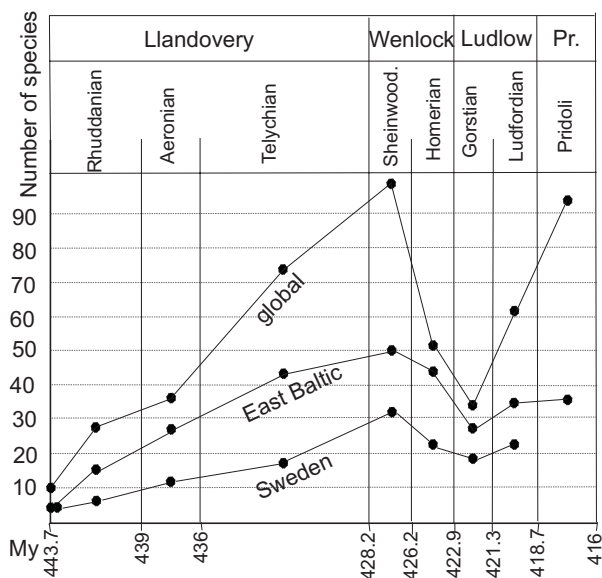


Fig. 3. The East Baltic Silurian chitinozoan diversity curve compared to the global and Swedish curves. Sheinwood., Sheinwoodian; Pr., Pridoli.

DIVERSITY AND ENVIRONMENTAL CYCLICITY

In Kaljo et al. (1998) mean values of the carbon isotope curves, global bathymetry, and glaciations have been tied to the generalized graptolite zones. To study the influence of these factors on chitinozoan diversity (Fig. 2), global biozones of the latter group were correlated with the generalized graptolite zones given in Koren et al. (1996). This correlation was compiled after Verniers et al. (1995), Loydell et al. (2003), and Nestor (2007, 2009). The eustatic curve from Kaljo et al. (1998, modified from Johnson et al. 1991) exhibits sea-level high- and lowstands in the Silurian (Fig. 2). The diversity of chitinozoans is clearly related to the transgression–regression phases. The high diversity values of chitinozoans from the Telychian to the lower Homerian and in the Gorstian are coeval with highstands of the global eustatic curve. The short-time sea-level fluctuations, connected with glaciations (Fig. 2), affected chitinozoan diversity, but are not expressed in the generalized diversity curve.

Carbon cycling is one feature of environmental cyclicity. In the East Baltic Silurian four main positive excursions in carbon isotopes have been recorded (Fig. 2). They occur usually during a low-diversity interval, after important extinctions of planktic organisms (Kaljo et al. 1998). This fits well with the severe chitinozoan extinction levels in the *M. margaritana* Biozone, followed by the Ireviken Event and in the uppermost *C. pachycephala* Biozone, followed by the Mulde Event at the lower boundary of the *S. lycoperdoides* Biozone. The Ludfordian extinction of chitinozoans takes place at the boundary of the *E. philipi* and *E. barrandei* biozones and is followed by the Lau Event (Nestor 2009).

Loydell (2007) has pointed out several causes of positive $\delta^{13}\text{C}$ excursions. Increased carbon burial, which is related to increased carbonate subareal weathering associated with glacial periods, as well as other causes of positive excursions, influenced chitinozoan biodiversity. These phenomena, however, have not been studied in detail yet.

THE REGIONAL DIVERSITY VERSUS GLOBAL DIVERSITY OF CHITINOZOANS

The East Baltic diversity pattern of chitinozoans, tied to the Silurian global standard stages and series, is shown in Fig. 3. The Silurian global chitinozoan diversity curve has been compiled by Paris using the CHITINOVOSP database, which was designed for recording all chitinozoan taxa described until the end of 1997 (Paris & Nölvak 1999). In addition, in the present paper the distribution data of new chitinozoan species published between 1998 and 2008 have been considered. Absolute ages (My) of stage boundaries from the home page of the ICS (www.stratigraphy.org) have been used (Fig. 3).

The chitinozoan diversity curve for the Silurian of Sweden was compiled using chitinozoan distribution data from Gotland (Laufeld 1974; Grahn 1995), Skåne (Grahn 1996), and other localities on the mainland of Sweden (Grahn 1998). At the level of the Silurian standard stages the diversity curves of the East Baltic and Swedish chitinozoans are similar (Fig. 3). The diversity increases from the Rhuddanian to the Sheinwoodian and decreases in the Homerian and Gorstian. A slight increase follows in the Ludfordian. The global diversity curve shows the same trend with the exception of the Pridoli, where the number of species increases considerably, contrary to the East Baltic.

At the end of the Pridoli the Baltic basin suffered from severe regression. The clastic sediments of the lowermost Devonian lack chitinozoans.

CONCLUSIONS

Chitinozoan diversity is related to the transgression–regression phases of the Silurian Baltic basin, which are linked to glaciations, global sea-level fluctuations, water temperature and chemistry. The turnover ratio and species origination and extinction are more or less regular throughout the Silurian, except the high peak in the *M. margaritana* Biozone, correlating partly with the Ireviken Event. At the level of the Silurian standard stages the East Baltic chitinozoan total diversity and global diversity curves show similar trends with the main positive peak in the Sheinwoodian. Chitinozoan diversity is also related to the evolutionary processes of the faunal group, but this aspect of diversity is still poorly studied.

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REFERENCES

- Achab, A. & Paris, F. 2007. The Ordovician chitinozoan biotransformation and its leading factors. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 5–19.
- Gailite, L., Ulst, R. & Jakovleva, V. 1987. *Stratotipicheskie i tipovye razrezy silura Latvii* [Stratotype and type sections of the Silurian of Latvia]. Zinatne, Riga, 182 pp. [in Russian].
- Grahn, Y. 1995. Silurian Chitinozoa and biostratigraphy of subsurface Gotland. *GFF*, **117**, 57–65.
- Grahn, Y. 1996. Upper Silurian (Upper Wenlock–Lower Pridoli) Chitinozoa and biostratigraphy of Skåne, southern Sweden. *GFF*, **118**, 237–250.
- Grahn, Y. 1998. Lower Silurian (Llandovery–Middle Wenlock) biostratigraphy of the mainland of Sweden. *GFF*, **120**, 273–283.
- Grahn, Y. & Caputo, M. V. 1992. Early Silurian glaciation in Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **99**, 9–15.
- Johnson, M. E., Kaljo, D. & Mckerrow, W. S. 1991. Sea level and faunal changes during the latest Llandovery and earliest Ludlow (Silurian). *Historical Biology*, **5**, 153–169.
- Kaljo, D. (ed.). 1970. *Silur Òstonii* [The Silurian of Estonia]. Valgus, Tallinn, 343 pp. [in Russian, with English summary].
- Kaljo, D., Paškevičius, J. & Ulst, R. 1984. Graptolite zones of the East Baltic Silurian. In *Stratigraphy of Early Paleozoic Sediments of the East Baltic* (Männil, R. & Mens, K., eds), pp. 94–118. Academy of Sciences of

- the Estonian SSR, Tallinn [in Russian, with English summary].
- Kaljo, D., Boucot, A. J., Corfield, R. M., Le Herisse, A., Koren, T. N., Kriz, J., Männik, P., Märss, T., Nestor, V., Shaver, R. H., Siveter, D. J. & Viira, V. 1995. Silurian bio-events. In *Global Events and Event Stratigraphy in the Phanerozoic* (Walliser, O. H., ed.), pp. 173–224. Springer, Berlin.
- Kaljo, D., Kiipli, T. & Martma, T. 1998. Correlation of carbon isotope events and environmental cyclicity in the East Baltic Silurian. In *Silurian Cycles – Linkages of Dynamic Stratigraphy with Atmospheric, Oceanic and Tectonic Changes* (Landing, E. & Johnson, M., eds), *New York State Museum Bulletin*, 491, 297–312.
- Koren, T., Lenz, A. C., Loydell, D. K., Melchin, M. J., Štorch, P. & Teller, L. 1996. Generalized graptolite zonal sequence defining Silurian time intervals for global paleogeographic studies. *Lethaia*, **29**, 59–69.
- Laufeld, S. 1974. Silurian Chitinozoa from Gotland. *Fossils and Strata*, **5**, 1–130.
- Loydell, D. K. 2007. Early Silurian positive $\delta^{13}\text{C}$ excursions and their relationship to glaciations, sea-level changes and extinction events. *Geological Journal*, **42**, 531–546.
- Loydell, D. K., Kaljo, D. & Männik, P. 1998. Integrated biostratigraphy of the lower Silurian of the Ohesaare core, Saaremaa, Estonia. *Geological Magazine*, **135**, 769–783.
- Loydell, D. K., Männik, P. & Nestor, V. 2003. Integrated biostratigraphy of the lower Silurian of the Aizpute-41 core, Latvia. *Geological Magazine*, **140**, 205–229.
- Melchin, M. J., Koren, T. N. & Štorch, P. 1998. Global diversity and survivorship patterns of Silurian graptoloids. In *Silurian Cycles – Linkages of Dynamic Stratigraphy with Atmospheric, Oceanic and Tectonic Changes* (Landing, E. & Johnson, M. E., eds), *New York State Museum Bulletin*, 491, 165–182.
- Nestor, H. & Nestor, V. 2002. Upper Llandovery to middle Wenlock (Silurian) lithostratigraphy and chitinozoan biostratigraphy in southwestern Estonia and northernmost Latvia. *Proceedings of the Estonian Academy of Sciences, Geology*, **51**, 67–87.
- Nestor, H., Einasto, R., Männik, P. & Nestor, V. 2003. Correlation of lower–middle Llandovery sections in central and southern Estonia and sedimentation cycles of lime muds. *Proceedings of the Estonian Academy of Sciences, Geology*, **52**, 3–27.
- Nestor, V. 1992. Chitinozoan diversity dynamics in the East Baltic Silurian. *Proceedings of the Estonian Academy of Sciences, Geology*, **41**, 215–224.
- Nestor, V. 1994. Early Silurian chitinozoans of Estonia and North Latvia. *Academia*, **4**, 1–163.
- Nestor, V. 2003. Distribution of Silurian chitinozoans. In *Ruhnu (500) Drill Core* (Pöldvere, A., ed.), *Estonian Geological Sections*, 5, 13–14.
- Nestor, V. 2005. Chitinozoans of the *Margachitina margaritana* Biozone and the Llandovery–Wenlock boundary in West Estonian drill cores. *Proceedings of the Estonian Academy of Sciences, Geology*, **54**, 87–111.
- Nestor, V. 2007. Chitinozoans in the Wenlock–Ludlow boundary beds of the East Baltic. *Estonian Journal of Earth Sciences*, **56**, 109–128.
- Nestor, V. 2009. Biostratigraphy of the Ludlow chitinozoans from East Baltic drill cores. *Estonian Journal of Earth Sciences*, **58**, 170–184.
- Nestor, V., Einasto, R. & Loydell, D. K. 2002. Chitinozoan biostratigraphy and lithological characteristics of the Lower and Upper Visby boundary beds in the Ireviken 3 section, Northwest Gotland. *Proceedings of the Estonian Academy of Sciences, Geology*, **51**, 215–226.
- Paris, F. & Nölvak, J. 1999. Biological interpretation and paleobiodiversity of a cryptic fossil group: the “chitinozoan animal”. *Geobios*, **32**, 315–324.
- Paris, F., Achab, A., Asselin, E., Chen, X.-H., Grahn, Y., Nölvak, J., Obut, O., Samuelsson, J., Sennikof, N., Vecoli, M., Verniers, J., Wang, X.-F. & Winchester-Seeto, T. 2004. Chitinozoa. In *The Great Ordovician Diversification Event* (Webby, B. D., Paris, F., Droser, M. & Percival, I., eds), pp. 294–311. Columbia University Press, New York.
- Verniers, J., Nestor, V., Paris, F., Dufka, P., Sutherland, S. & Van Grootel, G. 1995. A global Chitinozoa biozonation for the Silurian. *Geological Magazine*, **132**, 651–666.

Siluri kitiinikute mitmekesisus Baltikumi puuraukudes

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Baltimaade Siluri kitiinikute taksonoomilise mitmekesisuse andmed on artiklis seostatud kitiinikute globaalsete biotsoonidega, mis omakorda on rööbistatud graptoliidi skaalaga. Siluri kitiinikuud iseloomustavad kolm mitmekesisuse tiptaset Wenlockis ja Ludlow's ning madalseisud Llandovery ja Pridolis. Liike sureb välja kõige enam ja ilmub kõige vähem Wenlocki ea algul, mida võib seostada Irevikeni sündmusega. Liikide mitmekesisus on seotud veetaseme, vee kemismi ja temperatuuri muutustega, samuti evolutsiooniliste protsessidega. Siluri laajärkude alusel on Baltikumi puuraukude kitiinikute mitmekesisuse muutuste trend sarnane nii Rootsi kui ka kitiinikute mitmekesisuse globaalsete muutuste trendile.