

UDC 551.733.3:56.016(474)

Viiu NESTOR*

CHITINOZOAN DIVERSITY DYNAMICS IN THE EAST BALTIC SILURIAN



Project 216
Global Bioevents

Abstract. The species diversity of chitinozoans has undergone considerable changes throughout the East Baltic Silurian. Well-pronounced diversity maxima occur in the *sedgwickii*, *murchisoni bohemicus*, *testis*, and *formosus* zones and in the middle Pridoli; innovation maxima fall in the *turriculatus*, *flexilis*, *radians*, *scanicus*, and *formosus* zones. The major extinction events took place in the *sedgwickii*, *riccartonensis*, *testis*, and *balticus* zones. Most of these events were closely related to the transgression-regression phases of the Silurian Baltic Basin, global sea-level fluctuations, and evolutionary changes in the chitinozoan assemblage.

Introduction

During the Silurian the East Baltic cratonic basin was subjected to almost continuous sedimentation. In the geological record four major sedimentological cycles have been distinguished (Kaljo, 1971; Эйнасто, 1986), closely related to the sea-level changes, but also to the evolution and fluctuations in the relative abundance and diversity of chitinozoans. In this work attempts have been made to outline the character and general trends in chitinozoan dynamics in the Silurian sequence, which contains rich assemblages of over 150 species, most of them widely distributed all over the world. The curves showing the number of chitinozoan species in the Baltic Silurian are based on the samples studied from the Ikla (lower and middle Llandovery), Ohesaare (upper Llandovery, upper Ludlow and Pridoli), and Ventspils cores (middle and upper Wenlock and lower Ludlow). These sections and intervals were chosen as they show the co-occurrence of chitinozoans and graptolites (see Калъо, 1970; Ульст, 1987; Nestor, 1990), permitting to integrate directly the chitinozoan zonation and biotic events with the graptolite scale (Fig. 1). In all charts data are plotted in the middle of the graptolite zones.

Using published data, similar curves as for the East Baltic have tentatively been compiled also for the Welsh Basin (Dorning, 1981) and Palencia, North Spain (Schweineberg, 1987) (Figs. 2—5).

Geological Setting

The transgressive phase of the first main sedimentation cycle in the early and middle Llandovery was characterized by the rhythmically alternating accumulation of calcareous and terrigenous muds. It was followed by a rapid regression that reached the maximum in the *convolutus* Biozone. The second cycle began with a transgressive phase in the *sedgwickii* Zone and was characterized by the relative stability in sedimentation in the late Llandovery and early Wenlock, when argillaceous

* Eesti Teaduste Akadeemia Geoloogia Instituut (Institute of Geology, Estonian Academy of Sciences), Estonia pst. 7, EE0105 Tallinn, Estonia.

deposits covered large areas. Intensive regression followed at the end of the Wenlock (Nestor and Nestor, 1991), but in the deeper, middle part of the basin (Ventpils area) it was weakly expressed. The third cycle began with a transgressive phase in the lowermost Ludlow, when calcareous mudstones and marls accumulated. It was succeeded by a regression in the middle Ludlow, at the *tauragensis* Zone level, during which calcareous deposits began to form in the central part of the basin, terminating the graptolite succession in the East Baltic (see Ульст, 1987). The transgressive phase of the last cycle, which started in the late Ludlow, reached its maximum in the middle Pridoli. This phase was characterized by intense influx of terrigenous material and deposition of calcareous marls over a vast area. The cycle lasted until the late Pridoli, up to the final Silurian regression.

Event Patterns

The evolution of the Silurian Chitinozoa on the higher taxonomic level (genera, families) was rather slow. Most of the genera entered the Silurian from the Ordovician and continued in the Devonian. The species diversity of chitinozoans, however, underwent considerable changes throughout the Silurian, enabling to trace several bioevents of different scales. They reflect general tendencies in the evolution, but are also dependent on the sea-level changes and the water chemistry.

The diversity curve of the East Baltic Silurian chitinozoans (Fig. 2) shows four well-pronounced peaks and one modest peak for the *confertus* and *cyphus* zones. This first early Llandovery diversity maximum was followed by a steady decline in the diversity, lasting up to the short-time radiation in the *sedgwickii* Zone, which coincided with the beginning of the second main transgressive phase in the East Baltic Silurian. The third diversity maximum occurred at the *murchisoni bohemicus* Zone level and was followed by a major extinction event in the *riccartonensis* Zone (Fig. 4). A new radiation maximum was attained in the *testis* Zone, followed by another mass extinction event at the same level. The last Silurian radiation began in the early Ludlow *scanicus* Zone and, continuously increasing, extended up to the middle Pridoli. The most significant late Silurian chitinozoan extinction event occurred in the *balticus* Zone. Similarly to the *riccartonensis* Zone, it was characterized by the disappearance of more than 75% of the occurring species.

The bioevents which are more closely related to the evolutionary changes of chitinozoans are demonstrated in the innovation curve (Fig. 3). The most important innovation events occur at the base of the Silurian and within the *sedgwickii*, *turriculatus*, *flexilis*, *radians*, *scanicus*, and *formosus* zones, showing renewal of more than 50% of the species. A very high innovation peak characterizes the *turriculatus* Zone level, where 80% of the species were replaced. The innovation maxima well coincided with the global sea-level high stands in the Silurian (see Johnson et al., 1991); the extinction maxima usually corresponded to the sea-level low stands (see Fig. 1).

In order to minimize the influence of the time factor upon the interpretation of the chitinozoan diversity dynamics, the total rate, i.e. the number of the appearances and disappearances of species per one million years (Fig. 5 A, B) and the per taxon rate, i.e. the number of appearances and disappearances per chitinozoan species diversity (Fig. 5 C, D) have been calculated for all graptolite zones (after Jones and Nicol, 1986). The approximate duration of the graptolite zones in million years (Myr) is given (Table 1) according to D. Kaljo (pers. comm.).

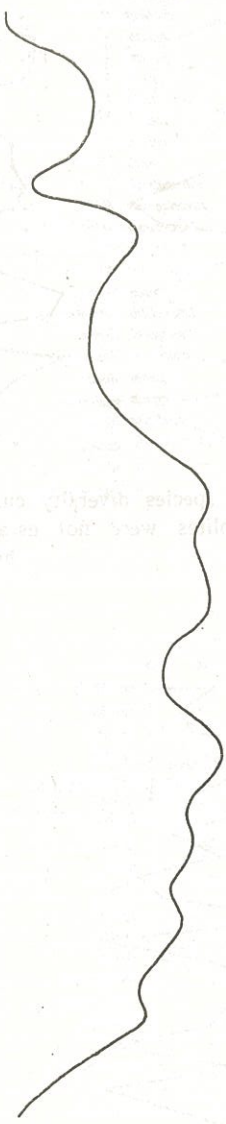
Series	Stage	Regional units		Graptolite scale	Global sea level curve	Chitinozoan biozones
		Stage	Graptolite biozones			
Pridoli		K ₄	?			Urnochitina
		K _{3b}		lochkovensis		E. filifera - F. pistilliformis
Ludlow	Ludfordian	K _{3a}	ultimus - formosus	ultimus - formosus		A. fragilis
						S. sphaeroccephala C. granosa
						E. philipi - E. lagenomorpha
	Gorstian	K ₂	balticus	Neocucullograpt.		C. latifrons
			tauragensis	leintwardinensis tumescens		G. militaris - C. sp. 2
			scanicus	scanicus		Conochitina sp. 1
			nilssoni	nilssoni		interzone V
Wenlock	Homerian	K ₁	ludensis	ludensis		S. indecora
			nassa	nassa		C. cribrosa
			testis	lundgreni		C. subcyatha
	Sheinwoodian	J ₂	radians			C. pachycephala
			perneri	ellesae		E. lagena
			flexilis	linnarssoni		C. cingulata
	J ₁		antennularius	rigidus		C. tuba
			riccartonensis	riccartonensis		C. cf. mamilla
			murchisoni	murchisoni		interzone IV
			bohemicus	centrifugus		M. margaritana
Llandovery	Telychian	H	spiralis	crenulata		C. proboscifera
			griestoniensis	griestoniensis		A. longicollis
			crispus	crispus		interzone III
			turriculatus	turriculatus		C. emmastensis
			sedgwickii	sedgwickii		interzone II
	Aeronian	G ₃	convolutus	convolutus		C. cf. protracta
			gregarius	gregarius		A. convexa
			cyphus	cyphus		C. electa
	Rhudda- nian	G ₁₋₂	confertus	vesiculosus		C. postrobusta
				acuminatus		interzone I A. laevaensis

Fig. 1. Correlation of the East Baltic graptolite and chitinozoan biozones with the Silurian standard graptolite scale (according to Решения..., 1987). Global sea-level curve after Johnson et al. (1991). Regional stages: G₁₋₂ — Juuru, G₃ — Raikküla, H — Adavere, J₁ — Jaani, J₂ — Jaagarahu, K₁ — Rootsiküla, K₂ — Paadla, K_{3a} — Kuresaare, K_{3b} — Kaugatuma, K₄ — Ohesaare.

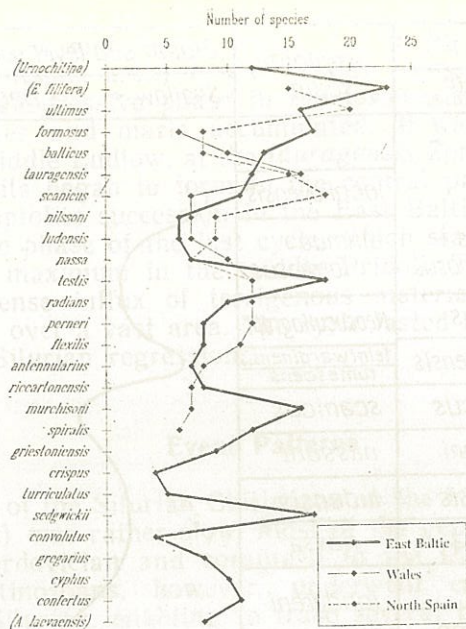


Fig. 2. Chitinozoan species diversity curves, plotted in the middle of each graptolite zone. Where graptolites were not established, chitinozoan biozones were used (in brackets).

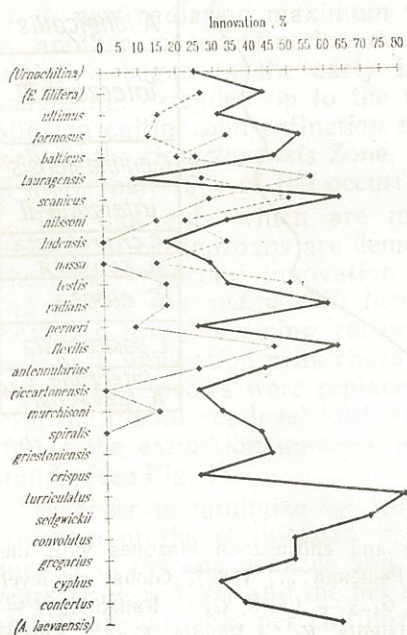


Fig. 3. Chitinozoan innovation curves.
For legend see Fig. 2.

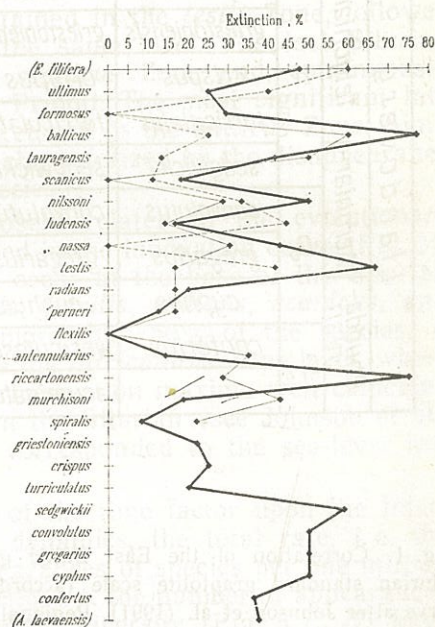


Fig. 4. Chitinozoan extinction curves.
For legend see Fig. 2.

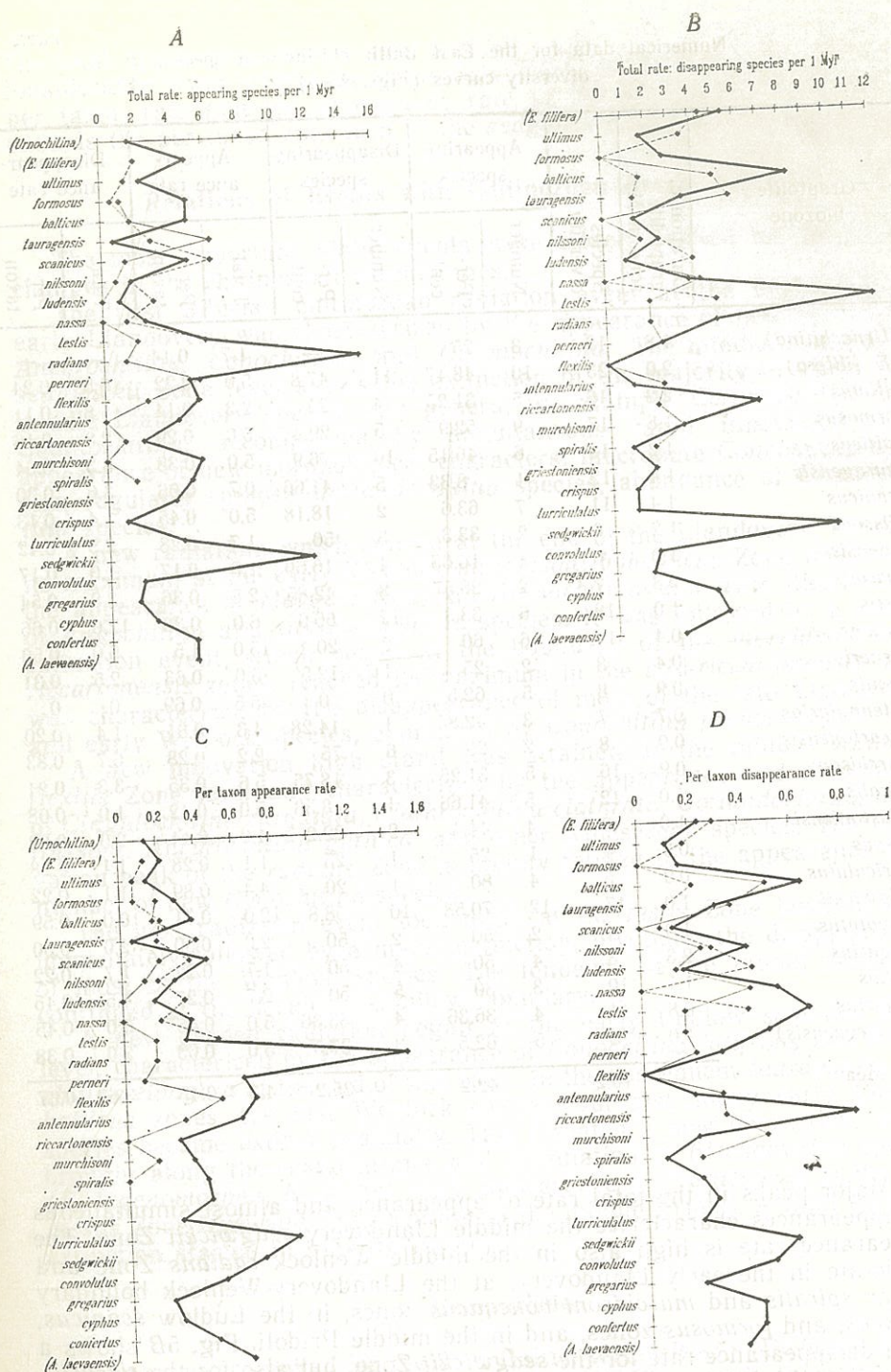


Fig. 5. Total appearance and disappearance rates of chitinozoan species per one million years (A, B). Per taxon appearance and disappearance rates of chitinozoan species per one million years per total species diversity (C, D).

Table 1

Numerical data for the East Baltic chitinozoan species diversity curves (Figs. 2—5)

Graptolite biozone	Duration of graptolite zone in Myr	Species diversity	Appearing species		Disappearing species		Appearance rate		Disappearance rate	
			Number	Per-cent	Number	Per-cent	Total	Per taxon	Total	Per taxon
(<i>Urnochitina</i>)	1.8	12	3	25	—	—	1.7	0.14	—	—
(<i>E. filifera</i>)	2.0	23	10	43.47	11	47.8	5.0	0.22	5.5	0.24
<i>ultimus</i>	2.2	16	5	31.25	4	25	2.3	0.14	1.8	0.11
<i>formosus</i>	1.8	17	9	52.9	5	29.4	5.0	0.29	2.8	0.16
<i>balticus</i>	1.2	13	6	46.15	10	76.9	5.0	0.38	8.3	0.64
<i>tauragensis</i>	1.4	12	1	8.33	5	41.66	0.7	0.06	3.6	0.30
<i>scanicus</i>	1.4	11	7	63.6	2	18.18	5.0	0.45	1.4	0.13
<i>nilssoni</i>	1.2	6	2	33.3	3	50	1.7	0.28	2.5	0.42
<i>ludensis</i>	1.0	6	1	16.66	1	16.66	1.0	0.17	1.0	0.17
<i>nassa</i>	0.8	7	2	28.57	3	42.85	2.5	0.36	3.8	0.54
<i>testis</i>	1.0	18	6	33.3	12	66.6	6.0	0.33	12.0	0.66
<i>radians</i>	0.4	10	6	60	2	20	15.0	1.5	5.0	0.50
<i>perneri</i>	0.4	8	2	25	1	12.5	5.0	0.63	2.5	0.31
<i>flexilis</i>	0.9	8	5	62.5	0	0	5.5	0.69	0	0
<i>antennularius</i>	0.7	7	3	42.85	1	14.28	4.3	0.61	1.4	0.20
<i>riccartonensis</i>	0.9	8	2	25	6	75	2.2	0.28	6.7	0.83
<i>murchisoni</i>	0.9	16	5	31.25	3	18.75	5.6	0.35	3.3	0.21
<i>spiralis</i>	1.0	12	5	41.66	1	8.33	5.0	0.42	1.0	0.08
<i>griestoniensis</i>	1.0	9	4	44.4	2	22.2	4.0	0.44	2.0	0.22
<i>crispus</i>	0.9	4	1	25	1	25	1.1	0.28	1.1	0.28
<i>turriculatus</i>	0.9	5	4	80	1	20	4.4	0.89	1.1	0.22
<i>sedgwickii</i>	1.0	17	12	70.58	10	58.8	12.0	0.71	10.0	0.59
<i>convolutus</i>	1.0	4	2	50	2	50	2.0	0.50	2.0	0.50
<i>gregarius</i>	2.3	8	4	50	4	50	1.7	0.22	1.7	0.22
<i>cyphus</i>	1.1	10	3	30	5	50	2.7	0.27	4.5	0.45
<i>confertus</i>	0.8	11	4	36.36	4	36.36	5.0	0.45	5.0	0.45
(<i>A. laevaensis</i>)	1.0	8	5	62.5	3	37.5	5.0	0.63	3.0	0.38
Mean:		10.2		42.2		35.2	4.3	0.45	3.6	0.37

Major peaks in the total rate of appearance and almost simultaneous disappearances characterize the middle Llandovery *sedgwickii* Zone. The appearance rate is high also in the middle Wenlock *radians* Zone and moderate in the early Llandovery, at the Llandovery-Wenlock boundary in the *spiralis* and *murchisoni bohemicus* zones, in the Ludlow *scanicus*, *balticus*, and *formosus* zones, and in the middle Pridoli. Fig. 5B shows a high disappearance rate for the *sedgwickii* Zone, but also for the *riccartonensis*, *testis*, *balticus* zones and for the middle Pridoli. Lower rates of disappearance characterize the lowermost middle Llandovery, the Wenlock *antennularius*, *flexilis*, *nassa*, and *ludensis* zones, the lower Ludlow and the Pridoli *ultimus* Zone.

The positions of the appearance and disappearance peaks in the per taxon rate plots (Fig. 5 C, D) are similar to those on the total rate charts. The main differences concern the *sedgwickii* and *turriculatus* zones.

The total appearance rate is very high at the *sedgwickii* Zone level, but considerably lower within the *turriculatus* Zone. At the same time, in the per taxon rate plot the appearance rate at the *turriculatus* Zone level exceeds the per taxon rate seen in the *sedgwickii* Zone.

Relations of Events with Chitinozoan Assemblages

The most important biotic events were closely related to the major changes in the chitinozoan assemblages.

The first Silurian chitinozoan radiation event at the beginning of early Llandovery was characterized by the appearance of new species of *Ancyrochitina*, *Conochitina*, and *Coronochitina*. The middle Llandovery *sedgwickii* Zone level shows the extinction of the majority of early and middle Llandovery species and genera, for example *Coronochitina* and *Cyathochitina*, accompanied by simultaneous rapid innovation and appearance of new morphological characters: mucronate *Conochitina* species, regularly spinose *Gotlandochitina* species, abundance of *Eisenackitina* species.

A new radiation, which started at the end of the Llandovery, reached its maximum at the early Wenlock *murchisoni bohemicus* Zone level with the appearance of *Margachitina* and *Anthochitina* and wide distribution of *Angochitina* and *Gotlandochitina* species. It was followed by a major extinction event, which began at the boundary of the *murchisoni* and *riccartonensis* zones, reached its maximum in the mid-*riccartonensis*, and was characterized by the disappearance of most of the late Llandovery and early Wenlock species, dominated by *Conochitina proboscifera*.

A new innovation high stand was attained at the middle Wenlock *flexilis* Zone level and characterized by the appearance and abundance of *Cingulochitina cingulata*, *Clathrochitina clathrata*, *Gotlandochitina martinssoni*, *Ancyrochitina guhnica*, and other widespread species. The innovation peak of the *radians* Zone is mainly related to the appearance of a number of new *Conochitina* species.

The next radiation event took place at the *testis* Zone level. It was immediately followed by a major extinction, involving the disappearance of most of the Wenlock species. The tendency of the faunal reduction continued at the Wenlock—Ludlow boundary.

A new graded radiation began at the early Ludlow *scanicus* Zone level, characterized by the appearance of *Conochitina latifrons* and *Angochitina elongata* at the end of this zone. In the subsequent *tauragensis* and *balticus* zones, the last Wenlock species, but also many early Ludlow species became extinct gradually. This initiated a new innovation, which brought along the reappearance and domination of *Eisenackitina* species (*E. lagenomorpha*, *E. philipi*, etc.), appearance of *Pterochitina* at the *formosus* Zone level and *Fungochitina* in the middle Pridoli. A final Silurian extinction started in the late Pridoli.

Comparison

The curves compiled for the East Baltic, Welsh Basin (Dorning, 1981), and Palencia, North Spain (Schweineberg, 1987) permit to make some comparisons between these areas (see Figs. 2—5, Tables 1 and 2).

The relative diversity and dynamics of chitinozoan species from the other two regions are comparable to the East Baltic only in general trends. The specific diversity increases gradually towards the middle Wenlock (in Wales) and decreases in the latest Wenlock, being low at the Wenlock—Ludlow boundary zones. Diversity is high again in the middle Ludlow, lowering in the topmost Ludlow. In the early Pridoli a new

diversity high stand followed (in North Spain). The major chitinozoan innovation occurred at the levels of the *flexilis* and *scanicus* zones; major extinction events have been recorded in the *testis*, *nilssoni*, and *balticus* zones and in the middle Pridoli.

Below some comparisons of chitinozoan and graptolite dynamics (after Koren, 1987) will be outlined. The most prominent graptolite diversity peak is assigned to the *gregarius* Zone, but chitinozoans at this level are already losing their relatively high diversity, occurring in the *confertus* and *cyphus* zones. The mass extinction event took place at the *riccartonensis* Zone level, involving both groups. Also the major radiation events coincide in the *lundgreni* (*testis*) Zone, followed immediately by drastic mass extinction in the topmost part of the zone. The early and late Ludlow graptolites show two well-pronounced diversity peaks in the *scanicus* and *formosus* zones and one smaller maximum occurs in the middle Pridoli. An analogous picture can be seen in the chitinozoan innovation chart.

Table 2

Numerical data for the diversity curves of the Welsh Basin (A) and North Spain (B) chitinozoan species (Figs. 2-5)

Graptolite biozone	Species diversity	Appearing species		Disappearing species		Appear- ance rate		Disappear- ance rate	
		Number	Per- cent	Number	Per- cent	Total	Per taxon	Total	Per taxon
A									
<i>formosus</i>	6	2	33.33	—	—	1.1	0.10	—	—
<i>bohemicus</i>	10	2	20	6	60	1.7	0.17	5.0	0.50
<i>leintwardinensis</i>	16	9	56	8	50	6.4	0.40	5.7	0.36
<i>scanicus</i>	7	2	28.57	0	0	1.4	0.20	0	0
<i>nilssoni</i>	7	1	14.28	2	28.57	0.8	0.12	1.7	0.24
<i>ludensis</i>	7	0	0	1	14.2	0	0	1.0	0.14
<i>nassa</i>	10	0	0	3	30.3	0	0	4.3	0.43
<i>lundgreni</i>	12	2	16.66	2	16.66	2.0	0.17	2.0	0.17
<i>ellesae</i>	12	1	8.33	2	16.66	1.3	0.10	2.5	0.21
<i>linnarssoni</i>	11	5	45.45	0	0	5.6	0.51	0	0
<i>rigidus</i>	8	2	25	2	25	2.5	0.31	2.5	0.31
<i>riccartonensis</i>	7	0	0	2	28.57	0	0	2.2	0.32
<i>centr. + murchis.</i>	7	1	14.28	3	42.85	1.1	0.16	3.3	0.48
<i>crenulata</i>	9	0	0	2	22	0	0	2.0	0.22
B									
<i>lochkovens</i>	15	4	26.6	9	60	2.0	0.13	4.5	0.30
<i>ultimus</i>	20	3	15	8	40	1.4	0.07	3.6	0.18
<i>formosus</i>	8	1	12.5	0	0	0.6	0.07	0	0
<i>bohemicus?</i>	8	2	2.5	2	25	1.7	0.21	1.7	0.21
<i>leintwardinensis</i>	15	4	26.6	2	13.3	2.9	0.19	1.4	0.10
<i>scanicus</i>	18	9	50	2	11.1	6.4	0.36	1.4	0.08
<i>nilssoni</i>	9	2	22	3	33.3	1.7	0.19	2.5	0.28
<i>ludensis</i>	9	3	33	4	44.4	3.0	0.33	4.0	0.44
<i>nassa</i>	7	1	14.2	0	0	1.4	0.20	0	0
<i>lundgreni</i>	12	6	50	5	41.66	6.0	0.50	5.0	0.42

Conclusions

1. Chitinozoan dynamics, i.e. their major innovation and extinction events were in good correlation with the transgression-regression phases of the Silurian Baltic Basin and with the global sea-level changes.

2. The maxima of different chitinozoan bioevents are close or coincide in most of the charts and occur at the *sedgwickii*, *riccartonensis*, *radians*, *testis*, *scanicus*, *balticus*, and *formosus* zones. These levels may serve as time markers for the global correlations.

3. The most important bioevents in chitinozoan dynamics during the Silurian were closely related to the evolutionary changes in the chitinozoan assemblages.

4. The prominent East Baltic chitinozoan radiation and extinction peaks show good correlation with the Silurian graptolite diversity and extinction maxima of other regions.

5. The fluctuations of the East Baltic Silurian chitinozoan diversity are not entirely concordant with those of Wales and North Spain, but comparable in general trends.

Acknowledgements. My thanks are due to Prof. D. Kaljo for many helpful suggestions, to Anne Noor for linguistic help, and Kaur Nestor for computer graphics.

REFERENCES

- Dorning, K. J. 1981. Silurian Chitinozoa from the type Wenlock and Ludlow of Shropshire, England. — *Rev. Palaeobot. Palynol.*, 34, 205—208.
- Johnson, M. E., Kaljo, D., and Rong, J.-Y. 1991. Silurian eustasy. — In: M. G. Bassett, P. D. Lane, and D. Edwards (eds.). *The Murchison Symposium. Special Papers in Palaeontology*, 44, 145—163.
- Jones, D. S. and Nicol, D. 1986. Origination, survivorship and extinction of rudist taxa. — *J. Paleont.*, 60, 107—115.
- Kaljo, D. 1971. The tectonic factor in the geological history of the East Baltic Basin during the Silurian. *Colloque Ordovicien-Silurien*, Brest, September 1971. — *Mémoires du B. R. G. M.*, 73, 275—279.
- Koren, T. N. 1987. Graptolite dynamics in Silurian and Devonian time. — *Bull. Geol. Soc. Denmark*, 35, 149—159.
- Nestor, V. 1990. Silurian chitinozoans. — In: D. Kaljo, H. Nestor (eds.). *An Excursion Guidebook*. Tallinn, 80—83.
- Nestor, V. and Nestor, H. 1991. Dating of the Wenlock carbonate sequences in Estonia and stratigraphic breaks. — *Proc. Estonian Acad. Sci. Geol.*, 40, 2, 50—60.
- Schweineberg, J. 1987. Silurische Chitinozoen aus der Provinz Palencia (Kantabrisches Gebirge, N-Spanien). — *Göttinger Arb. Geol. Paläont.*, 33, 1—94.
- Кальо Д. Л. 1970. Граптолиты. — In: *Силур Эстонии*. Таллинн, Валгус, 179—184.
- Решения Межведомственного стратиграфического совещания по ордовику и силуру Восточно-Европейской платформы 1984 г. с региональными стратиграфическими схемами. 1987. Ленинград, 1—114.
- Ульст Р. Ж. 1987. Распространение граптолитов в венлокских и лудловских отложениях скв. Вентспилс-ДЗ. — In: Л. К. Гайлите, Р. Ж. Ульст, В. И. Яковлева. *Стратотипические и типовые разрезы силура Латвии*. Рига, Зинатне, 129—136.
- Эйнасто Р. Э. 1986. Основные стадии развития и фацальные модели силурийского краевого бассейна Балтики. — In: Д. Л. Кальо, Э. Р. Клааманн (eds.). *Теория и опыт экостратиграфии*. Таллинн, 37—54.

Presented by D. Kaljo

Received
May 20, 1992

KITINOZOADE MITMEKESISUSE DÜNAAMIKA IDA-BALTI SILURIS

Kitinozoade liigiline mitmekesisus on siluri kestel pidevalt muutunud. Liikide arvukust on analüüsitud graptoliidi skaala alusel. Olulisemaid liikide ilmumise ja kadumise tasemeid on vaadeldud biosündmustena, mis ei ole tihedalt seotud mitte ainult grupisestev evolutsiooniliste muutustega, vaid ka Balti basseini transgressiooni- ja regressioonifaaside ning globaalsete merepinna kõikumistega.

Вийу НЕСТОР

ДИНАМИКА РАЗНООБРАЗИЯ ХИТИНОЗОЙ В СИЛУРЕ ПРИБАЛТИКИ

Видовое разнообразие хитиноз в силуре Прибалтики постоянно изменялось. Численность видов анализируется по региональной граптолитовой шкале. Наиболее массовые появления и исчезновения видов на определенных уровнях рассматриваются как биотические события, которые связаны не только с эволюционными изменениями внутри группы, но и с фазами трансгрессии и регрессии Балтийского бассейна и колебаниями уровня мирового океана.