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EVENTS IN THE CONODONT HISTORY DURING THE SILURIAN IN ESTONIA

Abstract. The evaluation of events in the Silurian conodont history is based on the stratigraphic distribution of all conodont species (including unpublished new ones) recognized in Estonia. The diversity of conodont species is the highest in the upper Llandovery and lowermost Wenlock (Velise Formation and lower Mustjala Member). In the main part of the Wenlock and in the upper Silurian the species diversity is below the average, except the Sauvere and Himmiste beds of the Paadla Stage, where the number of species is somewhat higher. The greatest declines in conodont diversity occurred in Mõhkküla, Mustjala, and Uduvere times. These disappearances coincide with the Sandvika, *amorphognathoides* resp. Ireviken, and *siluricus* resp. Lau extinction events by Jeppsson (1987, 1993). The total and per taxon rate charts show the same tendencies although in some intervals the per taxon rate tends to over-emphasize the appearances and disappearances.

The greatest innovations in the conodont evolution are noted in the Juuru and Adavere stages. Remarkable innovation is noted also in the lowermost Rootsiküla Stage. The appearance of new taxa in the Sauvere Beds is mostly connected with the radiation in some genera (*Ozarkodina*, *Oulodus*).

In the diversity changes of the conodonts four main cycles (early Llandovery—middle Llandovery, late Llandovery—early Wenlock, middle Wenlock—middle Ludlow, and late Ludlow—early Devonian) are established in Estonia.

Clark (1972, 1981) was the first to observe several generic and species diversity lows and peaks in the history of conodonts. Apart from Pennsylvanian—Permian the Silurian was noted as another period of a major evolutionary crisis.

Sweet's (1985) diversity curve is based on the changes in the number of conodontophorid species in 49 Lower Palaeozoic biozones. According to Sweet the species diversity started to decrease in the Late Ordovician and continued throughout the Silurian up to the Early Devonian. Nevertheless, the diversity curve has two peaks, in the late Llandovery and early Ludlow, showing the prevalence of the appearing species over the disappearing ones (Sweet, 1985, Fig. 7).

Aldridge (1988) documented in the Silurian only one clear generic origination event in the late Llandovery. It was preceded by relatively slow innovation in the earliest Silurian and followed by a rapid extinction in the early Wenlock. During this origination many new genera with new types of apparatuses (e. g., *Pterospathodus*, *Apsidognathus*, etc.) appeared

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in the late Llandovery. After the main extinction event only a few new genera were introduced in the late Wenlock and Ludlow (Aldridge, 1988, fig. 11.2).

Sweet (1988) recognized the cyclic pattern of the diversity changes and established 4 long-term and 20 second-order cycles. The Silurian history of conodonts belongs to second-order cycles IV and V with a high diversity episode in the late Llandovery and a smaller one in the early Ludlow. These cycles constitute the upper part of the late Cambrian—Silurian long-term cycle by Sweet (1988).

The results of the study of the Silurian conodonts from Estonia almost agree with the conclusions above. The aim of this paper is to test and detail the general diversity pattern describing the changes in the conodont diversity in the Silurian of Estonia.

Diversity Changes and Comments

The analysis presented below is based on the data of the stratigraphic distribution of all conodont species (including unpublished new ones) recognized in Estonia (Вийра, 1982, 1983; Viira, 1982; Männik, 1992). The total number of species and the numbers of appearing and disappearing taxa by beds (members) are given in the Table. Dates for the Llandovery—Wenlock, Wenlock—Ludlow, and Silurian—Devonian boundaries have been taken from Harland et al. (1982), and for the Ordovician—Silurian boundary from Tucker et al. (1990). The duration of beds (members) has been calculated by D. Kaljo proceeding from the above absolute datings and the number of the corresponding units.

The conodont species diversity (Fig. 1) is the highest in the upper Llandovery and lowermost Wenlock (Velise Formation and Mustjala Member). A rich and variable association is also identified from the uppermost lower Llandovery and middle Llandovery (Raikküla Formation, particularly from the Jõgeva Beds). In the Wenlock and upper Silurian the species diversity is below the average, except the Sauvere and Himmiste beds, where the number of species is somewhat higher.

The curves of the percentage of appearances and disappearances show greater changes (Fig. 1). The fauna is remarkably dominated by appearing taxa in the lower Velise Formation, Sauvere and Tahula beds, but also in the Viita Beds (Fig. 1). The greatest decreases in the diversity of conodont fauna took place in Mõhkküla, Mustjala, and Uduvere time. These disappearances coincide with the well-known Sandvika, *amorphognathoides* resp. Ireviken, and *siluricus* resp. Lau extinction events by Jeppsson (1987, 1993).

Although the total rate and per taxon rate charts show the same tendencies in the conodont diversity changes (Figs. 2 and 3), some comments are needed.

Very high species appearance rates in Mustjala and Viita beds may be the result of the extremely short duration of these units (Fig. 3). Moreover, the per taxon rate tends to over-emphasize the appearance and disappearance in the intervals with very low diversity (Johnson and Kauffman, 1990). As in Estonia the low diversity interval corresponds to the sediments of the Wenlock age (Fig. 1), the Mustjala, Viita, and Vesiku peaks on this chart may be over-accentuated. Also, the relatively low per taxon rate of appearance in Velise time (Fig. 3) may be due to the high faunal diversity in this interval (Fig. 1).

The main innovation intervals in the Silurian of Estonia are recognized in the lower Varbola and Velise formations. These are also well expressed in all three charts (Figs. 1—3).

The relatively high diversity, total appearance rate, and per taxon appearance rate in the Sauvere Beds (Figs. 1—3) could be considered as indicating a radiation phase connected with the morphological changes in the long-ranging *Ozarkodina*, *Oulodus*, and *Ctenognathodus* apparatuses.

Numerical data for appearance and disappearance plots of species diversity (Fig. 1), total rate (Fig. 2), and per taxon rate curves (Fig. 3)

Data are plotted in the middle of local units, but the appearance and disappearance of taxa could have occurred anywhere within the straton

Series	Boundary ages, Ma	Local unit	Duration, Ma	No. of spp.	Appearing spp.		Dis-appearing spp.		Appearances		Disappearances	
					No.	%	No.	%	Total rate	Per taxon rate	Total rate	Per taxon rate
	408											
Pridoli		K_4	1.8	9	5	55.6	7	77.8	2.8	0.31	3.9	0.43
		K_3bL	2.0	5	1	20.0	2	40.0	0.5	0.10	1.0	0.20
		$K_3bÄ$	2.2	6	2	33.3	2	33.3	0.9	0.15	0.9	0.15
	414											
Ludlow		K_3aK	1.7	6	2	33.3	2	33.3	1.2	0.20	1.2	0.20
		K_3aT	1.3	6	4	66.7	2	33.3	3.1	0.51	1.5	0.26
		K_2U	1.4	14	3	21.4	12	85.7	2.1	0.15	8.6	0.61
		K_2H	1.4	17	5	29.4	6	35.3	3.6	0.21	4.3	0.25
		K_2S	1.2	19	13	68.4	8	42.1	10.8	0.57	6.7	0.35
	421											
Wenlock		K_1Sn	0.5	9	1	11.1	3	33.3	2.0	0.22	6.0	0.67
		K_1Vs	0.5	9	3	33.3	1	11.1	6.0	0.67	2.0	0.22
		K_1Kn	0.4	8	0	0.0	2	25.0	0.0	0.0	5.0	0.63
		K_1Vt	0.4	11	6	54.5	3	27.3	15.0	1.36	7.5	0.68
		J_2T	1.8	7	1	14.3	2	28.6	0.6	0.08	1.1	0.16
		J_2M	0.4	8	3	37.5	2	25.0	7.5	0.94	5.0	0.63
		J_2V	0.5	6	0	0.0	1	16.7	0.0	0.0	2.0	0.33
		J_1P	0.7	9	1	11.1	1	11.1	1.4	0.16	1.4	0.16
		J_1N	0.9	13	4	30.8	4	30.8	4.4	0.34	4.4	0.34
		J_1M	0.9	35	5	14.3	25	71.4	5.6	0.16	27.8	0.79
	428											
Llandovery		$H'V_2$	2.0	37	8	21.6	0	0.0	4.0	0.11	0.0	0.0
		$H'V_1$	1.8	34	23	67.6	8	23.5	12.8	0.38	4.4	0.13
		$H'R$	1.0	7	1	14.3	0	0.0	1.0	0.14	0.0	0.0
		G_3Mh	1.0	15	3	20.0	9	60.0	3.0	0.20	9.0	0.60
		G_3Im	0.8	17	1	5.9	5	29.4	1.3	0.07	6.3	0.37
		G_3Jg	0.9	29	11	37.9	12	41.4	12.2	0.42	13.3	0.46
		G_3Vn	0.8	21	1	4.8	3	14.3	1.3	0.06	3.8	0.18
		G_3Jr	0.9	23	7	30.4	3	13.0	7.8	0.34	3.3	0.14
		$G_{1-2}T$	0.8	20	6	30.0	4	20.0	7.5	0.38	5.0	0.25
		$G_{1-2}V$	1.0	16	3	18.8	4	25.0	3.0	0.19	4.0	0.25
	441											

Abbreviations of local units: K_4 — Ohesaare Regional Stage, K_3bL — Lõo Beds, $K_3bÄ$ — Äigu Beds, K_3aK — Kudjape Beds, K_3aT — Tahula Beds, K_2U — Uduvere Beds, K_2H — Himmiste Beds, K_2S — Sauvere Beds, K_1Sn — Soeginina Beds, K_1Vs — Vesiku Beds, K_1Kn — Kuusnõmme Beds, K_1Vt — Viita Beds, J_2T — Tagavere Beds, J_2M — Maasi Beds, J_2V — Vilsandi Beds, J_1P — Paramaja Member, J_1N — Ninase Member, J_1M — Mustjala Member, $H'V_2$ — upper Velise Formation, $H'V_1$ — lower Velise Formation, $H'R$ — Rumba Formation, G_3Mh — Mõhkküla Beds, G_3Im — Imavere Beds, G_3Jg — Jõgeva Beds, G_3Vn — Vändra Beds, G_3Jr — Järva-Jaani Beds, $G_{1-2}T$ — Tamsalu Formation, $G_{1-2}V$ — Varbola Formation.

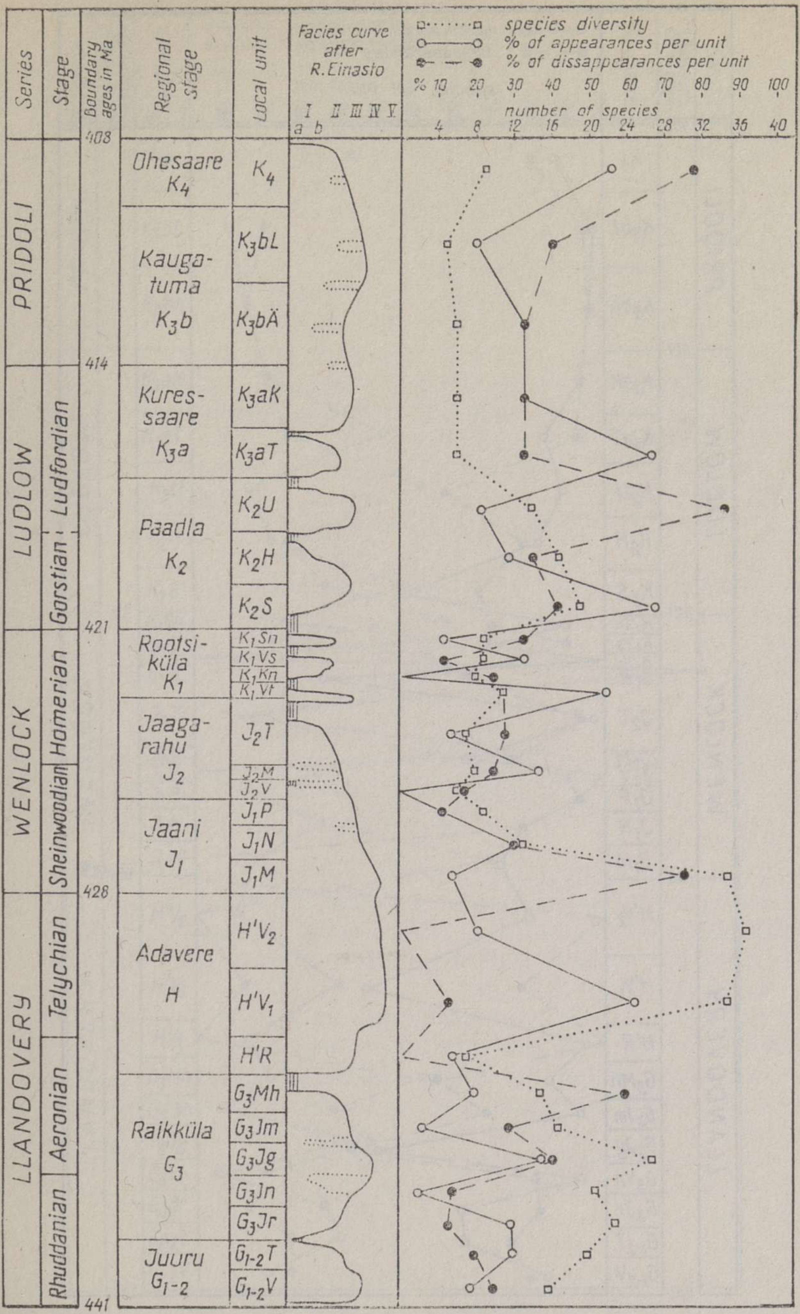

Fig. 1. Changes in the diversity of the conodont fauna: the species diversity and the percentage of appearing and disappearing species per local unit. The facies curve is given after Einasto (Кыртс et al., 1991); facies belts are as follows: I — lagoonal and restricted shelf, II — shoal, III — open shelf, IV — slope, V — depression (Нестор and Эйнасто, 1977).

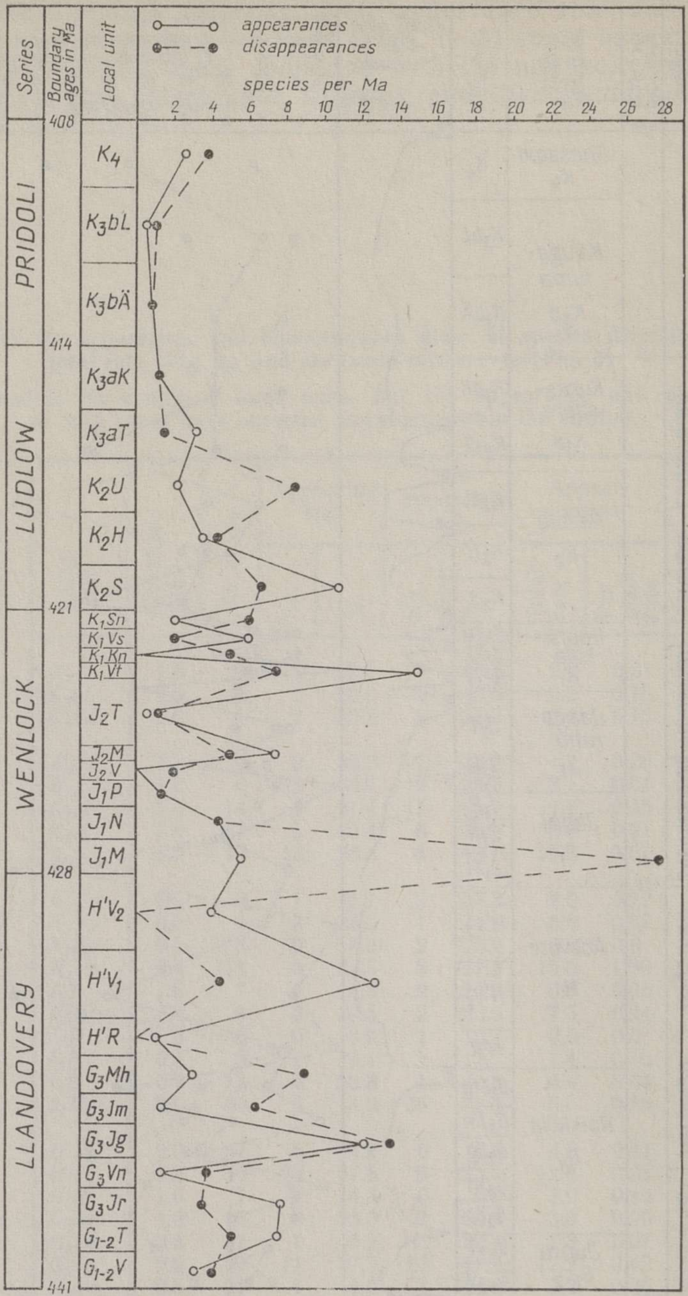

Fig. 2. Total appearance and disappearance rates of the conodont species. The total rate is calculated as the ratio of the number of appearing species and that of disappearing species per million years.

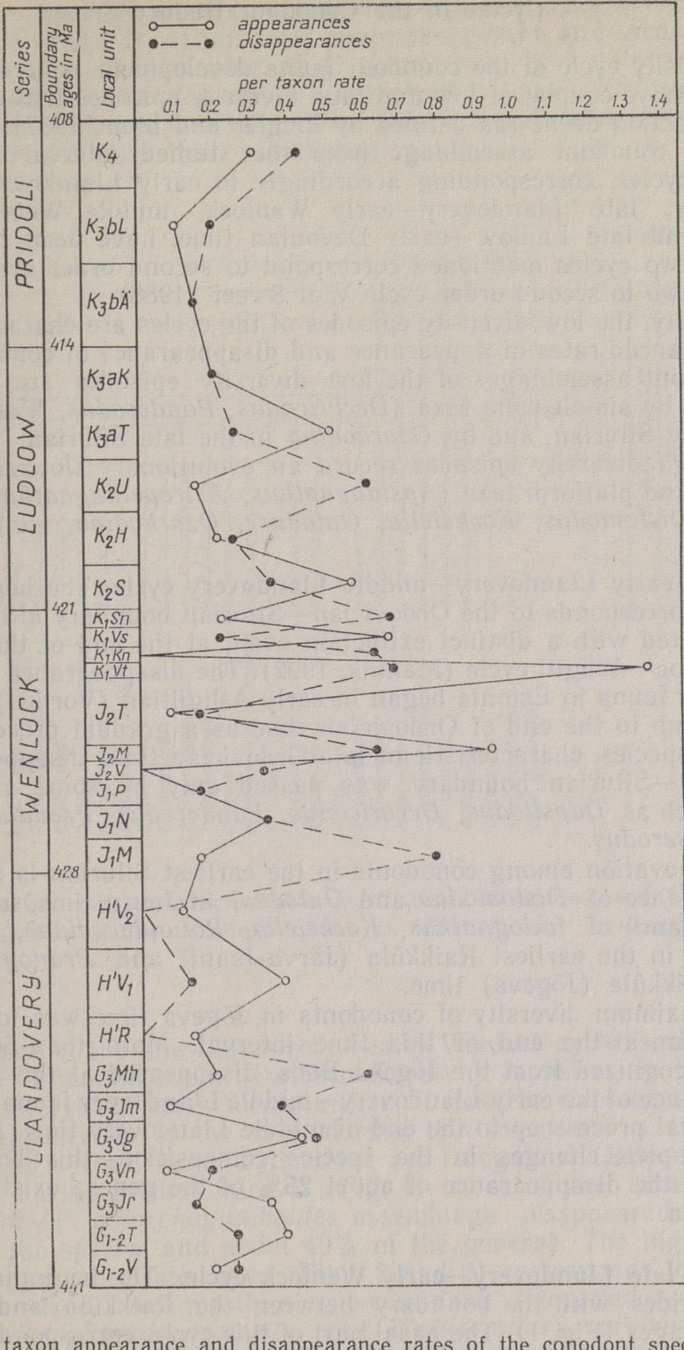

Fig. 3. Per taxon appearance and disappearance rates of the conodont species. The per taxon rate is the ratio of the number of appearances and disappearances per million years per diversity.

Cycles in the Conodont History

A diversity cycle of the conodont fauna development is here described as a successive couplet of low and high diversity episodes that culminates in an extinction event (as defined by Ziegler and Lane, 1987).

In the conodont assemblage from the studied interval four main diversity cycles, corresponding accordingly to early Llandovery—middle Llandovery, late Llandovery—early Wenlock, middle Wenlock—early Ludlow, and late Ludlow—early Devonian time, have been recognized. The first two cycles mentioned correspond to second order cycle IV and the other two to second order cycle V of Sweet (1988).

Generally, the low diversity episodes of the cycles are characterized by almost balanced rates of appearance and disappearance of conodont taxa. The conodont assemblages of the low diversity episodes are, as a rule, dominated by simple-cone taxa (*Decoriconus*, *Panderodus*, *Walliserodus*) in the early Silurian, and by *Ozarkodina* in the late Silurian.

The high diversity episodes record an evolutionary flowering of the ramiform and platform taxa (*Apsidognathus*, *Astropentagnathus*, *Aulacognathus*, *Distomodus*, *Kockelella*, *Oulodus*?, *Ozarkodina*, etc.).

1. The early Llandovery—middle Llandovery cycle. The beginning of the cycle corresponds to the Ordovician—Silurian boundary although it is not connected with a distinct extinction event at the end of the previous late Caradoc—Ashgill cycle (Männik, 1992). The disappearance of the late Ordovician fauna in Estonia began in early Ashgillian (Vormsi) time and continued up to the end of Ordovician time as a gradual process during which all species, characteristic of late Ordovician time, disappeared. The Ordovician—Silurian boundary was passed only by some simple-cone genera, such as *Dapsilodus*, *Decoriconus*, *Panderodus*, *Pseudooneotodus*, and *Walliserodus*.

The innovation among conodonts in the earliest Silurian is marked by the appearance of *Distomodus* and *Oulodus*? in Juuru time, followed by the appearance of *Icriognathus*, *Kockelella*, *Rotundacodina*?, and gen. et sp. n. 1 in the earliest Raikküla (Järva-Jaani) and *Pranognathus* in middle Raikküla (Jõgeva) time.

The maximum diversity of conodonts in Jõgeva time was followed by an extinction at the end of this time interval. More than 50% of the species, recognized from the Jõgeva Beds, disappeared at this level. The disappearance of the early Llandovery—middle Llandovery fauna continued as a gradual process up to the end of middle Llandovery time. Beside the almost complete changes in the species composition, this boundary is marked by the disappearance of about 25% of the genera existing in the older strata.

2. The late Llandovery—early Wenlock cycle. The beginning of this cycle coincides with the boundary between the Raikküla and Adavere regional stages (Fig. 1). The basal part of this cycle, corresponding to the main part of the Rumba Formation, contains an extremely poor assemblage of conodonts (only rare specimens of *Decoriconus*, *Ozarkodina*, *Panderodus*, and *Walliserodus* have been identified) and forms the low diversity episode of the cycle. This interval is characterized by extremely low rates of appearance and disappearance of conodont taxa (Figs. 2 and 3).

An extensive innovation in the conodont fauna at the end of Rumba (on NW Saaremaa Island and in continental Estonia) and at the beginning of Velise time (on SW Saaremaa) was connected with the main late Llandovery transgression, and indicates the beginning of the high diversity episode of the late Llandovery—early Wenlock cycle. This episode is marked by the highest rate of appearance of new taxa in early Silurian time (Figs. 2 and 3). At this level many new genera and species appeared. The occurrence of a number of platform taxa — *Astropentagnathus*, *Aulacognathus*, *Apsidognathus*, *Distomodus*, and *Kockelella* — is characteristic of this interval. From this interval also *Carniodus* and *Pterospathodus* have been established.

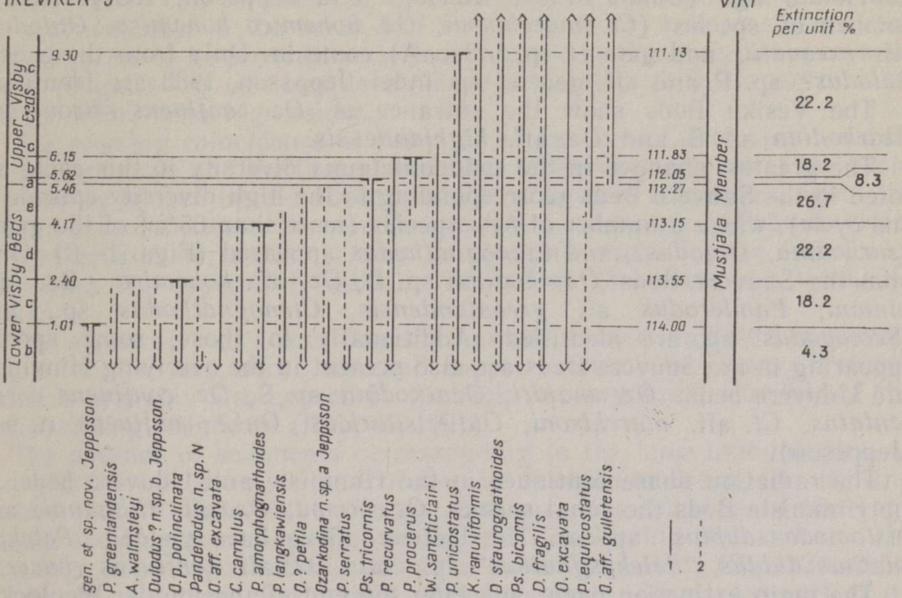

Fig. 4. Ireviken resp. *amorphognathoides* Event (based on Jeppsson and Männik, in prep.). The distribution of the conodont species in Viki (*1*) and Ireviken-3 (*2*) sections.

The end of the late Llandovery—early Wenlock cycle is marked by the sharpest extinction event (Ireviken Event by Jeppsson, in press) in the studied interval in early Wenlock time. It must be stressed that, actually, the disappearance of the taxa during this event has a "step-by-step" nature and several minor extinctions are recognized (Jeppsson, in press; Fig. 4). During a short interval (Fig. 4) most of the taxa of the rich *P. celloni—P. amorphognathoides* assemblage disappeared (more than 80% of the species and about 40% of the genera). The highest peak on the disappearance-rate curve (Figs. 2 and 3) corresponds to this event. In the Ireviken Event mostly simple-cone taxa (*Dapsilodus*, *Decoriconus*, *Panderodus*, *Pseudooneotodus*, and *Walliserodus*) survived. From the ramiform taxa only *Kockelella*, *Oulodus*?, and *Ozarkodina* have also descendants in the overlying strata.

3. The middle Wenlock—middle Ludlow cycle. The late Jaani, Jaagarahu, and Rootsiküla conodont faunas were characterized by low diversity (Fig. 1). The most significant appearances of new species during the middle and late Wenlock have been observed in Maasi, Viita, and Vesiku beds (Figs. 1—3). Presumably, these faunal changes are the result of recurrent ecological changes causing in several evolutionary lineages of conodonts (*Kockelella*, *Ozarkodina*, and *Oulodus*?) the appearance of new species and in one case even new genus (*Ctenognathodus*). In the Maasi Beds the most significant new species were *K. walliseri* and *Oz. confluens bucerus.*

Remarkable changes took place in the Viita Beds. In these beds, corresponding probably to a short innovation phase in the conodont evolution, the environmental changes led to the development of a new apparatus type. A new genus *Ctenognathodus* came into existence and is treated as an "ecological specialist" in near-shore environments of the Baltic basin in Rootsiküla age (Вийра, 1982; Aldridge and Jeppsson, 1984). Also a number of species (*Ct. murchisoni*, *Oz. bohemica bohemica*, *Oulodus*? aff. *excavata*, and gen. et sp. indet. A) come in. Only from these beds *Oulodus*? sp. R and aff. gen. et sp. indet. Jeppsson, 1983 are identified.

The Vesiku Beds show the entrance of *Oz. confluens retroversus*, *Ozarkodina* sp. B, and *Oz.* aff. *highlandensis*.

The greatest changes in the conodont fauna diversity in this cycle are noted in the Sauvere Beds (corresponding to the high diversity episode of this cycle), where a number of new species (more than 65%) of the genus *Ozarkodina*, *Oulodus*?, and *Ctenognathodus* appeared (Figs. 1—3). Only from the Sauvere Beds *Ozarkodina* sp. D, *Oz.* aff. *bohemica*, *Oz.* aff. *wimani*, *Panderodus* aff. *greenlandensis*, *Ctenognathodus* sp., and "*Scolopodus*" sp. are identified. Additionally to those, some species appearing in the Sauvere Beds are also present in the overlying Himmiste and Uduvere beds: *Oz. snajdri*, *Ozarkodina* sp. S, *Oz. confluens cornidentatus*, *Ct.* aff. *murchisoni*, *Oul.*? *siluricus*, *Oul.*? *confluens* n. ssp. (Jeppsson).

The radiation phase continues in the Himmiste and Uduvere beds. In the Himmiste Beds the zonal species *Oz. crispa*, *Oz.* aff. *tillmanni*, and *Distomodus dubius* appear. The Uduvere Beds have yielded *Pelekysgnathus dubius*, "*Pelekysgnathus*" sp., and *Oz.* aff. *confluens bucerus*.

The main extinction event, marking the end of the middle Wenlock—early Ludlow cycle, is identified near the boundary between the Uduvere and Tahula beds, where more than 75% of the species and 40% of the genera existing in the underlying beds disappeared.

4. The late Ludlow—early Devonian cycle. Only the low diversity episode of this cycle (the lower part of the late Silurian—Lochkovian cycle by Ziegler and Lane, 1987), corresponding to the sediments of the Kuressaare, Kaugatuma, and Ohesaare stages, has been studied in Estonia. In the Tahula Beds there appear *Oz. eosteinhornensis* and *Oul. elegans*, the different subspecies of which together with the two subspecies of *Oz. confluens* dominate in the fauna of the Kuressaare, Kaugatuma, and Ohesaare stages.

Conodont Diversity and the Evolution of the Basin

The comparison of the changes in the distribution of the conodont fauna and the evolution of the Paleobaltic Silurian Basin revealed some relations between them.

The initial stages of the high diversity episodes of three of the cycles discussed above coincide with the basal beds of the main stages of the development of the basin according to Einasto (Эйнасто, 1986): the innovative phase of the early Llandovery—middle Llandovery cycle coincides with the basal beds of the first macrophase (the basal beds of the Juuru Stage), the late Llandovery—early Wenlock cycle with the basal beds of the second macrophase (the uppermost Rumba or the lowermost

Velise formations), and the middle Wenlock—middle Ludlow cycle with the basal beds of the third macrophase (Sauvere Beds). The following high diversity episodes of these cycles almost correspond to the basal transgressions of the macrophases mentioned above. The ends of the studied cycles (the extinction events), however, have no correlation with the evolutionary stages of the basin.

It may be concluded that, although some correlation between the diversity cycles of conodonts and the main stages of the evolution of the basin (Fig. 1) can be observed, the evolution of the conodont fauna and the sedimentation in the basin had no direct causal relations. This conclusion seems to be proved by the fact that the appearance-disappearance peaks (Figs. 1—3) on some levels have correlation with transgressions, but on others with regressions.

The seeming coincidence of the ends of the early Llandovery—middle Llandovery cycle and the first macrophase of the development of the basin is probably caused by the absence of the sediments corresponding to the boundary beds between the middle and late Llandovery in Estonia (Нестор, 1976; Einasto, 1991). It may be also influenced by the scarcity of data from the uppermost Raikküla Formation (Imavere and Mõhkküla beds).

The absence(?) of a low diversity episode (lower—middle Llandovery cycle), or its very short interval (upper Llandovery—lower Wenlock cycle) is probably also caused by the lack (or very small amount) of the corresponding sediments (Einasto, 1991).

The absence of sediments corresponding to the long time-intervals is also established below, in and above the Rootsiküla Stage (Nestor and Nestor, 1991; Einasto, 1991). In the last case, the duration of the gaps exceeds the time represented by sediments. Considering this and also the quite high appearance rates of new taxa in the Viita Beds (Figs. 2 and 3), it may be assumed that, really, the Rootsiküla Stage (or part of it) represents the upper part of the middle Wenlock—early Ludlow cycle. In that case the Paadla Stage belongs to another (probably the middle Ludlow—late Ludlow) cycle.

To prove or disprove this assumption, a detailed study of conodonts from this interval (particularly from the middle part of the basin) is needed.

Conclusions

In the diversity changes of the conodont fauna four main cycles (early Llandovery—middle Llandovery, late Llandovery—early Wenlock, middle Wenlock—middle Ludlow, late Ludlow—early Devonian) are established in Estonia.

The greatest innovations in the conodont fauna are observed in the Juuru and Adavere stages. Remarkable innovation is noted also in the lowermost Rootsiküla Stage. The appearance of new taxa in the Sauvere Beds is mostly connected with the radiation of some genera (*Ozarkodina*, *Oulodus*, *Ctenognathodus*).

In the studied stratigraphic interval three main extinction events, marking the ends of diversity-cycles, are recognized: the Sandvika (at the end of the middle Llandovery), the *amorphognathoides* resp. Ireviken, and the *siluricus* resp. Lau events (Sweet, 1985; Aldridge, 1988; Jeppsson, 1987, 1993, in press).

The distribution and evolution of conodonts have some correlations with the development of the Silurian basin in Estonia.

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SÜNDMUSED SILURI KONODONTIDE ARENGUS EESTIS

Artiklis on käsitletud siluri konodondifauna muutumist Eestis. Selle iseloomustamisel on lähtutud liikide koguarvust stratigraafilistes üksustes, ilmuvate ja kaduvate liikide arvust miljoni aasta kohta ning ilmumiste ja kadumiste kiirusest.

Lähtudes liigilise koosseisu dünaamikast on Eesti siluris välja eraldatud neli (Vara-Llandovery—Kesk-Llandovery, Hilis-Llandovery—Vara-Wenlocki, Kesk-Wenlocki—Kesk-Ludlow ja Hilis-Ludlow—varadevoni) fauna arengu tsüklit.

Пээп МЯННИК, Вийве ВИЙРА

СОБЫТИЯ В ИСТОРИИ РАЗВИТИЯ СИЛУРИЙСКИХ КОНОДОНТОВ, ЭСТОНИЯ

Исходя из количества видов в местных стратиграфических подразделениях, из количества появлявшихся и исчезавших видов на протяжении миллиона лет и из скорости обновления и смены видового состава дана характеристика динамики изменений состава и разнообразия конодонтовой фауны.

В силуре Эстонии выделено четыре цикла развития конодонтовой фауны: ранний—средний лландовери, поздний лландовери—ранний венлок, средний венлок—средний лудлов, поздний лудлов—ранний девон.