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MACROEVOLUTION AND MACROECOLOGY OF CONODONTS OF THE SILURIAN BALTIC SEDIMENTARY BASIN

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Introduction

This work is dedicated to the study of macroevolution and macroecology of conodonts which lived in the Silurian Baltic basin and is based on the material collected from Lithuanian sections. Recent developments in paleontological, sedimentological and paleoclimatological research revealed that the Silurian period was very dynamic time interval (Cramer and Vanderbroucke 2012). During the studied period of time, Earth system experienced several so called „bioevents“ – large scale perturbations of climatic and oceanic states, during which there were significant biotal turnovers (increases of extinction and origination rates) (Jeppsson 1998). Conodonts are one of the most important components of nectobenthic and pelagic communities of the Paleozoic era. Moreover, for a long period of time conodonts were one of the most important subjects of Paleozoic biostratigraphy. Though, this clade is rarely used in paleobiological studies of their paleoecological and evolutionary dynamics. Due to the exquisite completeness and great thickness of Lithuanian Silurian geological sections, their studies promise novel insights in to the area of conodont macroevolution and macroecology. This work consists of high resolution studies of changes in conodont abundances, patterns of their species extinction selectivity, and also integrated conodont biostratigraphy and cyclostratigraphy.

The relevance of the study. At present, based on different estimates there are several million species of organisms – as a result it is just a fraction of a percent of a number of species which have ever lived on this planet (Raup 1992). Species diversity and its dynamics in time and space is a product of interaction between ecology and evolution. Deep time (geological) insight is essential for understanding the role of the listed factors in structuring modern biota. Paleobiological studies revealed very uneven patterns of evolutionary change, where “normal” time intervals are punctuated by the episodic mass extinctions (Bambach 2006). The causes of mass extinctions could differ, but their result always the same, i.e. – decrease in biodiversity and functional collapse of communities. The results of paleontological studies along with studies of modern ecosystems and climate, have shown that humanity’s expansion during the last several thousands of years (and especially in the modern times), forced major changes in the biotal functioning, which could negatively influence chances of survival for human species (Barnosky et al. 2012). The fossil record – is the only direct source of information, which allows us to evaluate impact of global changes on ecological dynamics, enabling comparison of past events with recent changes. The Silurian period the focal one in this study, experienced several strong climatic perturbations, during transitions from cold to warm climate (and even to the hothouse (Lehnert et al. 2013)) conditions and vice versa, during which there were appreciable evolutionary turnovers. Conodonts due to their abundance and excellent preservation qualities as well as having broad environmental distribution are ideally suited for studying macroecological and macroevolutionary processes which proceeded during episode of intense environmental change.

The study presented here includes a testing of selectivity of conodont extinctions, high resolution biostratigraphy as well as dynamics of conodont abundances and other paleoecological features. As a result, new patterns were revealed which statistically associate species level and organismic features with the probability of conodont species survival during the Ireviken mass extinction event. The chronology of development of conodont biota during and shortly after Mulde biotic event was refined. The long term controls of Pridoli conodont abundances by astronomic factors (i.e. Earth's orbit eccentricity modulation) were revealed as well.

Aim of the work. To reveal major features of macroevolution and macroecology of conodonts from the chosen time intervals of the Silurian Baltic basin of Lithuania:1) upper Llandovery – Lower Wenlock; 2) Upper Wenlock – Lowermost Ludlow; and 3) Middle and Upper Pridoli.

Main tasks:

- Reveal determinants of survival selectivity of conodont species during the Ireviken event, using bivariate and multivariate logistic regression and regression tree methodologies.
- Using natural gamma ray record and signal theoretical techniques construct an Upper Homerian cyclostratigraphic scale in the Viduklė-61 core section.

- Revise Upper Homerian conodont biostratigraphical time scale according to taxonomic analyses of conodont material from Lithuanian sections.
- Reveal patterns of paleoecological dynamics of upper Homerian conodonts from the shallow water environments, using as an example Ledai-179 core section.
- Reveal major dynamic pattern in the Middle and Upper Pridoli conodont abundances and suggest possible mechanisms which driven their change.

Novelty of the research. In the present study the influence of various ecological features of conodonts in their extinction selectivity during one of the most severe Silurian bioevents – the Ireviken mass extinction was investigated. Paleoecological features of abundance dynamics have never been studied before as possible determinants of survival (or contrary extinction) selectivity of species in macroevolutionary context. The current results suggest that species which had higher skewnesses of their local abundance distributions and higher levels of autocorrelation in their local abundance time series had higher chances of survival during this mass extinction event. Previous theoretical and empirical neo-ecological studies presented conflicting evidence concerning relations between levels of temporal autocorrelation in a time series of abundances and extinction risk. The results of this study could be used in evaluating extinction risk of modern species due to environmental alterations caused by human species, for example by estimating long-term autocorrelations of abundance time series of focal species in a quaternary fossil record. Moreover, this study confirmed the influence of conodont environmental preferences in modulating their extinction risk (it is lower in more shallow environments), which points to the specific deep (and open) ocean causes of the mass extinction.

Conodont biozones which were distinguished during a biostratigraphical study of the Lithuanian Upper Homerian sedimentary sequences will enable the possibility of correlation of patterns found in local sections with the information about global development of Mulde biotic event and post-extinction recovery of faunas.

The first quantitative cyclostratigraphical time scale of the Upper Homerian sequences in deep facies of the Baltic Silurian basin, which was created analyzing changes in natural gamma radiation intensity in the Viduklė-61 core section, could be used in further correlation and analysis of geobiological events for the later Wenlock.

It was demonstrated quantitatively for the first time, using spectral analytical techniques, that long term changes in the abundances of Middle and Upper Pridoli conodonts from Baltic basin are partially driven by periodic (and most possibly astronomical) processes. This finding enables us to use conodonts as an important indicator of astronomically driven environmental change and thus use their abundance dynamics in constructing high resolution astrochronological time scales.

Positions to be defended:

- Conodont species which had higher skewnesses of their local abundance distributions and those species which lived in shallower (located near shore) environments had higher chances of survival during the Ireviken extinction event.
- Conodont zones *Ozarkodina bohemica longa* and *Kockelella ortus absidata* are distinguished in Lithuanian sections (Viduklė-61 and Ledai-179).
- Paleoecological taxonomic dynamics of Upper Wenlock conodonts in shallow water environments experienced several state shifts. It was caused by development of physical environment and decrease in accommodation space in the eastern part of the Silurian Baltic basin (i.e. due to normal regression).
- Dynamics of Middle and Upper Pridoli conodonts abundances have a multifractal structure, which points to the multiplicative and hierarchical control mechanisms of change. Dynamics of their abundance change are also chaotic in their origin (i.e. they strongly depend on values of initial conditions). Three alternative states of ecosystem functioning existed during this time interval as evidenced by changes in correlation between stable carbon isotopes and conodont abundances. Dynamics of Middle and Upper Pridoli conodonts abundances are characterized by two cyclicities.

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1. Literature review

1.1 Conodont biostratigraphy of the Silurian Baltic basin and Silurian bioevents

Conodonts were small bilateral animals, which most probably belong to vertebrates or at least chordates (Friedman and Sallan 2012; Janvier 2013). Even though there are still some discussions which doubt their close relations to vertebrates (Turner et al. 2010). Biomechanical, microwear, and comparative anatomical studies revealed that their only biomineralized parts, or so called "elements", were used similarly as teeth of crown vertebrates (Goudemand et al. 2011; Jones et al. 2012; Purnell 1995). Discrepancies between observed conodont anatomy in exceptionally preserved fossils and anatomical features of crown vertebrates, could be explained by selective post-mortem degradation of advanced features, which is observed in taphonomical experiments with modern lampreys and amphioxuses (Janvier 2013; Sansom et al. 2010).

Most frequent conodont finds in the fossil record are their biomineralized elements, composed of bioapatite enriched with carbonates (Trotter and Eggins 2006). Remains of conodont elements are found in sedimentary strata ranging from Cambrian up to Late Triassic periods (Ogg et al. 2008). Due to their resistance to weathering, their small size, great abundance in samples and fairly complete fossil record, these conodont micro remains are widely used in biostratigraphy, paleoenvironmental analyses, sedimentary basin and tectonic studies (Foote and Sepkoski 1999; Harris 1979; Joachimski and Buggisch 2002; Märss and Männik 2013; Žigaitė et al. 2010). Thus conodonts have a great potential as a tool for understanding macroevolutionary, macroecological and Earth system dynamic processes.

Historically on the territory of the Baltic Basin (and indeed globally) conodonts were first described by Ch. Pander in the middle of the XIX century (Pander 1856), which described several species of Ordovician and Silurian conodonts. However, further developments in Silurian conodonts research were halted for approximately one century, until O. Wallliser presented the first conodont stratigraphical schemes of Carnic Alps (Walliser 1957; Walliser 1964). After that there was a great expansion of conodont biostratigraphical work in countries covering area of the Silurian Baltic basin. In Lithuania conodont biostratigraphy was initiated by V. Saladžius in 1966, and continues up to the present time by A. Brazauskas (Brazauskas 1993; Brazauskas et al. 2004; Šileikytė and Brazauskas 2008). Till now Silurian strata of Lithuania were subdivided in to the 20 conodont zones (Brazauskas et al. 2004).

At the same time conodont biostratigraphy research was developing in other countries. Based on studies of geological sections in Skåne region and Gotland Island, L. Jeppsson developed first detailed stratigraphical conodont time scales for this region (Jeppsson 1969; Jeppsson 1974; Jeppsson 1982). At present, Silurian strata of Gotland spanning from upper Llandovery to the Upper Ludlow, are subdivided in to the 23 conodont zones having many more local subzones (Calner et al. 2012; Jeppsson et al. 2006).

The northern part of the Silurian Basin is thoroughly studied by Estonian conodontologists. The earliest research there dates back in to the late seventies, when material from Estonian sections were compared to that of Lithuanian ones (Viira 1977). Conodont biostratigraphy research experienced great development during eighties as a part of ecostratigraphical correlation projects. The purpose of project was a comparison of development of benthic, nektonic and planktonic Silurian communities (Kaljo et al. 1986). Modern conodont stratigraphy of Estonian Silurian sections is well correlated with conodont time scales from other regions of the Baltic basin, and integrated with biostratigraphical time scale of other vertebrates (Jeppsson and Männik 1993; Märss and Männik 2013).

In other countries, which territories are parts of the Silurian Baltic basin (Poland, Latvia, Belarus, Ukraine and Russia (Kaliningrad district)); conodont biostratigraphy at a present time is in incipient stage (exceptions exist (Drygant 1984; Loydell et al. 2003; Männik and Małkowski 1998)). Recently there is surge of active work, which is centred on integrated stratigraphy of Ukrainian geological sections. During this work there were recorded critical geobiological intervals, and especially Silurian-Devonian transition (Jarochowska and Kozłowski 2014; Kaljo et al. 2012; Małkowski et al. 2009; Racki et al. 2012).

Described development of knowledge about temporal and spatial patterns of conodont species distributions served as a base for the development of theory of Silurian bioevents. The first who linked episodes of increased conodont species turnover to paleoceanographycally mediated environmental perturbation was L. Jeppsson who analyzed sedimentary successions of Upper Wenlock and Middle Ludlow (Jeppsson 1987). Further studies have show, that during Silurian period there were up to 15 global bioevents of varying strength and long-term impact on biota (Kaljo et al. 1996). However not all of those events are equally studied and proved to be significantly affecting different clades. The most widely used scheme for bioevents is proposed by L. Jeppsson. He, based on his own material and global compilations, distinguished 11 bioevents (Jeppsson 1998). Moreover, he proposed that there is distinctive pattern of environmental change that leads to the development of evolutionary and ecological turnovers. Jeppsson states that there are Primo and Secundo episodes of climate and oceanographic states. Primo episodes are characterized by cold and humid climate and active oceanic convection, and conversely Secundo episodes are characterized by hot and arid climate with sluggish salinity driven oceanic convection. Transitions between those episodes are characterized by destruction of species habitats and consequently synchronous multiple extinction episodes (Jeppsson 1997). Events which have a greatest impact on species macroevolution and environmental deterioration in general were Mid-Early Silurian (Earliest Wenlock) Ireviken event, Late- Early Silurian (Sheinwoodian) Mulde event, and Early-Late Silurian (Late Ludlow) Lau event (Calner 2008).

During this study three time intervals from the Silurian period were investigated. Two of them correspond to the Ireviken event and the Mulde event and its post-extinction recovery during latest Wenlock and earliest Ludlow. The third studied time interval corresponds to the middle and the latter parts of the Pridoli epoch, which is also characterized by intense changes in biota and climate (Lehnert et al. 2013).

1.2 Macroevolutionary and macroecological studies of the fossil record

Evolution is frequently defined as a “changes of allele frequencies in populations”. Even though this approach isn’t wrong, it is certainly incomplete and in many ways limiting. The approach does not considers the role of hierarchical levels of biological organisation in evolutionary dynamics (Eldredge 1985). Therefore, microevolutionary model of intrapopulational dynamics of gene frequency changes is inadequate in understanding and describing history of life, because it ignores origins, differential extinctions and durations of phylogenetic lineages, which define long-term evolution, by structuring taxonomic composition of biota (Williams 1992).

Complimentary to the microevolutionary studies is so called “taxic” approach (Eldredge 1979), which treats species and other taxa as ontological individuals in higher level sorting processes, simultaneously recognizing importance of cross-level evolutionary effects (Ghiselin 1974; Gould and Lloyd 1999; Vrba and Gould 1986). The major influence on the development of this macroevolutionary approach had the origin of a theory of punctuated equilibria during the early seventies, which states, that majority of morphological change in species evolution is concentrated in rapid cladogenetic events (Eldredge and Gould 1972). Consequently the pattern of punctuated equilibria was found to be one of the most common modes of macroevolution (Hunt 2007). Subsequently it was also been confirmed, based on the mathematical analyses of speciation models, that punctuated equilibria are the most expected result during parapatric mode of speciation (Gavrilets 2004). If majority of evolutionary change is concentrated in bursts of speciation, and direction of divergence during speciation is random with respect to long-term trends, then major driver of long-term changes should be species selection (Stanley 1975), or more generally species sorting which also includes phylogenetic drift and other processes (Stanley 1979; Stanley 1981; Vrba and Gould 1986). Thus macroevolution in this work is understood in the same way as it was recently defined by Lieberman and Eldredge: “the patterns and processes pertaining to the birth, death, and persistence of species” (Lieberman and Eldredge 2014).

Closely allied to macroevolutionary studies is so called macroecology research programme. The macroecology as an approach for the study of large scale ecological, biogeographic, and paleobiological patterns started its development in the latest part of the XX century, as a synthesis of approaches used in studies of biodiversity structure and its dynamics (Brown 1995; Brown and Maurer 1989). One of the founders of the science of macroecology J. Brown defines it as:"...a nonexperimental, statistical investigation of the relationships between the dynamics and interactions of species populations... and the processes of speciation, extinction, and expansion and contraction of ranges..." (Brown 1995). Macroecological approach is a necessary part of the ecological and evolutionary research, because processes which control biodiversity dynamics are scale dependant, i.e. there are different patterns of "species-area" curves which strongly depend on kinds of territories we measure – for example different areas of the same region or different isolated islands (Rosenzweig 1995). Also due to the nonlinearities of interactions between species, there could be qualitatively different ecological dynamic regimes, depending on the sheer number of species and their characteristic spatial scale of competition in a community (Laird and Schamp 2008).

Paleontological record is a very valuable source of material both for a macroecological and a macroevolutionary research. Fossils could potentially provide information about changes in local species abundances, their geographical ranges and structures of those ranges, and other macroecological parameters through significantly wider range of time scales in comparison to neo-ecological studies. Even more important role of the fossil record is in revealing macroevolutionary phenomena. The documentation of the fact of mass extinctions in the history of life, and their long term consequences for subsequent macroevolutionary regimes could serve as a premier example of unique insights that could be reached studying macroevolutionary patterns in paleobiological material (Jablonski 1986; Raup and Sepkoski 1982). Moreover, traditional macroecological research treats relations between explanatory variables as invariant in time. The relevance of evolutionary constraints in ecology is increasingly recognized (Futuyma 2010) and macroevolutionary research based on paleontological material could bring light in solving questions about the role of historical accidents (and contingency in general) in constraining rules of macroecological dynamics (Diniz-Filho et al. 2013).

In the present study conodont material was used in researching the influences of species abundance and the patterns of its temporal structure, and also habitat preferences in selectivity of species extinctions during the Ireviken mass extinction event. In addition, using high resolution integrated stratigraphy and taxonomic occurrence data was investigated along with the timing and possible paleoecological effects of Mulde bioevent. The conodont material was used for understanding long term macroecological determinants of abundance change in middle and upper Pridoli conodonts. Therefore results of this research ties large scale environmental changes (i.e. orbital forcing) documented in sedimentary successions with the biotic macroevolutionary and macroecological responses of conodonts.

2 Material

All research material used in this study comes from Lithuanian deep core sections. During the Silurian period, studied territory was a part of so called Silurian sedimentary basin which stretched on the territory of the Baltica paleocontinent, and which was located near the equator (Cocks and Torsvik 2005).

Three time intervals of the Silurian period were studied: the Ireviken event (late Llandovery – early Wenlock); Mulde event interval (upper Wenlock); and middle to upper parts of the Pridoli epoch. In order to reach the goals of the study, overall seven core sections were studied: Gėluva-99, Ledai-179, Butkūnai-241, Tverečius-336, Jočionys-299, Viduklė-61, Šešuvis-11. In the study of the Ireviken event, five deep cores were investigated for conodonts, which covered all major conodont biofacies belts (or paleocommunities *sensu* (Brazauskas 1993)): Gėluva-99 (26 samples), Ledai-179 (22 samples), Butkūnai-241 (27 samples), Tverečius-336 (26 samples), Jočionys-299 (36 samples). In the study of the „Big Crisis“ or Mulde biotic event two core sections (Viduklė-61 (66 samples), and Ledai-179 (53 samples)) were investigated. They reflected deep offshore and correspondingly nearshore shallow water settings. Finally, in the study of Pridoli conodonts two core sections were studies: Šešuvis-11 (77 samples) and Viduklė-61 (37 samples).

Conodont elements were extracted from rock matrix using standard buffered weak acid methods. Limestones and rocks with calcium carbonate cements were dissolved using 10 % buffered acetic acid, and dolostones and rocks with dolomitic cements were dissolved using 10 % buffered formic acid (Jeppsson and Anehus 1995). If there were abundant insolubles after acid treatment procedure, those residuals were additionally dissolved using heated (up to 60 C^{o}) 10 % hydrogen peroxide solution, which further oxidised organic cements. Dependant on the composition of samples, their chemical treatment spanned from 5 days up to several months. Residuals of chemical treatment were sieved through set of sieves from 0.1 up to 3 mm holes in diameter, which corresponds to the range of size of Silurian conodonts. Having sorted residuals conodont elements were picked under the MBS-9 binocular microscope.

The dataset of conodont taxonomy and their abundances, lithology, geophysical and stable isotopic data was compiled. Lithology has been described based on the visual inspection of core material and also using information from Lithuanian deep core lithology database. Natural gamma radiation logs were digitized from the analogical geophysical reports which are stored at the Geological Survey of Lithuania. The data of stable isotopic ratios ($\delta^{13}C$) of Viduklė-61 and Šešuvis-11 core sections was was extracted from the published articles (Kaljo et al. 2012; Martma et al. 2005). The in $\delta^{13}C$ data Ledai-179 section was obtained from the cooperative project MIP034/2012.

3 Methodologies

Protocols for statistical analyses of conodont extinction selectivity during the Ireviken event

The set of parameters describing species abundance structure and environmental preferences was studied in predicting conodont extinction selectivity during the Ireviken mass extinction event. Those parameters are: average abundance of the species at positive sampling sites (samples in which there were non-zero abundances of elements of given conodont species), averaged two timer variation coefficient of abundance, skewness of abundance distribution, Hurst exponent, spectral exponent, apparent extirpation rates of a species, apparent immigration rates of a species (both rate types were calculated using methodology described in (Legendre et al. 2008)), average gamma ray intensity at positive sampling sites (=amount of clayey material in samples), standard deviation of gamma ray intensity at positive sampling sites (width of environmental niche), and also skewness of distribution of gamma ray intensities at positive sampling sites.

All listed parameters were calculated from the conodont and environmental data from five Lithuanian core sections. Overall there was used information about 34 conodont species. In the statistical analyses of extinction selectivity species which survived extinction event were coded “0” and those that went extinct were coded “1”.

Due to the binomial error structure, extinction selectivity was studied using generalized linear modelling approach (in this case using logistic regressions) and also regression tree methodology. Initially simple bivariate logistic models were constructed, and then from the set of best predictors exhaustive set of multivariate logistic models was constructed which were compared using AICc information criterion and associated Akaike weights using *AICmodavg* package in R environment (Mazerolle 2011). Regression tree method was used as a complimentary approach to elucidate hierarchical and context dependant action (which is expected in macroevolutionary processes) of variables (Izenman 2008). For this purpose the CART algorithm in the Rpart package in the R environment for statistical computing was utilized (Therneau and Atkinson 1997).

Protocols for statistical analyses used in the cyclostratigraphy and the integrated biostratigraphy of the Mulde event interval

In order to test the possibility of cyclicities in sedimentary patterns during late Homerian time (lower Silurian) variability in natural gamma radiation in well studied Viduklė-61 core section was studied. The later section reflects deep shelf environments, in the depth interval between 1269 and 1320 m. For this purpose two kinds of spectral analyses: Lomb methods for testing statistical significance of cyclicities, and wavelet analysis (with Morlet "mother" wavelet) for time-frequency decomposition of spectral power and spatial localization of found cycles were used. Both types of analyses were performed using PAST statistical package (Hammer et al. 2001).

Based on distribution of conodont taxa in the same interval of the Viduklė-61 core section zonal biostratigraphic time scale for Mulde event and post-extinction recovery was constructed, integrated with the graptolite, lithology, stable carbon isotopic material and cyclostratigraphic model. For one taxon (*Kockelella orthus absidata)* which had sufficient number of occurrences (fossiliferous horizons) distribution free confidence interval was calculated for the first occurrence of this zonal species using PAST package (Hammer et al. 2001; Marshall 1994).

The core section Ledai-179 was studied because it reflects development of Mulde event in nearshore environments of the eastern part of the Baltic basin. In this core section based on abundant conodont material conodont biozones were distinguished, and performed quantitative paleoecological study of species turnover. In the description of species turnover three metrics were used: local species abundance, proportional immigration rates, and proportional extirpation (local and/or temporary extinction) rates. Proportional immigration rates were calculated, as a number of appearances of new species, in given sample, from the perspective of previous sample divided by a total number of species in previous sample (in the calculation of total number of species in a sample it was assumed that a species lives in a region during whole its stratigraphic range). Calculations of proportional extirpation rates were analogous, just in the place of number of appearance at given time we need to use number of disappearances of species at given time. Local species abundance was calculated as a raw number of conodont species found in a sample.

Describer parameters which reflected species turnover levels in the Ledai-179 core section were studied for the permanent changes in values of their averages and variances using so called change point analysis in R environment using *changepoint* package (Killick and Eckley 2013; R 2011). Approximate binary algorithm for sequence segmentation was used, which is superior to other analogous algorithms in allowing to set maximal number of change points, which reduces a probability of overfitting sequence (Killick and Eckley 2013).

Protocols for statistical analyses used in the study of the middle to upper Pridoli conodont abundance dynamics

At different temporal and spatial scales there are plentitude of differing controlling mechanism of ecological and evolutionary change (Bennington et al. 2009). In order to determine temporal scaling properties of conodont abundance change during the middle and the upper parts of the Pridoli epoch. Three kinds of statistical studies were performed: lacunarity analysis, estimation of Hurst exponents and also spectral density estimation (calculating so called spectral exponents).

Lacunarity analysis determines how heterogeneity in a given signal is distributed through range of scales by constructing graphs of dependencies of lacunarities against scales of measurement (or window sizes)(more information on methodology see in (Plotnick et al. 1996)). Different shapes of lacunarity profiles point to different patterns: exponentially decreasing profile points to white noise generating process, increases in a curve reveal clustering at that scale, and straight line decreasing profile points to multifractal nature of generation process (Plotnick 1995). In order to test robustness of found patters null distributions of lacunarity profiles for each dataset were generated, using 100 randomizations of each original stratigraphic time series. In addition to the null model testing, comparison of the patterns using information theoretical AICc approach was done (Claeskens and Hjort 2008) fitting multifractal (linear) and white noise (negative exponential) models to the lacunarity profiles in R statistical computing environment (R 2011).

In addition to lacunarity analyses, in order to determine properties of autocorrelational structure of time series Hurst estimates (H) was calculated. Later estimates how range of possible densities of outcomes grows with the passage of time (Ariño and Pimm 1995). The robustness of Hurst estimates was tested calculating null distribution of this parameter which is based on one hundred randomized sequences of each stratigraphic abundance time series of conodonts using package *gtools* in R environment (Warnes et al. 2008). The shapes of spectra of conodont abundance change were determined as well. Using implementation of the REDFIT algorithm in the PAST environment spectra and their slopes on log-log coordinates of spectral power against frequency have been determined. Slope coefficient, similarly to Hurst estimate, shows autocorrelational structure of the signal. For example spectrum of a white noise have a zero slope, and the processes which leave pink noise pattern have a slope between zero and minus one (Yacobucci 2005).

In an effort to determine stability properties of long-term conodont abundance dynamics so called maximal Lyapunov exponent for the conodont abundance time series from the most complete and sufficiently long (in number of samples) Šešuvis-11 core section was calculated. Maximal Lyapunov exponent shows how perturbations in initial conditions influence further evolution of a system (i.e. if it is positive, then system is highly sensitive to initial conditions – that is chaotic). For this purpose an R implementation of the TISEAN algorithm (package *tseriesChaos*) was employed, which allows accurate and consistent estimation of maximal Lyapunov exponent directly from short (in a number of observations) data (DiNarzo 2007; Hegger et al. 1999).

In order to determine possible relations of abundance change with environmental factors “global” and localized (or mowing window) correlation analyses between conodont abundances and gamma ray intensities (=amount of clay material) at sampling sites and also stable carbon isotopic ratios ($\delta^{13}C$) was performed. Initially, time series were normalized using Box-Cox transformation and also their averages were subtracted from them. Then generalized differencing procedure on transformed time series was performed, which relaxes an assumption of perfect autocorrelation (McKinney and Oyen 1989). During the analysis of localized mowing window correlations confidence intervals for correlation coefficients, based on their sample sizes (critical values for a given sample size were found in (Rohlf and Sokal 2012)) has been calculated.

In order to test hypothesis about presence of cyclicities in conodont abundance fluctuations two kinds of linear spectral analyses were performed. Box-Cox transformed and “Pre-whitened” (by subtracting mean and trend) signals were analyses using REDFIT algorithm in PAST environment, which is robust with respect to random variations in a position of stratigraphic samples with respect to time scale, and which allows to test the null hypothesis of lack of periodicities by estimating confidence intervals for AR(1) process (Schulz and Mudelsee 2002). Similarly as in the study of cyclostratigraphy of the Upper Homerian sequences, in order to determine time-frequency evolution of spectra of abundance change continuous wavelet transform with the Morlet “mother wavelet” was used (Hammer and Harper 2008).

4 Results and discussion

Determinant of conodont extinction selectivity during the Ireviken event

The results of bivariate logistic regression analyses of conodont survival selectivity during the Ireviken event have shown, that seven out of ten studied parameter were insignificant (at $p<0.1$ level) in explaining extinction patterns. Those are average abundances, averaged variation coefficients, Hurst exponents, rates of extirpation, and rates of colonization, the standard deviations of environmental proxies, and also the degrees and direction of skewnesses of the environmental preferences. Another three variables – scaling exponents (ν) of abundance power spectra, average substrate preferences as described by the gamma-ray proxies, and skewnesses of the local species abundances, were statistically significantly associated with conodont species survival during studied extinction event. Those three variables were used in constructing exhaustive set of multivariate models. AICc information theoretical comparison of four models, have shown that the best model which describes extinction patterns is the one which included as an explanatory variables skewnesses of the local species abundances, and also substrate preferences as described by the gamma-ray proxies (regression coefficient of both variables were statistically significant at $p<0.05$ level).

A regression tree approach has revealed very similar results to those of multivariate logistic model selection study. The best descriptor of the survival probability was a substrate preference of species, which was followed by skewnesses of the local species abundances, and local extirpation rates (which were surprisingly though, positively correlated with survival of species).

Revealed patterns show a great importance of temporal abundance structure of species, as revealed by values of spectral exponents and also skewnesses of their abundance distributions, in extinction selectivity during the Ireviken event. It was shown in theoretical modelling, and modern neo-ecological studies that temporal autocorrelation have an effect on probability of population survival. Though, the degree of importance and sign of effect (positive or negative) strongly depends on parameters of studied models of population dynamics (Halley and Inchausti 2004; Halley and Kunin 1999; Inchausti and Halley 2003). In this work it was shown that greater autocorrelation of abundance change is positively associated with the species survival. The positive association of skewnesses of abundance distribution with the survival of conodont species shows possible important effects of intra-species metapopulation and also metacommunity dynamics in creation of macroevolutionary patterns. In the paleoecological record, those species which are prone to large abundance excursions, are usually identified as “non-equlibrial” forms, which are characterized by higher rates of population growth (Hallam 1972). It was shown on theoretical grounds that in competitive communities there is subdivision of resources between species with linear and more non-linear growth rates. If resources fluctuate, first kind of species consume averages of resources, and another kind (more non-linear) consume variances of resources (Loreau 2010). It is possible that unstable conditions during Ireviken event created unstable functioning of ecosystems, which in this case would have positive effects on species with higher skewnesses of their local abundance distributions. It is also possible that there were positive effects which were related with episodes of unchecked growth of populations – i.e. increase of exaptive polymorphism pools (*sensu* (Gould 2002)) in conditions of relaxed natural selection (i.e. “waves of life” (Bennett 1997; Yablokov 1986)). That is, it is possible, that at least partially, survival of conodont species represented genuine case of narrow sense species selection (Gould 2002; Jablonski 2008; Okasha 2012).

Statistically significant and negative association between average natural gamma ray intensities at sampling sites (=amount of clay in sedimentary rocks) with the survival probability, reveals to open (or deep) ocean causes of Ireviken mass extinction event. To the possibility of differential survival of benthic versus nektonic and nekto-benthic species, also points the fact that taxa which were affected most – conodonts, graptolites and chitinozoans (Jeppsson 1997; Melchin et al. 1998; Paluveer et al. 2014), are mostly pelagic. The reason why pelagic species could be more vulnerable is that pelagic habitats are more homogenous, and the heterogeneity is supported by dynamic structuring of water masses, which could be easily lost during episodes of sudden climatic perturbations (Lipps 1986).

Late Wenlock conodonts and integrated stratigraphy

After performing Lomb periodogram and Morlet continuous wavelet analyses it was revealed that in the Viduklė-61 deep core section there are two statistically significant (at 99 % level) cyclicities in natural gamma ray intensities. Longer periodicity has period length of 16.7 m, and shorter one have period length of 6.7

m. Both cyclicities could be traced in whole studied (upper Wenlock) interval of the section. In order to determine the sources of periodicities most probable duration of the studied interval was estimated, based on two published radiometrically determined dates: age of Grötlingbo bentonite (428,45 ± 0,35 Ma), and also age of Wenlock-Ludlow boundary (427,86 ± 0,32 Ma) (Cramer et al. 2012). Based on these age estimates period length of longer cyclicity is about 300 Ka, and the period length of shorter cyclicity is approximately 120 Ka. Though, there are several tectonic mechanism of eustatic sea level change which could act at given time scales (unsteadiness of mantle convection in convergent tectonic settings (Miall 2010)), based on period lengths most probable mechanism of sedimentary cycles are 100 Ka and 400 Ka Milankovitch cyclicities, which are caused by changes in eccentricity of Earth's orbit (Zachos et al. 2001). Due to the abundant graptolite material, and rare finds of zonal conodont species in Viduklė-61 core, revealed cyclicities (regardless of their nature) could be tied to the international geochronological scale.

The analysis of conodont species distributions in the upper Wenlock strata of Viduklė-61 deep core revealed that majority of rarely found conodont remains belong to deep water and/or generalist species with long stratigraphic ranges, belonging to *Panderodus*, *Dapsilodus*, *Pseudooneotodus*, *Decoriconus* and *Wurmiella* genera. In the studied interval four species with significantly shorter durations were found. Those are *Ozarkodina bohemica longa* Jeppsson, *Kockelella orthus absidata* Barrick and Klapper, *Ctenognathodus murchisoni* Pander and also *Oulodus siluricus* (Branson and Mehl). Only *K. o. absidata* zonal species had sufficient number of samples in order to calculate confidence intervals for its FAD (first appearance datum). The first appearance of this species is observed at depth of 1283 m, and the last appearance at depth of 1249.2 m. Though, the calculation of the confidence interval shows that most probable location of FAD of this species should be at depth interval between 1283 and 1290 m. The inferred position is congruent with previous stratigraphic schemes, which places this species between two Mulde carbon isotopic excursions (Cramer et al. 2012)(as it is observed in this case). Another zonal species – *O. b. longa* is found just in two samples (at 1290.6m and 1267). There was no possibility to calculate non-parametric confidence intervals for appearance events for this species because of low number of observation. Rareness of this species in the shelfal deposits, points to unsuitability of this kind of environment for *O. b. longa*. Consequently, its stratigraphic interval should be significantly truncated. *O. siluricus* is found just in one sample (at depth of 1297.1 m). This species is usually found in Lithuanian sections lower than *O. b. longa* and its range overlaps in the lower part of the latter Zone (Brazauskas 1993).

Another species with relatively short duration – *C. murchisoni* was found in only one sample (at 1302 m). This positive find is stratigraphically much lower than expected (in *nassa* graptolite Zone), that is lower than the whole range (even considering confidence interval of the FAD) of *K. o. absidata*, which usually envisioned as originating significantly earlier than *C. murchisoni* (Calner and Jeppsson 2003). This indicates earlier than previously thought, origin of discussed species and possibly quicker recovery of conodont faunas after Mulde biotic event. It is possible, however, that this event represented turnover pulse type of biotic perturbation where the same factors (i.e. fragmentation of species geographic range) that enhance probability of species extinction, also increase probability of speciation (Stanley 1990; Vrba 1992).

Based on the comparison of conodont distributions with the δ^{13}C trend in the Ledai-179 core section two conodont chronozones were distinguished. Based on the finds of *O. b. longa* the Zone with the same name is distinguished in the interval between 649.9 and 637 m. In this core section there are no finds of the uppermost Wenlock zonal species *K. o. absidata*, but in other sections in Lithuanian part of the Baltic basin (see for example Viduklė-61 conodont data) it is usually found in the interval of the second Mulde positive isotopic excursion. Based on this observation and the pattern of carbon isotopic variability, *K. o. absidata* Zone is conditionally distinguished in the core interval between 637 and 618 m. In this core section which spans upper Wenlock and lower-most Ludlow two more temporally restricted conodont species: *Ctenognathodus murchisoni* and *Ctenognathodus sp. S* were found (*sensu* (Viira and Einasto 2003)) at depth of 609.2 m. Though *C. murchisoni* previously was considered as a zonal species, in this study it was shown that it had significantly longer stratigraphic interval than previously thought. Though, findings of *Ctenognathodus sp. S* are restricted to upper-most part of the Ludlow, its short stratigraphic distribution cannot be assumed from known occurrences which are statigraphically narrowly confined, because all species of the genus

Ctenognathodus lived in shallow water environments, and this kind of environment have the highest probability for development of large stratigraphic gaps in comparison to other basin settings (Patzkowsky and Holland 2012).

The results of change point analyses of paleoecological parameters of local conodont taxonomic turnover in Ledai-179 section have shown that there were two changes to lower conodont species richness: one in Jaagarahu regional stage, at depth of 660.8, m and another one at depth of 629.9 m in the Gėluva Regional Stage in the upper part of Nevėžis Formation. Per capita conodont immigration rates also experienced two changes to higher average and variance levels: one at depth of 698.3 m in Birštonas formation (though this change was very small and possibly represents an instance of statistical overfitting), and another one at depth of 637.7 m in the Gėluva regional stage. The changes in extirpation rates were distributed in the section similarly to the changes in immigration rates. The only change to higher levels of volatility in extirpation rates occurred at depth of 629.9 m (at the same point where occurred second change to the lower conodont species richness) in the Gėluva regional stage.

First change in local abundances observed in Ledai-179 core section represents permanent local extinction of deep water taxa (i.e. *Waliserodus curvatus*, *Pseudooneotodus bicornis*), shortly after abrupt changes to more volatile regime of shelfal sedimentation (as it is evident from natural gamma ray logs). Second change to even lower local species richness is approximately coincident with changes to higher levels of per capita immigration and extirpation rates. At the same time there was change to extremely shallow water lagoonal of sabkha environments, as reflected in lithology and natural gamma ray logs of the section. Only species which could exist in these environments belonged to the genera of *Ctenognathodus* and *Ozarkodina*. Extreme variations in extirpation and immigration rates could be attributed to intercalation of marginally livable and completely non-livable (for conodonts) habitats of nearshore environments. Interestingly though, none of changes in conodont paleoecological parameters occurred at the level of Mulde extinction at the beginning of the Mulde carbon isotopic excursion (at depth of 649.9 m).

Patterns and probable mechanisms of abundance dynamics of the mid- to late Pridoli conodonts

Visual inspection of conodont abundance curves in the Šešuvis-11 and Viduklė-61 cores, reflecting paleoecological changes during the Jūra time (mid- upper Pridoli), show wave like first order pattern with the lowest abundances in the lower and the upper-most parts of the formation and the highest average abundances in the middle part.

Analyses of lacunarity profiles have shown that sample weight standardized changes in the Šešuvis-11 core section have multifractal structure (fitted linear model have a high significance level:$r = -0.96, p = 0.0001$). The profile also does not overlap with the assemblage of lacunarity profiles which were generated using randomized sequences of conodont abundances. Model selection approach also confirmed higher support for multifractal (or linear) model (AICc = - 67.67 and Akaike weight ω= 1.0) than to random (or negative exponential) model (AICc = 7.41 and Akaike‘s weight ω= 0). Lacunarity profile for sample weight non-standardized conodont sequences from the same section was calculated as well. In this case lacunarity profile significantly overlapped with the assemblage of lacunarity profiles of randomized sequences. The model selection accurately predicted that the signal was generated by multifractal processes: linear model (AICc = -133 and ω= 1.0), and negative exponential model (AICc = -7.50 and ω= 0).

In contrast to described patterns in the Viduklė-61 core section signal of weight non-standardized conodont abundance sequences shows white noise pattern where empirical lacunarity profile completely overlaps with the null distribution of lacunarity profiles calculated from randomized empirical time series. The same pattern emerges from information theoretical model selection results: negative exponential model has higher support (AICc = -66.99, ω= 1.0) than linear model (AICc = -43.62, ω= 0).

Similar results are revealed during the estimation of Hurst exponents. Conodont abundance changes in the Šešuvis-11 core section exhibit $H=0.66$ ($p<0.01$), and in the Viduklė-61 section $H=0.53$ ($p=0.25$). It means that in the Šešuvis-11 section it exhibits statistically significant autocorrelated structure, and in the Viduklė-61 section structure of abundance change is indistinguishable from “white noise”. Similarly in the Šešuvis-11 section, regression slope coefficient of log-log power against frequency is $a= - 0.68$ ($r=-0.65$, $p=0.0001$); in the Viduklė-61 section the same parameter value is $a=0.41$ ($r=0.34$, $p=0.15$). These results confirm that signal in the Šešuvis-11 section is systematically more autocorrelated than in the Viduklė-61 section. Based on the value of the slope of regression on the power spectrum of Šešuvis-11 conodont abundances, the pattern of conodont abundance variation could be classified as a 1/f (or pink) noise.

The estimation of maximal Lyapunov exponent from weight-standardized abundance time series in the Šešuvis-11 core section revealed its positive value ($\lambda_{max}=0.37$). This means, that conodont abundance dynamics were sensitive to initial values of controlling parameters (i.e. chaotic in dynamical systems sense).

Correlation analyses of whole time series from both analyzed sections have shown that there are no “global” correlations between changes of conodont abundance, and stable carbon isotopes and also values of natural gamma radiation (=amount of clayey material in rock matrix). The contrasting results were found performing localized or gliding window correlation analyses of stable carbon isotopes and conodont abundances. It was found that in the Šešuvis-11 section were three episodes of statistically differing correlations (at $p<0.05$ level). In the lower third of the Jūra time there was positive and statistically insignificant correlation between changes in $\delta^{13}C$ and standardized conodont abundances. In the middle part there were negative and statistically significant correlations between these variables. During the last third of the Jūra time there was episode of positive and statistically insignificant correlations. Similar pattern was found in the Viduklė-61 section, but it was statistically insignificant (probably because of poorer material due to long between-sample intervals and non-availability of weights of samples for standardization procedures).

A REDFIT analysis of weight standardized conodont abundances from Šešuvis-11 section revealed two statistically significant periodicities in their abundance change: one with approximately 4.5 m long period (with 99 % confidence level), and another significantly longer with the period length of 57 m (with 95 % confidence level). In the Viduklė-61 I found just one statistically significant (at 99 % level) periodicity with approximate period length of 4.6 m. Wavelet analyses revealed similar patterns to those found using REDFIT approach. It is interesting though that amplitude of high frequency periodic fluctuations in both analyzed section was strongly modulated by low frequency component, which affirms multiplicative and interactive nature of long term abundance change, which was revealed by lacunarity analyses.

Revealed patterns generally show better quality of the signal in the Šešuvis-11 section if compared to the Viduklė-61 section. It was also shown that non-standardization of a data (by dividing absolute abundances of conodont elements by sample weights) could induce “whitening” of primary signal. The positive values of maximal Lyapunov exponent found during the analysis of conodont abundances from Šešuvis-11 section, have shown, that long-term conodont abundance dynamics exhibits sensitivity to initial conditions (i.e. paths of abundance change are contingent). Applying reasoning of Plotnick and Sepkoski in interpreting multifractal structure of a change (Plotnick and Sepkoski 2001) revealed by lacunarity analyses, it is most likely that conodont abundance dynamics were governed by hierarchical multiplicative interaction of mostly extrinsic factors varying at different rates. REDFIT and wavelet spectral analyses concur to this conclusion, since they show significant periodic components to the abundance change, which are probably forced by changes in climate which were most probably governed by quasi-cyclic Milankovitch astronomical mechanisms. There were three intervals of different correlation regimes between stable carbon isotopes and conodont abundances indicating extrinsically forced changes in a regional ecosystem functioning regime during the middle and the upper intervals of the Pridoli epoch. The first transition between positive correlation to the negative was also accompanied by significant acanthodian species turnover, which is documented by J. Valiukevičius in the Šešuvis-11 core section (Valiukevičius 2005). Thus this transition in ecosystem functioning was associated with species appearances and extinctions could be an example of a turnover pulse kind of biotic event (Vrba 1993).

Conclusions

The described macroevolutionary, macroecological and integrated stratigraphic study of Silurian conodonts from the Baltic Silurian basin led to the following conclusions:

Extinction selectivity during the Ireviken extinction event

- Skewnesses of conodont local abundance distributions were statistically significantly positively associated with the probability of species survival during the Ireviken mass extinction event.
- Average gamma radiation values at positive conodont sampling sites (which reflect amount of clayey material in carbonate rocks) are negatively associated with the probability of species survival during the Ireviken mass extinction event. This mean that preferentially survived those species which lived in the shallow environments. Revealed pattern points to open/deep ocean (offshore) causes of this mass extinction.
- Separate statistical analyses revealed spectral scaling exponents, which reflect degree of autocorrelation of abundance, and also extirpation rates, as possibly important factors in extinction selectivity. Both parameters were positively associated with the probability of species survival. This point to the importance of metacommunity and metapopulation dynamic regimes in survival of species.

Integrated biostratigraphy and conodont paleoecological dynamics during the Mulde event

- Two statistically significant cyclicities in gamma ray variability in the sedimentary succession of the upper Homerian strata in the Viduklė-61 core section were established: first one with $\approx$16.7 m (300 thousands of years) and second $\approx$6.7 m (120 thousands of years) period lengths.

- Two conodont zones were distinguished in the Viduklė-61 core section in the Gėluva regional stage: lower part of the Gėluva regional stage corresponds to the *Ozarkodina bohemica longa* Zone, and the upper part corresponds to the *Kockelella ortus absidata* Zone. On the other hand it is shown based on the finding of *Ctenognathodus murchisoni* species in the *nassa* graptolite interzone that this conodont species have much greater stratigraphic extent, and it is unsuitable for biostratigraphical zonation.
- *Ozarkodina bohemica longa* Zone could be distinguished in the lower part of the upper Homerian in the Ledai-179 section.
- Based on the analyses of parameters describing paleoecological conodont species turnover (local abundance, per capita immigration rates and per capita extirpation rates) in the Ledai-179 section it was found that there were several episodes of change in parameter values. Those changes probably were related to the developmental stages of the basin, during transition from deeper to shallower environments.

The dynamics of conodont abundances during the middle and the late Pridoli (Jūra time)

- The dynamics of conodont abundances in the studied time interval, as it was revealed by lacunarity, Hurst exponent, and spectral exponent analyses are characterized by multifractal structure, which points to the hierarchical and multiplicative nature of controlling mechanism. The complex nature of conodont abundance dynamics is confirmed by estimation of Lyapunov exponent, which points to chaotic (i.e. high sensitivity to initial conditions) nature of the change.
- The three episodes of differing correlation regimes between conodont abundances and $\delta^{13}C$ values, punctuated by sudden changes could be suggested. The episodes probably represent alternative states of function of the regional ecosystem.
- Abundance fluctuations in the Šešuvis-11 core section are characterized by two major cyclicities with estimated period lengths of approximately 74 and 950 thousands of years. The most probable mechanism which governed them was a

change in nutrient supply modulated by astronomically controlled Milankovitch climatic cycles.

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SILŪRO PERIODO BALTIJOS SEDIMENTACINIO BASEINO KONODONTŲ MAKROEVOLIUCIJA IR MAKROEKOLOGIJA

Reziumė

Šiame darbe nagrinėjamas silūro periodas, kaip rodo pastarųjų dviejų dešimtmečių tyrimai, yra vienas iš pačių dinamiškiausių fanerozojaus eono laikotarpių. Silūro periode kiek yra žinoma, Žemės sistema patyrė keletą (veikiausiai keliolika) stambių perturbacijų arba taip vadinamų bioįvykių, kurie pasižymėjo padidėjusiais taksonų išnykimo greičiais, paleobendrijų sandaros pokyčiais bei dideliais globalios klimatinės-okeanografinės sistemos pokyčiais. Savo ruožtu konodontai (primityvūs stuburiniai), kurie yra pagrindinis šio darbo tyrimasis objektas, buvo labai svarbi paleozojaus ekosistemų nektono ir nekto-bentoso dalis. Praeityje, dažniausiai šių stuburinių gyvūnų liekanos buvo naudojamos stratigrafinėms nuosėdinių uolienų koreliacijos ir suskirstymo problemoms spręsti. Dar daugiau, šių organizmų grupė pasižymi puikiu paleontologiniu metraščiu bei pakankamai didele gausa bandiniuose išgaunamuose iš Lietuvos giliųjų gręžinių kerno. Tai savo ruožtu įgalina jų naudojimą detaliuose evoliuciniuose ir paleoekologiniuose tyrimuose.

Norint atskleisti silūro periodo Baltijos sedimentacinio baseino konodontų pagrindinius makroevoliucijos ir makroekologijos bruožus, buvo pasirinkti trys dinamiškiausi nagrinėjamo periodo laiko intervalai: vėlyvojo landoverio – ankstyvojo uenlokio (Ireviken‘o masinio išmirimo įvykis); vėlyvojo uenlokio – ankstyviausiojo ludlovio (Mulde‘s bioįvykis); viduriniojo ir viršutinio pržidolio epochų dalys. Šiam tikslui pasiekti buvo ištirti septyni gręžiniai: Gėluva-99, Ledai-179, Butkūnai-241, Tverečius-336, Jočionys-299, Viduklė-61, Šešuvis-11. Jie padengė visas konodontų biofacijas ir tokiu būdu leido optimaliai įvertinti biotinių įvykių poveikį rūšims pasižyminčioms skirtinga ekologija bei gyvenusioms skirtingose baseino aplinkose.

Darbo metu buvo iškelti tokie uždaviniai, kurie leido geriausiai panaudoti turimą medžiagą ir įvairiapusiškai įvertinti makroekologinius ir makroevoliucinius procesus, kurie veikė kritinių geobiologinių intervalų metu:

- Naudojantis dvimatės ir daugialypės logistinių regresijų bei regresinių medžių metodikomis nustatyti Ireviken‘o masinio išmirimo selektyvumo veiksnius.
- Patikslinti homerio (viršutinio uenlokio) konodontų biostratigrafinę skalę, bei integruoti ją su ciklo- ir chemostratigrafinėmis laiko skalėmis.
- Atskleisti viršutinio homerio konodontų taksonominės paleoekologinės dinamikos bruožus sekliose aplinkose.
- Nustatyti viduriniojo ir viršutinio pržidolio konodontų gausumo pokyčių dinamines savybes ir pagrindinius varomuosius mechanizmus.

Ireviken‘o masinio išmirimo selektyvumo statistinio tyrimo metu buvo ištirti dešimt parametrų apibūdinančių konodontų rūšių gausumo dinamiką ir struktūrą, bei jų mėgstamas aplinkas: vidutinis konodontų elementų gausumas bandiniuose; suvidurkintas konodontų elementų gausumo variacijos koeficientas; konodontų gausumo bandiniuose asimetrijos koeficientas, Hurst‘o eksponentė; gausumo pokyčių spektro normavimo eksponentė; imigracijos greičiai; ekstirpacijos greičiai; vidutinės gama spinduliuotės reikšmės konodontų radinių vietose (=aplinkos molingumo laipsnis); gama spinduliuotės vidutiniai kvadratiniai nuokrypiai konodontų radimo vietose(=aplinkos sąlygų tolerancijos ribos); gama spinduliuotės konodontų radimo vietose asimetrijos koeficientai (=tendencingumas gyventi mažesnio arba didesnio molingumo aplinkoje). Statistinių analizių metu buvo nustatyta, kad iš visų šių veiksnių statistiškai patikimai asocijuojasi su išgyvenimo masinio išmirimo metu tikimybe konodontų gausumų asimetrijos koeficientai, gausumo pokyčių normavimo eksponentės bei vidutinės gama spinduliuotės reikšmės (=molingumas) konodontų aptikimo taškuose. Šios statistinės asociacijos nurodo, kad svarbų vaidmenį rūšių išgyvenime turėjo vidinė rūšių metapopuliacinė struktūra, kuri nulemia jų gausumo dinamikos ypatumus (daug ar mažai autokoreliuota) ir fenotipinio kintamumo erdvinį ir laikinį rūšiavimą. Taip pat, neigiama asociacija tarp rūšių išgyvenamumo ir molingesnių (gilesnių) aplinkų, nurodo į tai, kad Ireviken‘o masinio išmirimo priežastys nebuvo susijusios su jūros lygio kritimu bet buvo nulemtos vandenynų struktūrizacijos pokyčių.

Viršutinio uenlokio konodontų biostratigrafijos tyrimai parodė, kad apatinėje Gėluvos regioninio aukšto dalyje galima išskirti *Ozarkodina bohemica longa* Zoną, o viršutinėje dalyje *Kockelella ortus absidata* konodontų Zoną. Tuo tarpu

Ctenognathodus murchisoni konodontų rūšis, kuri anksčiau buvo priimama kaip Zona, buvo įrodyta, kad atsirado kur kas anksčiau nei manyta prieš tai (*nassa* graptolitų interzonoje). Taip pat ankstyvas šios rūšies atsiradimas (daugiausiai po kelių šimtų tūkstančių metų pasibaigus Mulde‘s išmirimo įvykiui) nurodo, kad tie patys veiksniai kurie padidindavo rūšių išnykimo riziką (pvz. buveinių fragmentacija), veikiausiai turėjo teigiamos įtakos naujų rūšių atsiradimui, padidinant atskirų populiacijų izoliacijos efektyvumą.

Paleoekologinių taksonominių pokyčių laiko eilučių tyrimai sekliose aplinkose vėlyvojo uenlokio ir ankstyviausiojo ludlovio epochų metu parodė, kad konodontai šiame laiko intervale patyrė kelis sisteminius pokyčius jų vidutiniame lokaliame gausume, proporcinguose imigracijos ir ekstirpacijos greičiuose. Visi šie pokyčiai įvyko arba Jagarahu regioniniame aukšte arba Gėluvos regioninio aukšto viduryje. Taigi, nei vienas iš jų nesutapo su Mulde‘s išmirimo įvykiu, kas nurodo į šio biotinių perturbacijų epizodo nedidelį praeinamą poveikį konodontų biotai.

Kelių tipų laiko eilučių analizės, kuriu metu buvo nagrinėjama viduriniojo ir viršutinio pržidolio konodontų gausumo dinamika, atskleidė sudėtingą ir daugiasluoksnę pokyčių struktūrą. Lakūnariškumo analizė, kurios dėka galima nustatyti laiko eilučių heteregoneškumo pasiskirstymą skirtinguose laiko masteliuose, parodė, kad konodontų gausumo kintamumas pasižymi multifraktaline struktūra, kuri nurodo į hierarchinę ir dauginamąją pokyčių kontrolę. Į hierarchinį konodontų gausumo pokyčių pobūdį taip pat nurodo ir spektrinės analizės, kurių dėka buvo atskleista, kad konodontų kiekio svyravimai pasižymėjo mažiausiai dviem statistiškai patikimais periodiškumais su labai skirtingais svyravimų periodų ilgiais (≈74 ir ≈950 tūkst. metų), kurių tikėtiniausias varomasis mechanizmas yra astronominiai Milankovičiaus cikšliškumai. Taip pat buvo nustatyta, kad konodontų ekologinė dinamika, nagrinėjamame laikotarpyje patyrė du struktūrinius pokyčius. Apatinėje Jūros regioninio aukšto dalyje koreliacija tarp konodontų gausumo ir stabiliųjų anglies izotopų santykių buvo teigiama, bet statistiškai nepatikima, po to ji perėjo į neigiamą ir statistiškai patikimą, ir vėliau viršutinėje Jūros regioninio aukšto dalyje ji vėl tapo teigiama bet statistiškai nepatikima. Taipogi, vykstant šiems perėjimams įvykdavo padidėjimai konodontų gausumų ir stabiliųjų izotopų svyravimų amplitudėse. Tai yra svarbus požymis, kuris nurodo į tai, kad šie perėjimai tarp skirtingų koreliacinių režimų pasižymėjo kritiniu pobūdžiu (dinaminių sistemų prasme).

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