



# Bayesian analysis of ultra-high-resolution ostracod record reveals the tempo and structure of the late Wenlock Mulde Event

SIMONA RINKEVIČIŪTĖ, LIUDAS DAUMANTAS, SIGITAS RADZEVIČIUS AND ANDREJ SPIRIDONOV

## LETHAIA



The late Wenlock Mulde/*lundgreni* Event or the ‘Big Crisis’ was one of the most significant extinction events, sea level regressions and global carbon cycle perturbations of the early Palaeozoic. It was first detected in graptolite and conodont fossil records which represent the pelagic realm. The impact of the event on benthic communities is less understood, and the overall understanding of the community collapse and recovery suffers from lack of resolution. Here we present an ultra-high-resolution (<10 Ka) record of benthic ostracod assemblages from the shelfal zone of the Silurian Baltic Basin (Lithuania). This record is segmented using newly developed time-contiguous community clustering algorithm which revealed the stages of collapse and recovery. The Bayesian geochronology approach constrained the most probable duration of event to 260 Ka, which suggest half an order of magnitude shorter duration than previous estimates. The collapse leading to and recovery from the Mulde/*lundgreni* Event happened on time scales of tens of thousands of years. This sharp event did not result in apparent ostracod extinctions; it caused the state shift in their biodiversity metrics and their relation to abundance. This pattern implies the transition of ecosystems through a critical tipping point to an alternative community assemblage pattern in the mid-Silurian. □ Tipping points, extinction, ‘Big Crisis’, palaeocommunities

Simona Rinkevičiūtė ✉ [simona.rinkeviciute@chgf.vu.lt], Liudas Daumantas [liudas.daumantas@chgf.vu.lt], Sigitas Radzevičius [sigitas.radzevicius@gf.vu.lt] and Andrej Spiridonov [andrej.spiridonov@gf.vu.lt], Vilnius University, Department of Geology and Mineralogy, M. K. Čiurlionio 21, LT-03101 Vilnius, Lithuania; manuscript received on 16/05/2024; manuscript accepted on 13/11/2024; manuscript published on 27/02/2025 in Lethaia 58(1).

The Mulde/*lundgreni* Event, or the ‘Big Crisis’ (Jaeger 1991) of the late Wenlock is a global Silurian biotic and oceanic perturbation that was first recognized in the fossil record of extinctions of graptolites and conodonts, and which also correlates to changes in oceanic circulation, chemistry, and the stable carbon and oxygen isotopes (Jeppsson *et al.* 1995; Jeppsson & Calner 2002; Koren’ 1991; Trotter *et al.* 2016; Whittingham *et al.* 2020), and presumably related to the interference of 4<sup>th</sup> and 5<sup>th</sup> order (long and short eccentricity) cycles (Radzevičius *et al.* 2017; Rinkevičiūtė *et al.* 2022; Spiridonov *et al.* 2017a). The mid-Homerian ‘Big Crisis’ is part of a pattern of Late Ordovician and Silurian repeating high-magnitude extinction events detected in the marine realm (Frýda *et al.* 2021; Spiridonov *et al.* 2020), which are tied either to the transition to ice-house megacclimate regime (Crampton *et al.* 2016) and/or radical transitions in biogeochemistry of the planet due to expansion of terrestrial plants (Lenton *et al.* 2016) among other possible mechanisms (Jeppsson 1998).

The precise and accurate estimation of the rates and stages of great extinction and turnover events is necessary in order to reveal the factors responsible for oceanic perturbations and also in understanding the mechanism of ecosystem transitions (Cramer *et al.* 2015). Earlier geochronological and integrated stratigraphical studies suggested that the duration of the Mulde/*lundgreni* Event was ~1 Ma (Cramer *et al.* 2012). Other studies suggested that the event itself could be an artefact in completeness of the fossil record in general (Jarochovska & Munnecke 2016). Certainly, the completeness of the fossil record affected the perception of the event making it look longer, by smearing the first appearances of some conodonts forward in time (Radzevičius *et al.* 2016; Radzevičius *et al.* 2014c). Although, the cross taxa comparison shows, that the main stress pulse was concentrated in a rather narrow window of time (Rinkevičiūtė *et al.* 2022; Spiridonov 2017; Whittingham *et al.* 2020, 2022), while the ‘post-Big Crisis’ interval of the Homerian was rich in events of smaller significance

modulated by constant hierarchical environmental change (Rinkevičiūtė *et al.* 2022).

Here we present a study of ultra-high-resolution (bed-by-bed) record of ostracods from the Jaagarahu and Gėluva regional stages of the mid- to late Homeric Stage of the eastern Baltic Basin, Lithuania. The sampled Gėluva-118 section is situated in shallow shelf palaeoenvironments, rich in calcareous benthic fauna (Fig. 1). The resolution of any stratigraphical data confines and modifies the apparent rate of sedimentations as well as the apparent speed of events (Kemp & Sadler 2014). Therefore we aim to reach the highest resolution possible in core section, and determine the structure, duration and quantitative palaeoecological characteristics of benthic communities through different stages, as well as times before and after the ‘Big Crisis’. The published ostracod dataset (Rinkevičiūtė *et al.* 2022) which indicated the approximate interval of the event, documented by the graptolite fauna, was significantly detailed, so that the final resolution inside and around the event was increased fourfold. Together with this enhanced dataset, we employed newly developed temporal contiguous hierarchical segmentation algorithm to distinguish stages of the ‘Big Crisis’. Later we employed community similarity indices to characterize these stages, and in combination with Bayesian geochronological modeling estimated the absolute rate and duration of the event and its stages.

## Material and methods

The published mid- to upper Homeric ostracod taxonomic and abundance data from the Gėluva-118 core (55° 15′ 30.89″ N, 23° 23′ 24″ E; Fig. 1), comprising 97 samples (Rinkevičiūtė *et al.* 2022), were augmented with 44 newly collected and processed samples from the ‘Big Crisis’ interval and its immediate surroundings, obtained in order to achieve ultra-high resolution (Fig. 2). The depth range of the up-sampled interval spans from 1008 to 1018.8 m with sampling resolution of  $\Delta 0.2$  m, which according to the correlation of cyclic patterns of sedimentation and graptolite record in the Silurian Baltic Basin, approximately corresponds to the upper *lundgreni* to *nassa* graptolite Zones (Radzevičius *et al.* 2014a). New samples were processed (Green 2001), and overall 2429 new specimens of ostracod carapace and disarticulated valves were collected and recognized to species/genus level. The ostracod collection produced by this study is stored at the Geological Museum at Vilnius University. The section itself is composed of

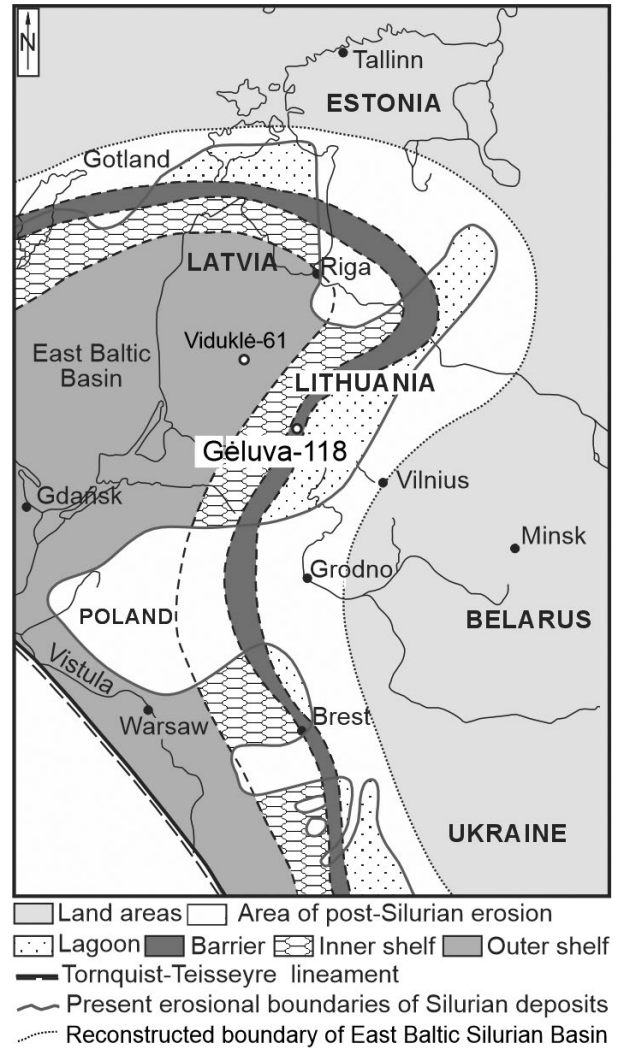


Fig. 1. Palaeogeographical location of the studied core (Gėluva-118) and contextual core Viduklė-61. Map reproduced from Einasto *et al.* (1986).

mudstones and muddy packstones of the Riga and Gėluva Formations, which vary continuously in clay content, reflecting aggradational sequence of shelfal environments (Rinkevičiūtė *et al.* 2022).

The Gėluva-118 core section has been correlated with the Viduklė-61 and Šiupyliai-69 core sections (Paškevičius 1997; Radzevičius & Paškevičius 2000, 2005; Rinkevičiūtė *et al.* 2022; Spiridonov *et al.* 2020). This age inference is supported by  $\delta^{13}\text{C}_{\text{carb}}$  and conodont data, with the presence of *Kockelella absidata* corresponding to the descending limb of the second peak of the upper Homeric  $\delta^{13}\text{C}$  excursion in the lower and middle parts of the studied section (Spiridonov *et al.* 2020). These data constrain the location of the Wenlock and Ludlow boundary which is used in the construction of the age-depth model

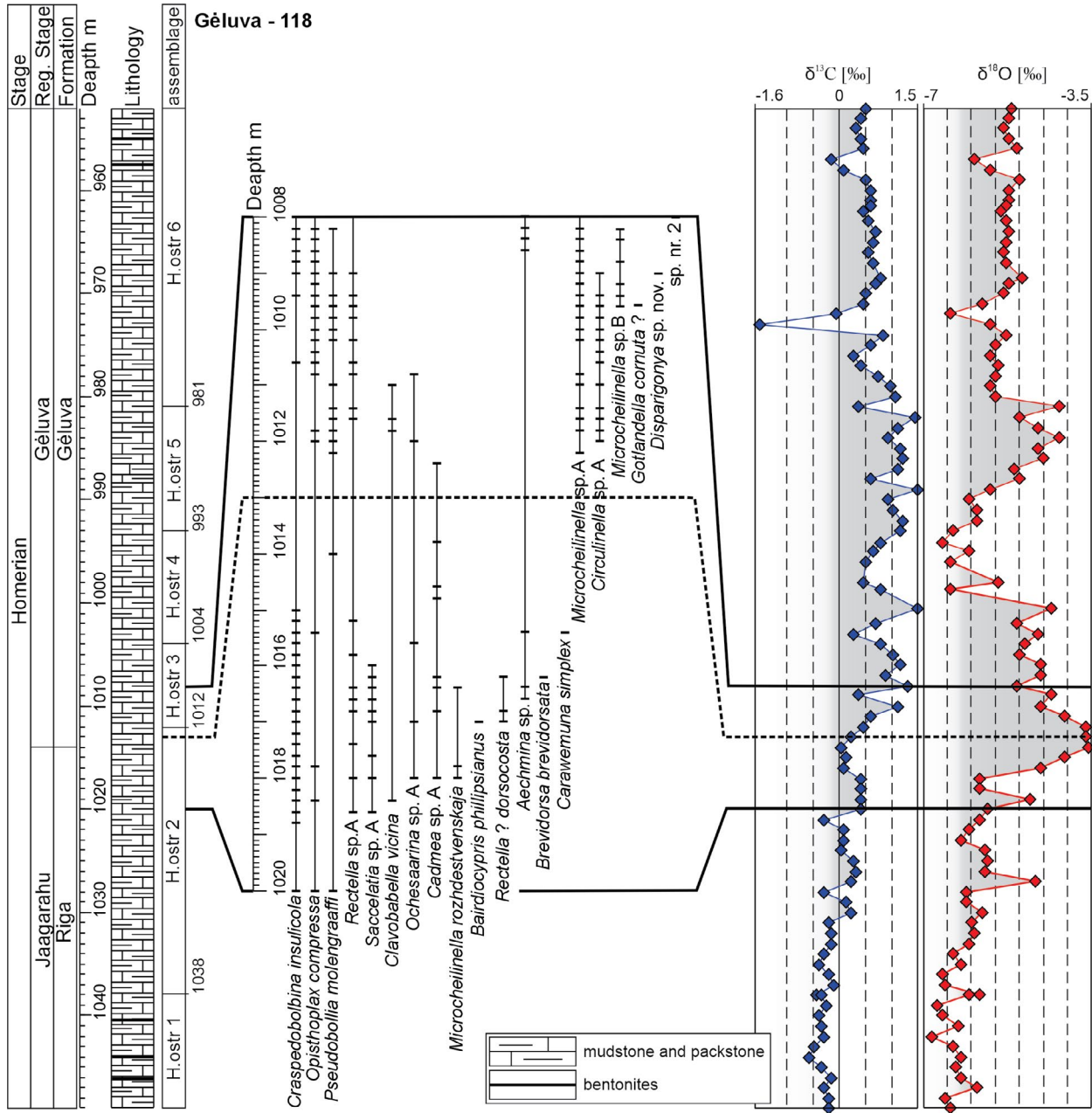


Fig. 2. Stratigraphical distribution of lithology, ostracods, and ostracod compositional assemblages (identified with a 99% significance level), along with trends in carbonate  $\delta^{13}C$  and  $\delta^{18}O$ , is presented. Data on lithology, carbonate  $\delta^{13}C$  and  $\delta^{18}O$ , and ostracod compositional assemblages are sourced from Rinkevičiūtė *et al.* (2022).

and the estimation of the speed of the Mulde/*lundgreni* Event.

Typical strata of the Mulde/*lundgreni* bioevent are found in Gotland, Sweden, belonging belong to the Fröjel and Halla formations. A regional stratigraphical hiatus at the top of the Fröjel Formation marks the final stage of the event and the lowest sea level in the Homerician stage (Calner 1999; Jeppsson & Calner 2003). These formations correlate with horizontally

stratified marls in deeper parts of the Silurian Baltic Basin in Latvia, Poland, and Lithuania (Calner *et al.* 2004; Radzevičius *et al.* 2014) and can be used as a significant lithological event marker at least at the regional (Silurian Baltic Basin) scale. During the mid-Homerician, sea-level regression was presumably caused by the hierarchical interference of 4th and 5th order sea level cycles related to the eccentricity variations of Earth's orbit (Radzevičius *et al.* 2017).

The Mulde/*lundgreni* bioevent can also be identified using  $\delta^{13}\text{C}$  data, which shows a positive carbon isotope anomaly, typically displaying two peaks in the relatively complete stratigraphical section. This positive nature of the anomaly suggests a sequestration of the organic carbon from the ocean-atmosphere system, and the anomaly itself is linked to the global climate changes, 4th order sea-level fluctuations, carbon cycle restructuring (Kaljo *et al.* 1997; Saltzman 2001; Martma *et al.* 2005; Calner *et al.* 2006; Lenz *et al.* 2006; Jarochovska *et al.* 2016; Radzevičius *et al.* 2019). If the sedimentary record in the studied interval was incomplete, it would not display the characteristic two-peaked curve of the late Wenlock  $\delta^{13}\text{C}$  carbon isotopic event (Radzevičius *et al.* 2017; Rinkevičiūtė *et al.* 2022). The completeness of the sedimentary record is further supported by the presence of zonal graptolite species in expected portions of the section in relation to the  $\delta^{13}\text{C}$  data (Radzevičius *et al.* 2014; Rinkevičiūtė *et al.* 2022). The relative completeness of the studied event strata is also corroborated by the relatively smooth transitions and distinctiveness of the stages of the event. Stratigraphical gaps are expected to produce spurious jumps. Additionally, the distinctness of composition of neighbouring ostracod assemblages (separated by 0.2 m intervals) points to the preservation of the original assemblage compositions and the limited role of time-averaging at these high-resolution sampling scales.

In order to characterize the structure of the mid-Homerian Event interval we used a newly developed recursive binary segmentation algorithm tailored for the temporal/stratigraphical segmentation of contiguous assemblages, according to their compositional similarity, an extension of the hierarchical spatial data subdivision method HespDiv (Daumantas & Spiridonov 2024). The algorithm works by making recursive section partitions at minimal Morisita-Horn similarity index (Horn 1966) values (see Supplementary Information).

To track changes in ostracod communities throughout the Mulde/*lundgreni* Event, we distinguished the following five stages: 1) Pre-Event; 2) Collapse; 3) Maximal Stress; 4) Recovery; and, 5) Post-Event. The stages were characterized by distributions of bootstrapped sample averages of three diversity indices: Pielou evenness, inverse Simpson index and abundance. The Pielou evenness index (Pielou 1966) reflects the evenness of species representation in a sample. It is standardized by the number of species in a sample, making it useful for comparing palaeocommunities of different species richness. The Simpson index (Simpson 1949) is a measure of species concentration or dominance.

The apparent abundance, preserved in the studied Gėluva-118 core section, gives a glimpse on the evolution of biomass in palaeocommunities.

Durations of stages and Nyquist frequency were estimated using a Bayesian age-depth model, built using ‘modifiedBChron’ R package, v. 0.7.0 (Trayler *et al.* 2020). It is an adaptation of ‘BChron’ package (Haslett & Parnell 2008) for deep-time applications. Its independence on time scales is important given the scaling properties of sedimentation rates (Kemp & Sadler 2014). The age-depth model was based on the chronology of the Gėluva-118 section. For its construction we used: the Llandovery-Wenlock boundary (1120.5 m) determined based on the lithostratigraphy, the correlated/projected depth of the Grötlingbo Bentonite (1012 m) using Viduklė-61 core as the reference (Radzevičius & Paškevičius 2000); the correlated/projected depth of the base Homerian (1059 m) using as the reference closely located Šiupyliai-69 core (Radzevičius *et al.* 2017, Radzevičius & Paškevičius 2000); and also the Wenlock-Ludlow boundary (930 m).

Biostratigraphical and lithostratigraphical proxies used for correlation of the Gėluva-118 and Šiupyliai-69 core sections are based on graptolite and conodonts biostratigraphy, chemostratigraphy and lithostratigraphy. In the Šiupyliai-69 core section, the lower boundary of the Sheinwoodian and of the Wenlock Epoch (at a depth of 1123.5 m) is identified by the first appearance of *Cyrtograptus purchisoni* Carruthers (Radzevičius & Paškevičius 2000). This lithological interval correlates with the boundary between the Llandovery and Wenlock in the Gėluva-118 core section (at 1120.5 m depth), marking the beginning of the Riga Formation (Paškevičius 1997).

The boundary between the Sheinwoodian and Homerian stages in the Šiupyliai-69 core section (at a depth of 1055 m) is marked by the first appearance of *Cyrtograptus lundgreni* Tullberg (Radzevičius & Paškevičius 2000). The corresponding level in the Gėluva-118 core section was found using graphical correlation with the geographically close and visibly similar Šiupyliai-69 core (Rinkevičiūtė *et al.* 2022), to be at approximately the 1059 m depth.

The lower boundary of the Gėluva Regional Stage in the Šiupyliai-69 core section (at 1004.8 m depth) is marked by the first appearance of *Gothograptus nassa* Holm and *Pristiograptus parvus* Ulst (Radzevičius & Paškevičius 2005). In the Gėluva-118 core section, this same boundary is characterized by the last appearance of *Monograptus flemingi* (Salter) and *Pristiograptus pseudodubius* Bouček, alongside a steady increase in  $\delta^{13}\text{C}$  values — the start of the late Homerian positive carbon isotopic excursion also informally known as the ‘Mulde Excursion’ (Rinkevičiūtė *et al.* 2022).

The lower boundary of the Ludlow in the Šiupyliai-69 core section (at 973 m depth) is indicated by the first appearance of *Neodiversograptus nilssoni* (Barrande) (Radzevičius & Paškevičius 2005). In the Gėluva-118 core section, this boundary is identified using detailed conodont biostratigraphy in combination with the  $\delta^{13}\text{C}$  trends and numerical crossrecurrence plot correlation (Spiridonov *et al.* 2020).

## Results and discussion

The Maximal Stress stage, defined as the longest continuous interval with significantly reduced ostracod abundances and fewer than two species present, was identified between 1015.1 m and 1012.3 m. In contrast, the entire extent of the Mulde/*lundgreni* Event, estimated from the hierarchical segmentation analysis, was determined to fall between 1016.3 m and 1009.1 m in the core section. The event interval exhibits a distinct structure, revealing a conspicuously changing composition of ostracod assemblages. The Morisita-Horn similarity values of established splits inside the interval were 0.01 and 0.1, and the value of split that identified the interval was 0.25 (Fig. 3). In contrast,

other subdivisions were much weaker, with Morisita-Horn similarity values ranging from 0.55 to 1.00. Just before the event interval, the compositions were so stable that there were two splits established inside the 1038.5 – 1016.3 m interval, which are even indistinguishable in the figure (Fig. 3). The hierarchical dissimilarity structure of ostracod palaeocommunities in the Pre-Event interval highlights the exceptional nature of the ‘Big Crisis’ compared to post-event interval.

The frequency distributions of durations estimated for each stage of the Mulde/*lundgreni* Event were all positively skewed (Fig. 4B, C). The median and 95% HDI durations of each stage and of the whole event are as follows: Collapse – 50 Ka (11 – 171 Ka), Maximal Stress – 120 Ka (31 – 601 Ka), Recovery – 80 Ka (21 – 576 Ka), and the entire Mulde/*lundgreni* Event – 260 Ka (100 – 1136 Ka). The Nyquist (Median 13 Ka, 95% HDI 2.5 – 74 Ka) frequency of our samples was more than sufficient for the detection of these dynamic states (see Supplementary Information).

Although originally based mostly on local Gotland data (Calner & Jeppsson 2003; Cramer *et al.* 2012; Jeppsson & Calner 2002), the Mulde/*lundgreni* Event was envisioned as a multi-stage extinction-stress-recovery episode spanning about 1 Ma in the mid-Homerian

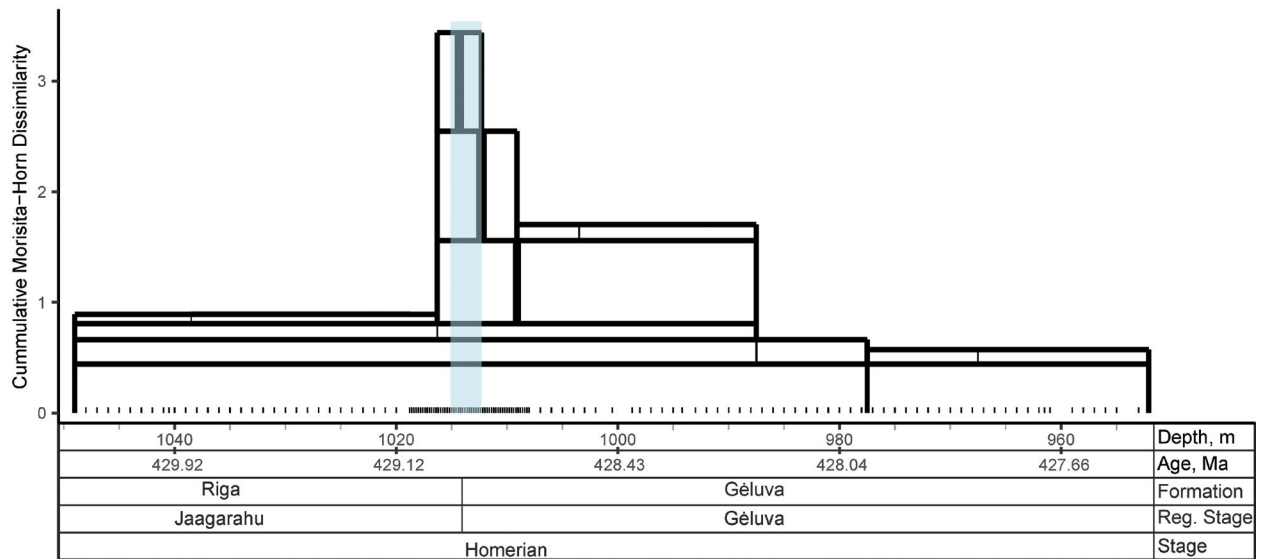


Fig. 3. Hierarchical segmentation of the Gėluva-118 section ostracods. Each rectangle represents a segment of the section partitioned based on compositional differences in ostracod assemblages. For example, the bottom rectangle represents the entire section, while the rectangles above it represent segments created by subsequent partitions. The vertical line within each rectangle marks the partition location, where the compositional similarity between assemblages was lowest in the segment. Both the height of the rectangle and the width of the partition line reflect the Morisita-Horn dissimilarity ( $1 - \text{Morisita-Horn similarity}$ ) between the ostracod assemblages on either side of the partition. Taller rectangles and wider lines indicate greater compositional contrast. Also, the taller the topmost rectangles, the more compositionally heterogeneous the ostracod assemblages are in the corresponding section segments. The Morisita-Horn dissimilarity represented by the rectangle heights can be read from the vertical axis of the figure, which shows cumulative dissimilarity values for the stacked rectangles. Small ticks below segmentation plot shows sampling locations. Light-blue interval corresponds to Maximal Stress stage. The 80 cm discrepancy between the beginning of Maximal Stress stage and the split of the tallest segment is an artefact of an imposed requirement for segments to contain at least 10 samples. This artefact only effects the segmentation of narrow and rarely sampled segments. Thus, it should not have affected the distinction of total Mulde/*lundgreni* Event interval.

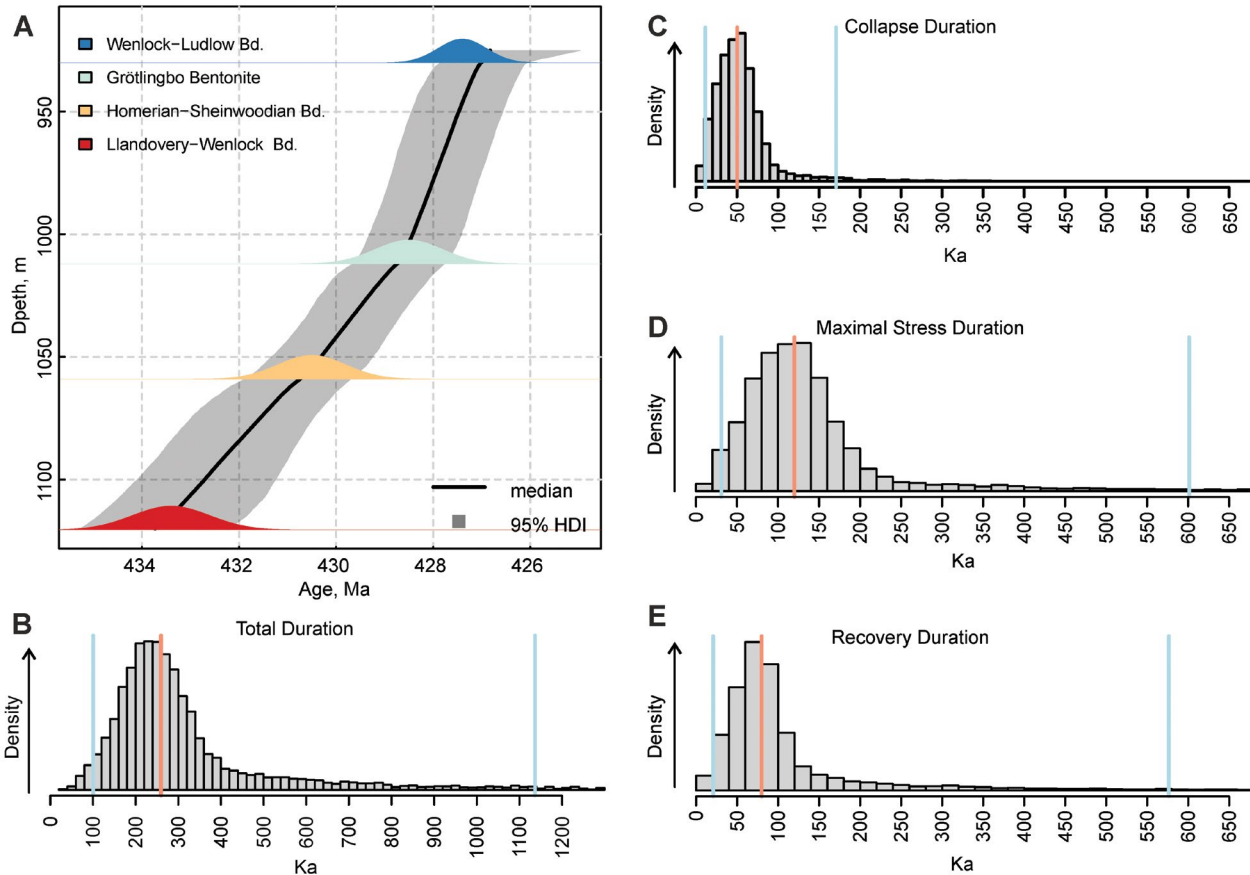


Fig. 4. Bayesian age-depth model for Gėluva-118 section (A), and durations estimated from it for (B) all *Mulde/lundgreni* events, and (C–E) different stages of its progression. Age interval between light-blue lines in B–E is 95% highest density interval (HDI), whereas the orange line marks median (the most likely) duration.

(Cramer *et al.* 2012). Now new data on conodonts, graptolites and acritarchs, show that the stress interval should have been far shorter than previously envisioned, and the recovery of conodonts happened essentially simultaneously with extinction of old taxa (Radzevičius *et al.* 2016; Venckutė-Aleksienė *et al.* 2016). The effects of the *Mulde/lundgreni* Event were rather ephemeral for the diversity of microphytoplankton, and overall the diversity apparently followed the 4th order (presumably related to the 405 Ka eccentricity term) cycles (Radzevičius *et al.* 2014a, b; Venckutė-Aleksienė *et al.* 2016). On the other hand, the cyst sizes of sphaeromorphs (the dominant phytoplankton) significantly decreased during the *Mulde/lundgreni* Event, which can be interpreted as a sign of severe decrease of nutrient flux (Spiridonov *et al.* 2017b). This in turn should have affected up the food chain, suggested by recent findings of the coupling of phytoplankton and graptolite diversity changes (Stankevič *et al.* 2024). The temporal pattern of sicular annuli disappearance in graptolites during the *Mulde/lundgreni* Event was

interpreted as reflective of the decrease of episodic ocean mixing activity (the decrease in frequency and energy of hurricanes which enhance upwelling) (Whittingham *et al.* 2022). This nutrient starvation and oceanic perturbation episode resulted in a severe and quick (confined to the end-*lundgreni* Zone) extinction of graptolite species and almost immediate (as determined by stratocladistic analysis) radiation of post-extinction taxa (Whittingham *et al.* 2020).

Based on Gotland data, it was previously proposed that the conodonts, which were the primary taxa used in the recognition of the *Mulde/lundgreni* Event, recovered in stages, following step-like origination of new zonal taxa in following succession: *Ozarkodina longa* – *Kockelella absidata* – *Ctenognathodus purchisoni* (Jeppsson *et al.* 1995; Jeppsson & Calner 2002). Later analyses from other locations in Baltica (Radzevičius *et al.* 2014a; Radzevičius *et al.* 2016; Radzevičius *et al.* 2014c), as well as Bohemia (Slavík 2014) revealed that these zonal species originated essentially simultaneously during the extinction episode itself, just leaving

a heterogeneous mark of their first appearances in different locations. This led to the proposition of so called 'delay phase' model of turnovers, when extinctions are globally simultaneous but new species originate in confined locations, and it takes significant time for them to disperse to their maximal spatial extent (Radzevičius *et al.* 2016). In such a case the pattern of First Appearance Datum of new taxa in a single stratigraphical section would look like a series successive step-like originations of new species. The interpretation that the turnover was quick and severe is confirmed by the spatially and temporally coherent drop in abundance and the transition to simpler population dynamics in conodonts, as was revealed by the recurrence and cross-recurrence plot analyses (Spiridonov 2017) of Polish and Lithuanian core sections (Jarochowska & Munnecke 2016; Radzevičius *et al.* 2016; Radzevičius *et al.* 2014c). The step-like change at the beginning of the late Homeric carbon isotopic excursion, was also detected in conodont species rank abundance distributions, and the transitions from more complex to simpler and more even communities (Spiridonov *et al.* 2017a). This range of patterns is expected under the coordinated stasis mechanism of coherent ecological and phylogenetic turnover, which envisions multitaxic macroevolutionary changes initiated by intermittent regional to global perturbations punctuating long periods of reversible changes in community compositions (Brett & Baird 1995; Ivany *et al.* 2009).

These studies point toward much shorter (although with spatially heterogeneous impact overprinted by the stratigraphical features of the fossil record) duration of the Mulde/*lundgreni* Event than was previously envisioned. Our current contribution, based on previously published ostracod dataset (Rinkevičiūtė *et al.* 2022), was specifically upsampled in the focal interval of maximal changes. This feature allows an exact bed-by-bed characterization of this sharp perturbation in all of its 'anatomical' details (fall of diversity, maximal stress, and the return to new equilibrium). To our knowledge all other studies on the Mulde/*lundgreni* Event either lacked the resolution or the sufficient duration of time series in order to characterize both — the speed of the process on the one hand (which requires time resolution), and the characterization of states which were before, during and after the extinction/extirpation/turnover event (which requires sufficient duration of the record). Current record is restricted to a single, although major, taxonomic group, and a single geological section. Therefore, the results should be seen as provisional, and without a doubt will be updated with additional studies in the Silurian Baltic Basin and other palaeobioprovinces.

Ostracod assemblages corresponding to different stages of the Mulde/*lundgreni* Event each exhibit distinct distributions of bootstrapped sample averages of diversity indices and abundance (Fig 5). The Maximal Stress stage stands out with its extremely low diversity. The diversity states observed across the rest of stages appear to be influenced by two primary factors: the 'pull of equilibrium' and the presence of stress. Stress sets apart the equilibrium populations from the transitional stages of the event, contributing to lower abundances and higher evenness in the Collapse and Recovery populations. Conversely, the 'pull of equilibrium' significantly anchors the transient stages (Collapse and Recovery) to their respective equilibrium states (Old Equilibrium and New Equilibrium), inhibiting change except during the Maximal Stress stage when total community collapse leads to a new equilibrium. Ostracod populations from the old equilibrium state (early Homeric) were generally less diverse, exhibiting a lower inverse Simpson index and lower evenness compared to their counterparts from the new (late Homeric) equilibrium state.

Interestingly, ostracod assemblages assigned to the old equilibrium state display a steeper slope in the evenness – inverse Simpson plot (Fig. 5A), indicating a distinct community assemblage pattern. These populations had more variable evenness, while new equilibrium populations showed greater variability in the inverse Simpson index. Given the positive relationship between evenness and the inverse Simpson index, and the fact that the Simpson index better reflects species richness, these observations suggest that the less diverse old equilibrium populations had a less stable dominance structure as well. In these populations, small increases in species richness led to larger increases in evenness. In contrast, the new equilibrium populations, with generally higher species richness, showed only small changes in evenness despite greater fluctuations in species richness, indicating a more stable community dominance structure. This could suggest that the Mulde/*lundgreni* event played a role in the emergence of ostracod communities that were ecologically more mature and better saturated with species, either locally or more broadly.

Another point of interest is the bi- or tri-modality observed in the density distributions of Recovery assemblage indices. These three modes suggest that the recovery was not a smooth process but involved some setback and stabilization events. Similarly bi- or tri-modal distributions could be expected for the Collapse population, but sample size on which its distribution is based is too small to observe these more nuanced patterns.

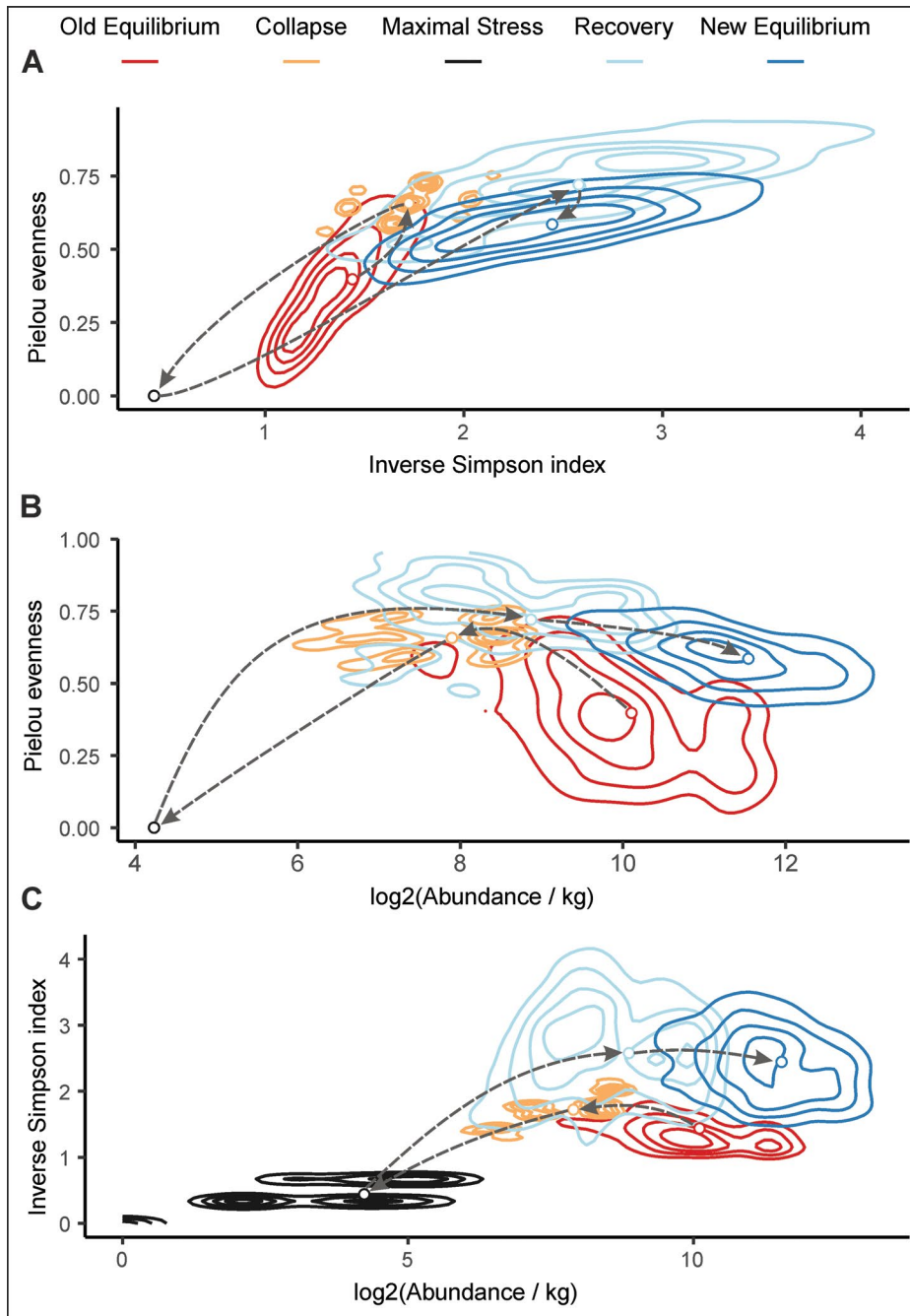


Fig. 5. Contour plots of bootstrapped sample averages of diversity indices depicted for each ostracod population, corresponding to different stages of Mulde/lundgreni event progression. Points represent the centroids of distributions, and arrows connect them in the order of time progression. For each stage there are four contour lines, dividing the range of empirical probability density distribution into five equal intervals.

Many studies of the Mulde/lundgreni Event interval focus on pelagic fauna, while studies of benthic groups are scarce (Calner *et al.* 2012). Often, they suggest that in the Maximal Stress interval, benthic clades had small or no changes, which could be an artefact of low resolution data and the short duration of the event (Jeppsson *et al.* 1995). Moreover it

was suggested that the event could have been a stratigraphical artefact of lateral movement of biofacies due to high-magnitude sea level changes (Jarochowska & Munnecke 2016). Although ostracods are much more prevalent in shallow oxygenated palaeoenvironments, and in the case of pure biofacies lateral movement, ostracod assemblages should have become richer and



more abundant in deeper parts of the basin. But we do not see this pattern. During the 'Big Crisis', abundance drops by orders of magnitude, and some samples even become barren. This barren level is also correlatable with barren micro-laminated deep-water facies in distal parts of the Baltic Basin, the so called Ančia Member (Radzevičius *et al.* 2014b). This scarcity of both benthic and nektonic life implies toxicity or spread of anoxic zones across water column, or presence of other cross-environmental stressor.

The 'Big Crisis' did not cause the complete extirpation of any ostracod species at the section scale, but did prompt a systemic shift in their composition and abundance patterns. This points to crossing of an eco-systemic tipping point on a time scale of ~260 Ka (up to the full recovery), after which palaeocommunities become 'frozen' for hundreds of thousands and possibly up to a million of years or more ('coordinated stasis' of Brett 2012 at shorter time scales). In the aftermath of the Mulde/*lundgreni* event similar synchronous shift was also detected in conodonts, although in it was in opposite direction of lower abundance and diversity, and higher evenness (Spiridonov 2017; Spiridonov *et al.* 2017). The graptolite zooplankton turnover likely impacted marine ecosystem organization due to its role in food and nutrient transport. Such a connection across functional tiers of ecosystems and spatial locations could have been the reason of such a synchronous shift in functioning of clades less affected by extinction process.

## Conclusions

The mid-Homerian biotic turnover and extinction event is recognized as one of the most important geobiological perturbations of the early Palaeozoic, although its impact and structure beyond biostratigraphically important groups (conodonts and graptolites) was uncertain. Here using a high-resolution record of ostracods, which allowed the detection of perturbations longer than 13 Ka, and applying Bayesian geochronology approach we estimated the timing and duration of different stages of the Mulde/*lundgreni* Event in shallow shelf benthos. It was found that the most probable duration of the mid-Homerian turnover event was around 260 Ka. This perturbation corresponded to the regressive phase of the 4<sup>th</sup> order sea level cycle (Radzevičius *et al.* 2017), which agrees well that it was approximately half of the duration of long orbital eccentricity (405 Ka) cycle. Contrary to some previous semi-quantitative interpretations which suggested that probable crisis up to the final recovery lasted around 1Ma (Cramer *et al.* 2012), the

current Géluva-118 record shows that it is much more restricted (almost by an order of magnitude) duration including full recovery and transition to a new state. The benthic ostracod assemblage collapse, restructuring and transition to new diversity-abundance condition happened on time scales comparable to that of major late Quaternary glaciations. The 'post-Big Crisis' corresponded to relative compositional stability of ostracod assemblages, thus confirming the generality of so called 'coordinated stasis' hypothesis of marine faunal change in mid Palaeozoic (Koren' 1991). The current work confirms the relatively fast pace of the 'Big Crisis' first suggested by the fossil records of pelagic graptolites and semi-pelagic conodonts, and shows significant and fast impact and later reorganization dynamics of the benthic realm, therefore revealing the uniformity in rates of the turnover across the whole range of marine environments.

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