Cyst size trends in the genus *Leiosphaeridia* across the Mulde (lower Silurian) biogeochemical event

ANDREJ SPIRIDONOV, AGNĖ VENCKUTĖ-ALEKSIENĖ & SIGITAS RADZEVIČIUS

The upper Wenlock epoch (Homerian age) of the Silurian period was an interval of intense changes in biotic composition, oceanic chemistry and sea level, which also witnessed a double-peaked positive stable carbon isotopic excursion. These biotic and environmental perturbations are thought to have originated due to reorganizations of the ocean system and high-amplitude sea level fluctuations. However, the evolutionary responses of the size of the micro-phytoplankton, which would help comprehension of the oceanographic mechanisms of these global perturbations, are currently unknown. Therefore, in this contribution we present morphometric data on the size changes of cysts of the dominant acritarch genus *Leiosphaeridia* during the middle and upper parts of the Homerian, which includes the *lundgreni* and Mulde bioevents, from the deep shelf facies of the eastern Baltic Basin (western Lithuania, Viduklė-61 core). Three parameters were measured for size distributions. Those are namely: average size, range of sizes, and power law exponent, which measures degree of "heavy-tailedness" and thus complexity of the distribution of cyst sizes. The average of the cyst sizes increased in the post-*lundgreni* interval of the Homerian, which points to the fundamental shift in the acritarch communities. The uncovered trends in cyst size ranges and power law exponents of their cyst size distributions revealed their close correspondence to the 4th order sea level fluctuations. Probable paleoclimatic and paleoecological mechanisms for this connection are presented. • Key words: Acritarchs, green algae, Silurian, Mulde Event, size evolution, Eastern Baltic.

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The Silurian period was one of the least stable time intervals throughout the entire Phanerozoic (Melchin *et al.* 2012). It is characterized by a set of conodont and graptolite extinctions, extirpations (regional disappearances), as well as general turnover events (Jeppsson 1987, 1993, 1997; Aldridge *et al.* 1993; Jeppsson *et al.* 1995; Jeppsson & Aldridge, 2000; Jeppsson & Calner, 2002; Calner & Jeppsson 2003; Radzevičius *et al.* 2014c, 2016; Spiridonov *et al.* 2015, 2016; Jarochowska & Munnecke 2016), which resulted in highly volatile (*sensu* Lieberman & Melott 2013) diversity patterns of graptolites (Cooper *et al.* 2014, Crampton *et al.* 2016). These events were accompanied by globally recognized positive stable carbon isotopic excursions, which point to deep oceanographic, paleoclimatological, and geobiological perturbations (Samtleben *et al.* 1996, Martma *et al.* 2005, Saltzman 2005, Loydell 2007, Cramer *et al.* 2011, Jeppsson *et al.* 2012, Kaljo *et al.* 2012, Racki *et al.* 2012, Lenton *et al.* 2016).

The focus of this study is the so-called global Mulde Event interval, which spans the mid- to upper Homerian (Calner & Jeppsson 2003; Cramer *et al.* 2006, 2012; Radzevičius *et al.* 2014b). The beginning of this interval is characterized by one of the most severe crises in the history of animal plankton, namely the extinction of the majority of graptolites [the "Big Crisis" of Jaeger (1991) or *lundgreni* event of Koren' (1987, 1991)], a significant decrease in the diversity of chitinozoans (Lenz *et al.* 2006, Cooper *et al.* 2014, Paluveer *et al.* 2014), and changes in the community composition of conodonts and possibly other vertebrates (Jeppsson 1998; Jarochowska *et al.* 2016; Radzevičius *et al.* 2014c, 2016). Synoptic coarse-grained compilations revealed that toward the end of the Homerian there was a global decrease in standing acritarch diversity and a simultaneous increase in disappearance rates (Kaljo *et al.* 1996). Similarly, perturbations in the abundance and diversity of acritarchs were observed in the mid-to-late

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Wenlock in north-western Poland (Porębska *et al.* 2004). Preliminary coarse-grained data on the Wenlock succession of the Cape Phillips Formation from northern Canada suggest a reduction in phytoplankton diversity (Noble *et al.* 2012). On the other hand, a high resolution study of the Viduklė-61 section does not show any significant taxonomic compositional changes in acritarch and prasinophyte assemblages at the genus level during the *lundgreni* event (lower Mulde event interval) in the Baltic Basin (Venckutė-Aleksienė *et al.* 2016). In addition to the biotic perturbations, one of the most characteristic features of this time interval is the development of a double-peaked, easily recognizable, positive stable carbon isotopic excursion, and the occurrence of high-magnitude 4th order [usually defined as 80 to 500 ka in duration (Catueanu 2006); here understood as 300 to 500 ka in duration] sea level fluctuations (Calner & Jeppsson 2003; Martma *et al.* 2005; Lehnert *et al.* 2007; Ray *et al.* 2010; Cramer *et al.* 2012; Radzevičius *et al.* 2014a, b).

In this study we examined the fossil record of size changes of the genus *Leiosphaeridia* spp., which is represented by simple cysts that are spherical in shape. The studied specimens are spherical to ovoidal in shape, without processes or divisions into fields, and the surface is smooth with some folds. The specimens vary in color (light yellow to brown) and in wall thickness (thin to moderate thick-walled). No pores are observed in the cell wall. Some specimens possess an excystment opening as a partial rupture or median split, a characteristic feature of microscopic algae (Moczydłowska 2010).

The organic-walled acid resistant spherical forms without processes were described in the first half of the twentieth century as the genus *Leiosphaera* by Eisenack (1938). Spherical forms with wall pores have been assigned to the older genus *Tasmanites* Newton, 1875 *in* Wall (1962) (previously regarded as spores) and forms without pores with thin walls have been assigned to the new genus *Leiosphaeridia* Eisenack, 1958. Since then, the morphology, biological affinity and classification of *Leiosphaeridia* have attracted the attention and puzzled many researchers. Wall (1962) suggested that *Leiosphaeridia* resembled the modern prasinophyte species *Halosphaera minor*. However, *Leiosphaeridia* has been referred to acritarchs by Evitt (1963). For a long time there were references that classified leiospheres as acritarchs (Martin 1993, Servais 1996, Strother 1996, Fatka & Brocke 2008, Mullins & Servais 2008, Vecoli 2008). Currently, some researchers support the idea of *Leiosphaeridia*'s affinity to a group of green algae named Prasinophyta (Tappan 1980, Le Herissé 1984, Guy-Ohlson 1996), which was confirmed based on ultrastructural and microchemical analyses of *Leiosphaeridia* cell walls (Arouri *et al.* 2000, Javaux *et al.* 2004). According to some other authors, remains of the genus *Leiosphaeridia* Eisenack, 1958 may represent vegetative green algal cells (Kazmierczak & Kremer 2009, Moczydłowska & Willman 2009). However, it was argued that in general Leiospheres (informal name of thin walled smooth surfaced palynomorphs), although having algal affinities, might represent a polyphyletic assemblage (Prauss *et al.* 1991).

The studied palynomorph genus is the most abundant phytoplanton taxon in the mid-to-upper Homerian of the Viduklė-61 core section, representing 85.5% of all counted nano- to microphytoplankton specimens (Venckutė-Aleksienė *et al.* 2016). Very similar percentages were found in the shallow water assemblages of the English Wenlock (Dorning & Bell 1987). Even though the exact biological affinity of the researched genus is still debatable (Vecoli 2008), this group is an important component of the early Paleozoic and especially in the Ordovician and Silurian phytoplankton communities (Brocke *et al.* 2006; Jun *et al.* 2010; Delabroye *et al.* 2011; Le Hérissé *et al.* 2009, 2013; Venckutė-Aleksienė *et al.* 2016).

The studied genus, judged by its morphology and size, is mostly micro-phytoplankton, although smaller individuals with a diameter of < 20 μm could be regarded as being nanophytoplankton. The knowledge on the contribution of other plankton components, namely other nano- and especially picoplankton in the Paleozoic seas is to date very limited. However, there is some rare direct (Agić 2015) and indirect (Strother 2008, Riding 2009) evidence of their occurrence and geobiological effects. Although nano- and picoplankton in today's oceans are a very important component of marine ecosystems (Buitenhuis *et al.* 2012), the small cell sizes of these groups significantly constrain energy transfer to higher trophic levels. Longer trophic chains are needed in order to transfer the produced energy to macroscopic animals, *i.e.*, their size is most frequently too small for direct consumption (Sommer *et al.* 2002). On the other hand, larger phytoplankton (*e.g.*, those studied here) were directly accessible to metazoan grazers, and thus were very important for the emergence and maintenance of complex communities of multicellular organisms in oceanic ecosystems.

Size is one of the most important parameters of living creatures, having an effect on almost any property – it controls the life history, physiology, morphology and to some extent even the genome size, evolutionary selectivity regimes, as well as the potential for complexity increase in lineages (Van Valen 1973, LaBarbera 1989, Kapraun & Buratti 1998, Gould 2002, Payne *et al.* 2009, McShea & Brandon 2010, Bonner 2013, Smith *et al.* 2016). The oceanic and marine ecosystem's function is totally dependent on the size distribution of phytoplankton, which affects the length of the food chains and energy transfer to the higher trophic levels, and as a consequence the potential and rates of organic carbon and nutrient burial (the so-called "biological pump") in deep-sea sediments (Chisholm 1992, Kiørboe 1993, Cortese *et al.* 2012, Marañón 2015). *Leiosphaeridia* spp. is characterized by relatively large individuals (5–175 µm in our samples) for phytoplankton, and size is a major determinant of sinking speed (Kiørboe 1993), and consequently carbon sequestration in the ocean. Therefore, it is crucial to document and understand the size trends of key phytoplankton groups in order to build realistic models of the, to this day puzzling, Silurian oceanic events and stable carbon isotopic excursions which accompany them.

Therefore, in order to test the impact of the Homerian environmental change we calculated a set of measurements describing the size distributions, and later compared these measurements with a model of 4th order sea level changes. Moreover sea level fluctuations are accompanied by other climatic and biotic effects, which could affect phytoplankton communities. The first factor is increased flux and recycling of nutrients in photic zone due to increased turbulence (Kiørboe 1993) of surface waters, due to stronger winds in hotter climate state (*e.g.*, Toggweiler & Russell 2008), which is ussually associated with the highstands of the sea level (there are certain indications that in the late Homerian there was a warming trend (Radzevičius *et al.* 2016). This factor could promote increase in size of unicellular algae. Another factor is a proliferation of phytoplankton predators in the aftermath of the *lundgreni* extinction event. We would expect for metazoan predators (grazers), which constitute the largest individuals in the zooplankton (organic matter consuming part of plankton), to selectively target larger fractions of the phytoplankton, mostly due to mechanical and energetic limits of the filtering of smaller particles (Sommer *et al.* 2002). This selective grazing (predation) could affect size frequency distributions by depleting large size individual classes. The fossil record shows that the graptolites were one of the most important components of the mid-Paleozoic zooplankton. Therefore in this contribution, based on literature survey, we also compared peaks of their diversity during the late Homerian to the fluctuations in the studied cyst size distribution parameters of *Leiosphaeridia* spp.

Materials and Methods

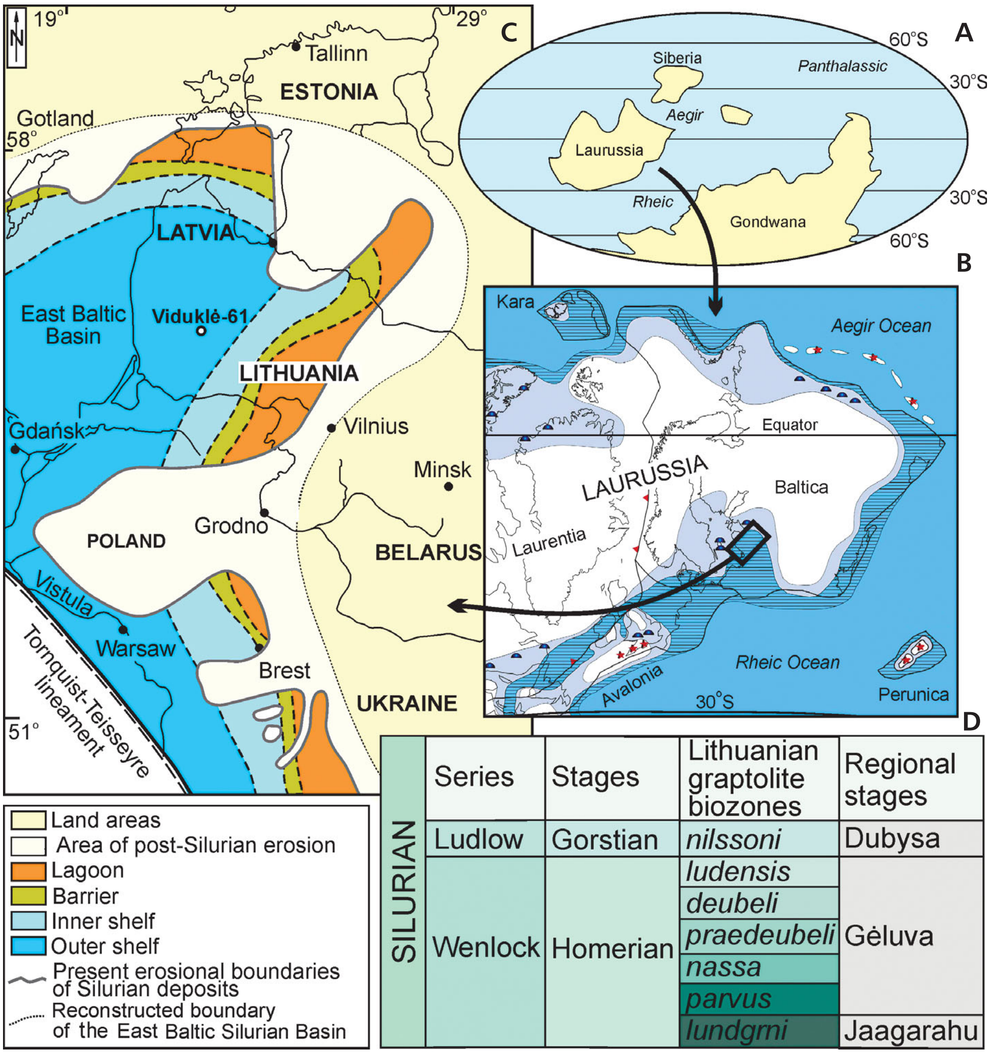
Geological Setting

The Viduklė-61 well is located in the western part of Lithuania: 55° 23´ 43.08˝ N, 22° 54´ 37.01˝ E (Fig. 1). During the Silurian period this site was a part of the so-called Silurian Baltic (or Baltoscandian) Basin, whose strata now stretch from the Teisseyre-Tornquist Zone in the south Baltic Sea area, central Poland, and the north-west of Ukraine to Estonia in the north-east (Einasto *et al.* 1986, Paškevičius 1997, Cocks & Torsvik 2005). The thickness and completeness of the strata of the Silurian System in this basin increases toward the south-west due to a convergent tectonics regime which dominated the region during the Caledonian Orogeny (Paškevičius 1997, Lazauskienė *et al.* 2003). Paleogeographically, during the studied Wenlock epoch the Silurian Baltic Basin stretched along the south-eastern flank of the Laurussia supercontinent in the southern tropical latitudes near the equator, and was a marginal sea of the greater Rheic Ocean (Cocks & Torsvik 2002, 2005).

During the upper Wenlock the studied Viduklė-61 site was characterized sedimentologically by the deposition of clayey carbonates and to a lesser extent microlaminated limestones, and it is located in the outer shelfal zone of the Silurian Baltic Basin (Radzevičius *et al.* 2014b). The studied core yielded one of the richest arrays of data in the world on the paleoenvironmental changes during the Mulde Event, ranging from graptolite, conodont, brachiopod, polychaete and microphytoplankton biostratigraphy and paleoecology, to stable carbon isotope chemostratigraphy and natural gamma ray cyclostratigraphy (Brazauskas & Paškevičius 1981; Paškevičius 1997; Martma *et al.* 2005; Ekleris & Radzevičius 2014; Radzevičius *et al.* 2014b, 2017; Venckutė-Aleksienė *et al.* 2016). Additionally, this core contains a stratotype of the lower boundary of the Gėluva regional stage (Kojelė *et al.* 2014), and therefore it is a reference section for the detailed regional stratigraphical correlation and the detection of paleoclimatological and paleobiological patterns.

Morphometric data

For the purpose of analysis the same set of 56 samples (three being barren), which was the basis of a phytoplankton biodiversity change study (Venckutė-Aleksienė *et al.* 2016), was examined for the linear size measurement analysis of the microphytoplankton genus *Leiosphaeridia.* The sampled interval spanned the upper *lundgreni* through the *ludensis* graptolite zones – a depth interval of between 1312.8 and 1276.1 m (Radzevičius *et al.* 2014b, Venckutė-Aleksienė *et al.* 2016). The green algae cysts were measured using a Nikon Eclipse 200 LED Binocular Microscope under × 400 magnification. The maximal linear dimension was used as a surrogate for a cyst's diameter, assuming the original spherical shape. Overall, 53 samples with *Leiosphaeridia* spp. (19,238 measured individuals) were used in the analysis (the measurements and derived parameters can be found in the electronic supplementary appendix). The samples are kept in the Nature Research Centre in Vilnius, Lithuania.



	Series	Stages	Lithuanian graptolite biozones	Regional stages
SILURIAN	Ludlow	Gorstian	*nilssoni*	Dubysa
	Wenlock	Homerian	*ludensis*	Gėluva
			deubeli	
			praedeubeli	
			nassa	
			parvus	
			lundgrni	Jaagarahu

Figure 1. A – continental reconstruction of the Early Silurian (Torsvik & Cocks 2013). B – paleogeography of Laurussia during the mid-Silurian (Cocks & Torsvik 2005). C – paleogeographic location of the Viduklė-61 well in the Silurian Baltic Basin (Einasto *et al.* 1986). D – stratigraphical time scale of the upper Wenlock and the lowermost Ludlow in Lithuania (Radzevičius 2006).

Statistical techniques

It has been determined in other studies that cyst sizes are generally very similar to the motile phase during the life cycle of unicellular eukaryotes (Finkel *et al.* 2007). Therefore, in this study it is assumed that cyst sizes are proportional to cell sizes in the active stage. During the analysis we estimated the parameters (average diameters, ranges of diameters, and power law exponents of diameter size frequency distributions), comprehensively describing the distributions of the cyst sizes. First, we calculated averages (μ) of the cysts' diameters (d) of the genus for each productive sample. The next two parameters (range and shape of distribution) could be seen as proxies for the bioenergetic niche of a genus. Total range of sizes is related to the total availability of nutrients – larger the range, less nutrient restrictive environments is for the algae. Shape of the distribution, on the other hand shows how the nutrients and produced biomass are distributed in the planktonic community. It is increasingly recognized that inferred paleoniches are dynamic states which evolve in response to physical perturbations as well as biogeographic and evolutionary turnovers (Myers *et al.* 2015, Lieberman & Saupe 2016, Patzkowsky & Holland 2016). Therefore, the quantification of these parameters is a crucial step in narrowing down the probable determinants and understanding the geobiological consequences of the eco-evolutionary change of phytoplankton.

Total range (the difference between min. and max. values) is a statistically unreliable measurement due to its sensitivity to outliers. Therefore, as a surrogate for the range we used the difference between the average of the three largest specimens and the average of the three smallest specimens in a sample. Suppose we have ranked the sequence of cyst sizes from the smallest to the largest: $1,2,3,......j-1,j$, then the minimal consistent range, or here just range (R), can be found in the following way (see the explanation of measures used in this study in Fig. 2):

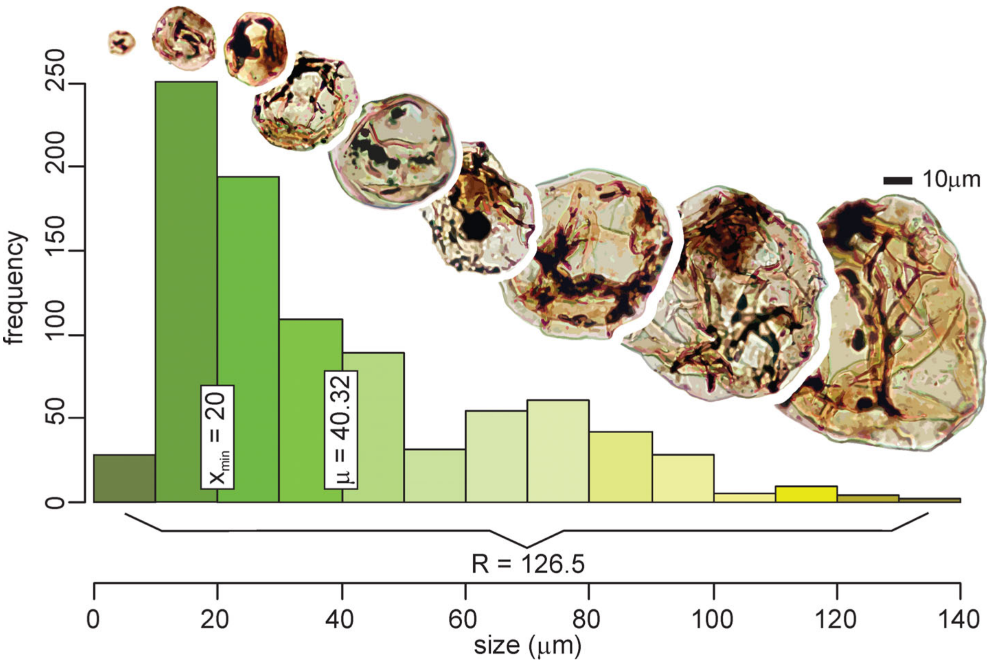


Figure 2. Explanation of the parameters used in the description of size distributions: d_{min}– minimal diameter used for the estimation of the power law exponent; μ– average diameter; R– minimal consistent size range of a sample. In the upper part of the diagram representatives of the different size classes of *Leiosphaeridia* spp. are shown (sample depth 1312.8 m).

$$R = \mu_{i=j-2}^{n=j} - \mu_{i=1}^{n=3} \qquad \text{(eq. 1)}$$

Here μ is an average. The described method requires at least six occurrences of individuals from one genus in a sample. Therefore, the samples of a given genus which had fewer than that were omitted from the analysis. Additionally, since the range measure increases monotonically with an increase in sample size (Foote 1997, Wainwright 2007), this bias should be mitigated. Therefore, we performed a logistic regression of range sizes against sample sizes and later subtracted this sample size-related trend from the data and used residuals for further analysis. Logistical regression was used because it is suitable for modeling monotonically increasing quantities with a definite level of saturation (*i.e.*, increasing the range of an empirical distribution as a function of sample size). It could be argued that this technique should perform better than subsampling on theoretical grounds since it actively compensates for the monotonic sample size-related bias in the estimation of the range statistic. The subsampling, on the other hand, would severely under-use the available data, as it requires the use of sub-samples at least as small as the smallest sample in the studied set, *e.g.*, Alroy *et al.* (2001).

Most of the size distributions studied here exhibited strong positive skewness (Fig. 3). This fact points to the great diversity of size classes in the samples. Smaller size classes are almost always numerically more prevalent than the larger classes. Therefore, if we have strong positive skewness, even though larger size classes are less abundant than the smaller ones, we should have decent amount of large individuals in a sample. High positive skewness is usually associated with the larger range of a distribution. On the other hand power law exponent measures "thickness" of the right hand tail of a distribution, which shows how numbers of individuals are distributed through this tail. Therefore, both parameters (range and power law exponent) complement each other in describing cyst size histograms in a meaningful way.

For each distribution (with > 15 measurements) we calculated the so-called power law exponents (α). We approximated the shape of the right-hand side of a distribution using the discrete version of a power law:

$$p(d = D) = \frac{d^{-\alpha}}{\zeta(\alpha, d_{min})} \qquad \text{(eq. 2)}$$

Here, (ζ) is the generalized Zeta function, and d_{min} is the minimum (cut-off) value of a cyst's diameter (Fig. 2), which still follows the power law (Clauset *et al.* 2009). A larger exponent value points to the quick decay of the right-hand side tail of a distribution, and a lower value indicates that even though smaller individuals dominate the sample, there is a good probability of finding very large ones (that is, the tail of the distribution is very heavy). Other distributions can be used for parameterizing histograms of cyst sizes (*e.g.*, exponential), but power law distribution is more flexible in accommodating "heavy tail" distributions which are abundant here. Moreover power law exponent is inversely related to ecological metric of standardized entropy, and therefore can be meaningfully interpreted in an ecological context.

It has been shown mathematically that the fractal dimension of the distribution could be measured as the reciprocal of the power law exponent ($1/\alpha$), and it is linearly related to the sample size's standardized entropy or the evenness of the distribution (Frontier 1985, pp. 296, 297). Thus, smaller values of α indicate a higher diversity and complexity of a measured distribution (its higher evenness). That is, we can observe wider range of size classes with a greater chance. Therefore a sample from this distribution is expectedly should be more diverse (Frontier 1985) with regard to cyst sizes. In this case, different cyst size classes are represented more evenly, and therefore they are available in considerable abundances for the higher diversity of prey size restricted consumers. The estimation of the minimum values and power law exponents were performed using the 'poweRlaw' package in the R statistical computing environment (Gillespie 2015, R Development Core Team 2015). More detailed summary on the application of power law (or Zipf) distribution can be found in the Appendix.

In order to gain insights into the mechanisms controlling body size distribution changes of the analyzed green algae we also plotted the time series of proxies: the filtered curve of 4th order sea level fluctuations (Radzevičius *et al.* 2017) which were proposed to represent the 400 ka eccentricity Milankovitch cycles (Radzevičius *et al.* 2014a). The 4th order sedimentary cycles were distinguished based on the REDFIT statistical testing (Schulz & Mudelsee 2002) of the natural gamma ray signal with the subsequent band-pass Gaussian filtering of the ≈ 20 m long (measured on the thickness scale) cycles from the original signal using package 'astrochron' in the R computational environment (Meyers 2015, R Development Core Team 2015) (more details can be found in Radzevičius *et al.* 2017). The symmetry of the distinguished sea level cycles (the rising and falling limbs are almost symmetrical) is expected since we are dealing with a deep-water sedimentary system. This kind of setting is much less prone to significant perturbations in the sedimentation rates than in near-shore systems and thus it is much more suitable for cyclostratigraphical analyses (Weedon 2003).

Results

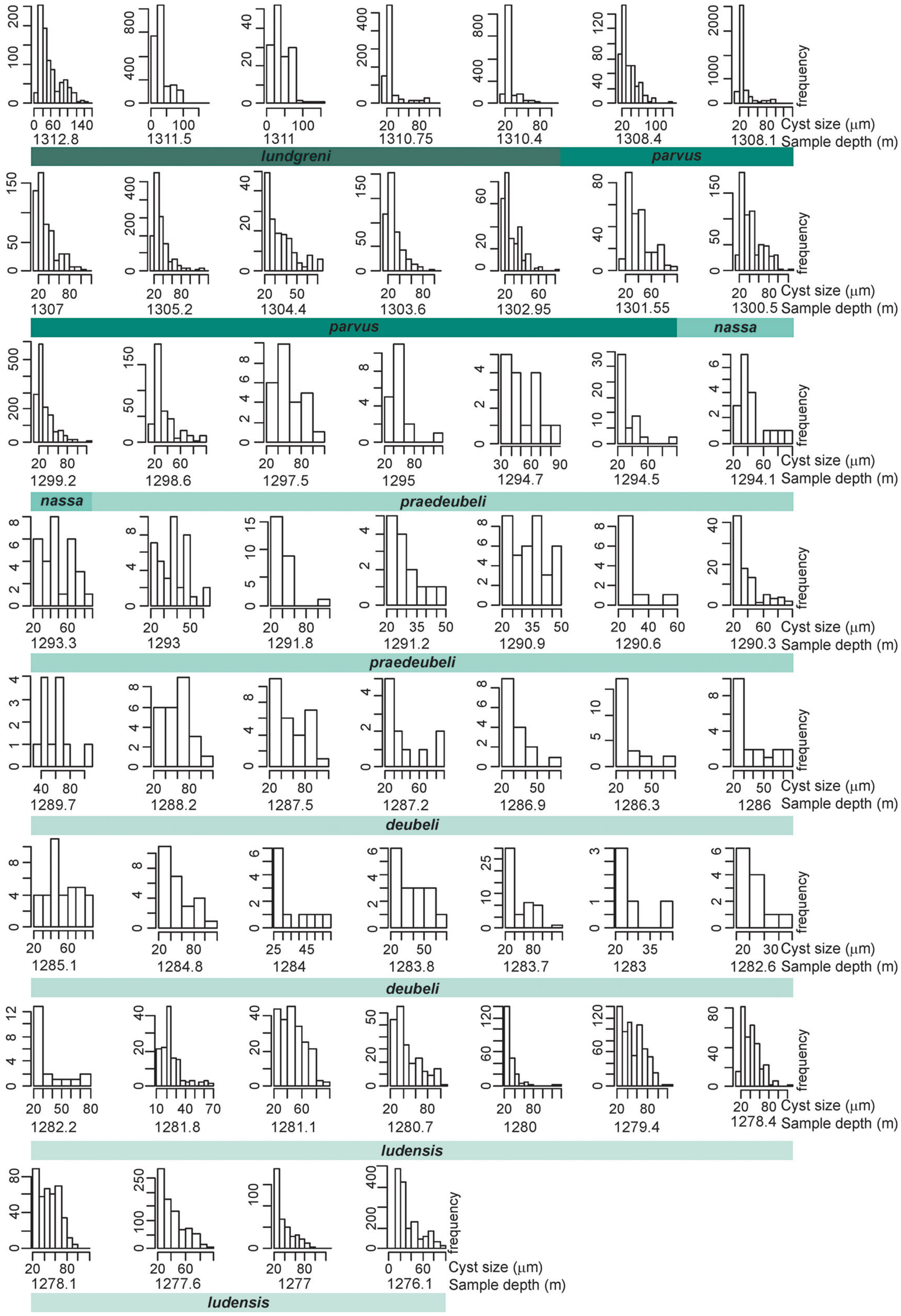
A visual examination of the size histograms of *Leiosphaeridia* spp. during the mid-to-late Homerian reveals several interesting patterns. The upper *lundgreni* interval up to a depth of 1311 was characterized by a fairly even distribution of body sizes (Fig. 3). On the other hand, the interval of the uppermost *lundgreni* and the lower *parvus* zones (1310.75–1308.1 m) was characterized by an extremely asymmetrical distribution with an exceptionally pronounced mode (≈ 20–25 μm) of very small cysts [also known as the "Lilliput effect" of Urbanek (1993)] which dominated the assemblages. Later on the distributions assumed a more even but still right-skewed form up to the start of the *praedeubeli* Zone, where they started to become very even and irregular, partly due to their lower absolute abundance. Starting from the *deubeli* Zone, more right-skewed cyst size distributions appeared with more abundant large size classes.

A comparison of the trends in cyst size distribution parameters with 4th order sea level cycles reveals more specific details about the scaling of *Leiosphaeridia* spp. specimens through time (Fig. 4). The smoothed trend in the average size (Fig. 4A) shows that the lower parts of the section (the uppermost *lundgreni* and *parvus* zones) were characterized by smaller sizes than their later descendants in the upper Homerian. There was a steady growth from a long-term average of 33–35 μm in the lower portion of the interval to around 40 μm in the *praedeubeli* and later zones. However, this increase was accompanied by pronounced high-frequency fluctuations and should be seen as a first-order (at the scale of analysis) pattern.

The long-term changes in the sample size bias-corrected cyst size range estimate (Fig. 4B) reveal somewhat different patterns to those exhibited by the long-term averages of cyst diameters. It appears that there is a close similarity between the long-term trends in range sizes and 4th order sea level cycles (Fig. 4D). There was a drop in range size during the earliest *parvus* time, which was followed by increase in range size during the *nassa* time, which was later followed by a decrease in size ranges during the late *predeubeli* and early *deubeli* times, as well as a subsequent rise in range size and a third long-term peak in the *ludensis* Zone.

The long-term values of the power law exponents (α) of cyst size distributions apparently also followed the trajectory, which is very similar to the 4th order sea level cycles (Fig. 4C, D). The minima of the 4th order sea level curve during the latest *lundgreni* and the earliest *parvus* zones, at the end of *praedeubeli* Zone and at the end of *ludensis* Zone, corresponded to the minima of the long-term trends in the power law exponents. Therefore, in general, these intervals were characterized by flatter, heavier-tailed cyst size distributions. However, similar to the case of average size and ranges of the size distributions, there is an abundant high-frequency variation in the

Figure 3. Histograms of the cyst diameters of *Leiosphaeridia* spp. in the mid-to-upper Homerian from the Viduklė-61 well. The histograms show the raw morphometric data on the taxon from the studied interval shown by graptolite zones. The graptolite zones are based on Radzevičius *et al.* (2014b).


frequency
Cyst size (µm)
Sample depth (m)
0 60 140 1312.8
0 100 1311.5
0 100 1311
20 80 1310.75
20 80 1310.4
20 100 1308.4
20 80 1308.1
lundgreni
parvus
20 80 1307
20 80 1305.2
20 50 1304.4
20 80 1303.6
20 60 1302.95
20 60 1301.55
20 80 1300.5
parvus
nassa
20 80 1299.2
20 60 1298.6
20 80 1297.5
20 80 1295
30 60 90 1294.7
20 60 1294.5
20 60 1294.1
nassa
praedeubeli
20 60 1293.3
20 50 1293
20 80 1291.8
20 35 50 1291.2
20 35 50 1290.9
20 40 60 1290.6
20 60 1290.3
praedeubeli
40 80 1289.7
20 80 1288.2
20 80 1287.5
20 60 1287.2
20 50 1286.9
20 50 1286.3
20 50 1286
deubeli
20 60 1285.1
20 80 1284.8
25 45 1284
20 50 1283.8
20 80 1283.7
20 35 1283
20 30 1282.6
deubeli
20 50 80 1282.2
10 40 70 1281.8
20 60 1281.1
20 80 1280.7
20 80 1280
20 80 1279.4
20 80 1278.4
ludensis
20 80 1278.1
20 60 1277.6
20 80 1277
0 60 1276.1
ludensis

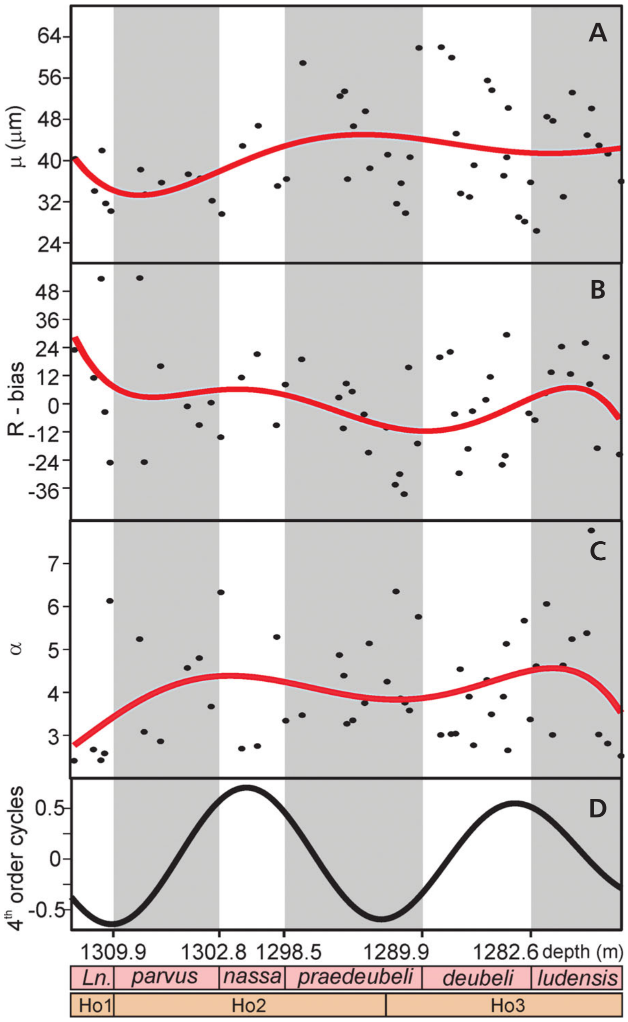


Figure 4. Trends in A – average size (μ) of cysts; B – corrected range (R-bias) of cyst sizes; C – power law exponents (α) of cyst size distributions; and D – filtered 4th order sea level cycles (from (Radzevičius *et al.* 2017). The smoothed non-linear trends in A–C were determined using 5th order orthogonal polynomial regression. The graptolite zones were according to Radzevičius *et al.* (2014b). The Homerian stage slices (Cramer *et al.* 2011) (Ho1–Ho3) were correlated based on conodont, graptolite, and δ^{13}C data applying an integrated stratigraphy approach.

examined parameter. This indicates the quick response times of the cyst size distributions to perturbations.

Discussion

Trends in the average of cyst size diameters

The most pervasive pattern in the average of *Leiosphaeridia* spp. cyst sizes revealed by the analysis is its increase and stabilization during the post-*parvus* time interval. This pattern is congruent with what is known about the paleoclimate of the Homerian. The *lundgreni* Event and the beginning of the Mulde Event was characterized by a pronounced eustatic sea level fall (Loydell 1998, 2007; Calner & Jeppsson 2003), and a significant decrease in tropical sea water temperatures (Radzevičius *et al.* 2016, Trotter *et al.* 2016). The later part of the Homerian was characterized by an increase in sea level with significant secular variations which can be traced in different geographical regions, therefore pointing to their eustatic origin (Loydell 1998, 2007; Ray & Butcher 2010; Radzevičius *et al.* 2014a). However, at this time a quantitative test of the association of water paleotemperatures with the size trends of leiosphere cysts is rather difficult. This difficulty arises from the sparseness of paleotemperature estimates and the possible problems related to scaling these estimates to the densely sampled record presented here.

Studies of Cenozoic phytoplankton have revealed that the recent transition to an icehouse climatic state was followed by a pervasive size decrease in the dominant phytoplankton groups (diatoms and dinoflagellates), which was probably related to the changes in trophic states, turbulence, and the stratification levels of the oceans (Finkel *et al.* 2005, 2007; Falkowski & Oliver 2007). Therefore, the post-*lundgreni* increase in overall cyst size can be explained as a response to the warming-induced oceanographic changes in water masses during the late Homerian (*i.e.*, lower stratification and more effective recycling of nutrients). On the other hand, given in mind spatial restrictions of this study, there is possibility that the patterns revealed not necessary reflect in situ changes in populations but could also be caused by the systemic regional displacements of water masses (more stratified by less stratified) and with them indigenous *Leiosphaeridia* spp. populations.

Trends in the range of sizes

The smaller ranges of cyst size distributions were associated with the 4th order sea level regressions. The maximum range was achieved in the upper *lundgreni* and lower *parvus* zones, and later on during the studied interval it was never matched. It is probable that the *lundgreni* event decimated the cyst size diversity of *Leiosphaeridia* spp., although the focus of this size diversity decrease (intra- or inter-specific) and the mechanism responsible for it (natural *vs.* species selection and drift (Stanley 1975, Gould 2002) are currently unknown. Similarly, previous synoptic studies have shown a close association of acritarch and prasinophyte diversity with global and regional fluctuations in sea level on time scales of millions to tens of millions of years (Servais *et al.* 2008, Delabroye *et al.* 2011, Venckutė-Aleksienė *et al.* 2016). This suggests the importance of sea level dynamics in modulating evolutionary and ecological change in Paleozoic marine phytoplankton assemblages. On the other hand there is large amount of smaller scale variability which cannot be attributed to this single determinant, and therefore other unaccounted factors could have played role.

Trends in the power law exponents of size distribution

The higher values of power law scaling exponents α (the thinner right-hand side tails of body size distributions) during transgressions should be seen as the first-order approximation of the revealed patters. As in the case with the time series of ranges of size distributions, there is abundant high frequency variability in the described parameter.

Nevertheless, apparent association of high values with the long-term (4th order) sea level high-stands can be explained by the proliferation of new species of graptolites (probable consumers of *Leiosphaeridia* spp.) during the inferred high stands of the sea level at the given site. The local diversity of graptolites peaked in the lower *praedeubeli* Zone and at the start of the *ludensis* Zone (Radzevičius *et al.* 2014b). Assuming that the power law relation appears to be a result of the mixture of several normal (or log-normal) distributions of diminishing amplitude (larger species are progressively less abundant), the action of predators could decrease the diversity of prey and narrow down the distribution of cyst sizes to the most resilient size class, and in this way make the cyst size distributions look more Gaussian (or normal), *i.e.*, symmetrical with steeper slopes.

The patterns of first and the last occurrences of graptolite species in the studied section are highly congruent with those recognized in other regions, *i.e.*, (Koren' 1987, Kozłowska-Dawidziuk *et al.* 2001, Lenz *et al.* 2006, Melchin *et al.* 2012). Therefore the observed pattern of graptolite species turnover in the studied section could have been controlled on the long time scales by large scale macroevolutionary processes in interaction with spatial dispersal, and not just a result of the local peculiarities of community change.

An increase in the diversity and productivity of prey could occur during the aftermath of an extinction event when the prey experiences relief from the negative effects of predation (Solé *et al.* 2010), but eventually the long-term diversification of predators during the recovery phase following extinction (Sallan *et al.* 2011) or delayed dispersal after immediate rediversification (Radzevičius *et al.* 2016) will down-regulate the prey to the presumed equilibrium values. Therefore, this indirectly shows that top-down trophic controls (*i.e.*, predation) could be an important factor in macroevolution and long-term changes in phenotype distributions (Stanley 2008, Sallan *et al.* 2011, Voje *et al.* 2015). In this way the association of the higher values of α with 4th order highstands of the sea level is an indirect effect of higher diversities of potential consumers of leiospheres (in this case graptolites), with the high sea level conditions.

High values of α of size distributions could be also explained in other ways. For example if there is strong limitation of nutrients, then larger size classes would be less represented, since the effectiveness of diffusive nutrient intake to the larger cells is increasingly ineffective. On the other hand the trends in average cyst sizes point out that there is pervasive trend toward larger cysts in post-*lundgreni* time, which deems this alternative less likely.

Conclusions

The major changes in the evolutionary and ecological dynamics of *Leiosphaeridia* spp. in the Viduklė-61 section occurred at the transitions between low and high sea level stands during 4th order cycles. The *lundgreni* extinction interval and the following survival interval, which are associated with the bottom of a 4th order sea level cycle, were characterized by small average cyst sizes and a narrow mode of small sizes. The remainder of the Homerian was characterized by significantly larger average cyst sizes. It appears that the range of cyst sizes and the power law exponents that described the shapes of the cyst size distributions were also modulated by the same 4th order cycles. Larger cyst size ranges were more frequent in high-stand situations. The long term changes in power law exponents (larger values during intervals of increased diversity of graptolites) of the cyst size distributions studied here indirectly point to the possible long term predation effects of the dominant fossilized zooplankton (graptolites) on the studied acritarch group.

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Appendix

Present application of the power law or Zipf model to the size distributions of cysts of acritarchs is based on the interpretation of this model by Frontier (1985) in the context of ecological systems. The Zipf model written in a discrete form is expressed in the following way $f_r = f_0 . r^{-\alpha}$, here f_r is a rank of r^{th} species, $f_0 = f_1$ is the frequency of the species with the highest abundance, and α is the power law exponent. This model was put forward in order to reveal dynamical patterns of ecosystem assembly by means of ecological succession, when arrival of later species is conditioned on the appearance of former (more abundant) species. The frequency of each class (it could be species or other ecological meaningful entity) of this distribution shows its probability of appearance, when all necessary conditions are satisfied. The parameter of interest α is inversely related to the evenness of the distribution. There is an extension of this model, so called Zipf-Mandelbrot model with one additional term (β), which discrete version is expressed mathematically in the following way $f_r = f_0 \cdot (r + \beta)–\alpha$ (Frontier 1985). This model being more flexible and informative is less straight-forward for the interpretation.

The described Zipf model was widely applied to the whole range of complex systems, ranging from linguistics, electronics, and natural sciences, as a way of describing complex self-organizing systems which exhibit long-tailed distributions (Clauset *et al.* 2009).