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Spontaneous Article

Dynamic ecophenotypy in the Silurian Monograptidae (Graptolithina)

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ABSTRACT: The monograptids from the Wenlock and Ludlow (mid- to late Silurian) of the palaeotropical Baltic Basin exhibit thickened ring structures (sicular annuli) over their initial phase of growth. Appearing before the *lundgreni* extinction event, they persisted throughout the remainder of the Silurian, fluctuating in number over that period. To better understand the mechanisms controlling their development and variation, counts of sicular annuli were taken from three well cores in Lithuania, compared between species in each sample and compared with contemporaneous gamma ray data, accompanied by the stable isotope ($\delta^{13}C$), and acritarch diversity data. Mean counts of annuli fluctuated greatly over the studied interval, but showed negligible variation between species, indicating that the trait is ecophenotypic. The fluctuation in annulus presence aligned with variations in fourth- and fifth-order cycles derived from the gamma ray trends, which represent significant sea level fluctuations, $\delta^{13}C$ ratios, and primary productivity, suggesting that annuli were more plentiful in high-stand states which are associated with the wetter climate and more productive conditions, whereas dryer, less productive conditions were not conducive to annulus development. In light of this evidence, we hypothesise that the action of upwelling as a result of intensified storm events during wetter periods would have encouraged phytoplankton blooms, increasing construction of annuli. These results show the potential utility of sicular annuli in the study of Silurian climate change and give new insights into graptolite palaeoecology.

KEY WORDS: climate change, graptolites, Mulde event, sicular annuli, ecology, zooplankton.

The Silurian Period was marked by a series of climatic disturbances that had a significant impact on the evolution of marine life. In the late Wenlock, one of these disturbances, the Mulde Event, is associated with sea level fluctuations (Calner *et al.* 2006) and two probable glaciations at the beginning and middle of the event (Jeppsson & Calner 2003). These severe climatic shifts coincided with a collapse in the abundance and diversity of marine fauna (Lenz *et al.* 2006; Calner 2008; Steeman *et al.* 2016; Venckutė-Aleksienė *et al.* 2016; Spiridonov 2017). Among the most striking of the biotic disturbances of the Mulde interval was the early Homerian *lundgreni* graptolite extinction event (Koren' & Urbanek 1994; Urbanek *et al.* 2012), a severe, although short-lived, biodiversity disturbance detected in the fossil record of Baltic ostracods (Rinkevičiutė *et al.* 2021) and graptolites (Urbanek *et al.* 2012). This disturbance saw the family Monograptidae reduced to a single species, *Pristiograptus dubius parvus* Ulst (Koren' & Urbanek 1994; Urbanek *et al.* 2012). *Pristiograptus dubius parvus* was followed by an anagenic successor in *Pristiograptus dubius frequens* (Jaekel), and during and following the Mulde interval that stem lineage gave rise to a broad swath of morphologically disparate taxa (Urbanek 1997; Rickards & Wright 2003; Urbanek *et al.* 2012; Whittingham *et al.* 2020). The diverse monograptids from that time are especially remarkable as many species both from the low paleolatitudes of the Baltic Basin (Urbanek *et al.* 2012), Canadian High Arctic (Lenz & Kozłowska-Dawidziuk 1998), and Australia (Rickards *et al.* 1995; Rickards & Wright 1999), and from the mid-paleolatitude Bohemia (Štorch *et al.* 2014) possess the same novel trait, known as 'sicular annuli'.

Annuli are thickened bands on the sicula (Fig. 1) or, very rarely, on the first theca (Fig. 1a) of some monograptids. These were observed to be disassociated with the growth rings (fusellae) of the sicula (Kozłowski 1948; Walker 1953), refuting claims that the annuli were representative of slowed periods of growth in the sicula (Kraft 1926). Walker (1953) also showed that sicular annuli were formed during the development of the sicula, instead of being constructed after its completion. Later observations (Urbanek 1958) revealed the consistent presence of an initial annulus, at the boundary of the prosicula and metasicula (Figs 1c, d), and showed that the initial annulus consisted of material deposited on both the inside and outside surfaces of the sicula, contrasting with the metasicular annuli, which exist only on the inside of the sicula. Urbanek also noted broad variation in the number of sicular annuli per specimen in a given species, including some specimens with none. This variability has been since expanded upon through two key findings: (1) that sicular annuli at the boundary of the prosicula and metasicula are first consistently identifiable across multiple species after the *lundgreni* Biozone of the lower Homerian

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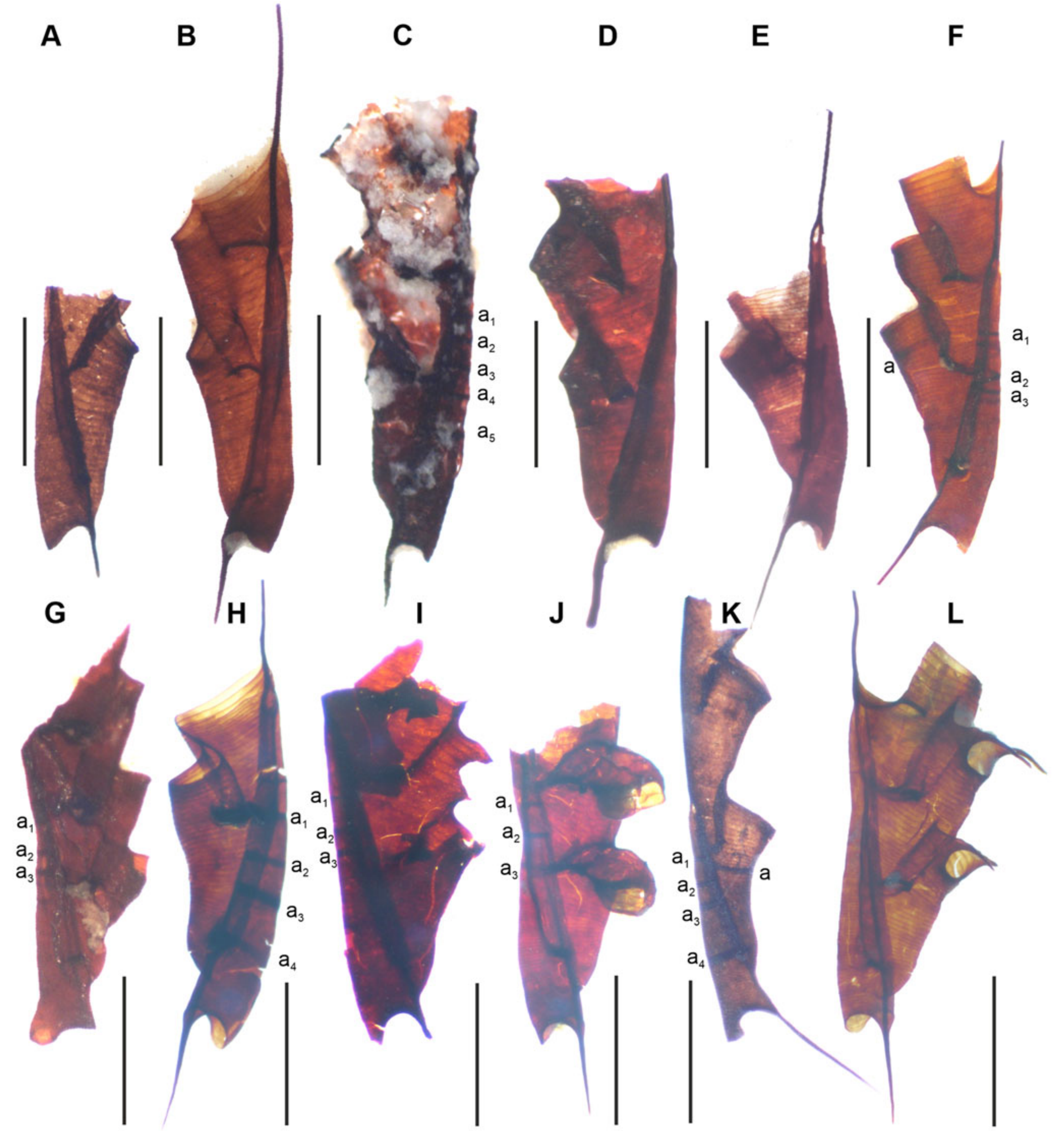

Figure 1 (A) *Pristiograptus parvus* Ulst; no. VU-S.V-131_356b, Vilkaviškis – 131 borehole, depth 1085.8 m, *parvus* Biozone, Gėluva Regional Stage, Homerian, Wenlock; (B, C) *Pristiograptus dubius frequens* Jaekel, Šiupyliai – 69 borehole: (B) without sicula annuli no. VU-P.S-69_292, depth 998.4 m, *nassa* Biozone, Gėluva Regional Stage, Homerian Wenlock; (C) with sicula annuli, VU-S.S-69_011b, depth 952.4 m, *progenitor* Biozone, Dubysa Regional Stage, Gorstian, Ludlow; (D) *Pristiograptus virbalensis* Paškevičius, no. VU-S.V-131_012, Vilkaviškis – 131 borehole, depth 1076.3 m, *praedeubeli* Biozone, Gėluva Regional Stage, Homerian, Wenlock; (E, F) – *Colonograptus praedeubeli* (Jaeger), Vilkaviškis – 131 borehole, *praedeubeli* Biozone, Gėluva Regional Stage, Homerian, Wenlock: (E) without sicula annuli, no. VU-S.V-131_015, depth 1076.3 m; (F) no. VU.MW.V-131_022, depth 1077.3 m; (G) *Colonograptus deubeli* (Jaeger), no. VU-S.V-131_016, Vilkaviškis – 131 borehole, depth 1067.3 m, *deubeli* Biozone, Gėluva Regional Stage, Homerian, Wenlock; (H) *Pseudomonoclimacis dalejensis* (Bouček), no. VU.MW.S-69_018, Šiupylai – 69 borehole, depth 964.3 m, *nilssoni* Biozone, Dubysa Regional Stage, Gorstian, Ludlow; (I) *Colonograptus gerhardi* (Kühne), no. VU.MW.B-2_019, Baubliai – 2 borehole, depth 1641.1 m, *nilssoni* Biozone, Dubysa Regional Stage, Gorstian, Ludlow; (J) *Uncinatograptus uncinatus* (Tullberg), no. VU.MW.S-69_025, Šiupylai – 69 borehole, depth 964.3 m, *nilssoni* Biozone, Dubysa Regional Stage, Gorstian, Ludlow; (K) *Bohemograptus bohemicus bohemicus* (Barrande), no. VU.S.B-2_016, Baubliai – 2 borehole, depth 1628.8 m, *scanicus* Biozone, Dubysa Regional Stage, Gorstian, Ludlow; (L) *Saetograptus chimaera* (Barrande), no. VU.MW.S-96_012, Šiupylai – 69 borehole, depth 951.2 m, *progenitor* Biozone, Dubysa Regional Stage, Gorstian, Ludlow. Abbreviations: a = dense fusellae marking interrupted growth; a_n = annuli of sicula. Scale bars = 1 mm.

(Lenz & Kozłowska-Dawidziuk 1998), and (2) that annuli vary in number between the *nassa* graptolite Biozone of middle Homerian and the *leintwardinensis* graptolite Biozone of the earliest Ludfordian (Urbanek 1997; Urbanek *et al.* 2012).

The fluctuation of annuli between the middle Homerian and Ludfordian was recognised as occurring in phylogenetically independent lineages by Urbanek (1997), with the veracity of that phylogenetic independence later being supported via stratocladistics (Whittingham *et al.* 2020). However, the ecological and evolutionary significance of sicular annuli remains unclear. It is that fluctuation in the number of annuli per specimen during the *nassa–leintwardinensis* Biozone interval that may provide insight into the life habit of middle–late Silurian graptolites and, if the fluctuations are independent of species, the changing climate of the Mulde interval. The purpose of this study is to establish whether the fluctuations in sicular annuli through the late Homerian and early Gorstian are independent of taxonomy, as predicted by Urbanek (1958), and if so, what factors may instead be responsible for that fluctuation.

1. Material and methods

Material consists of 367 graptolites (see Supplementary material available at https://doi.org/10.1017/) from the Viduklė-61 [56.049°N, 23.090°E] (upper *nassa–scanicus* biozones), Šiupyliai-69 [55.395°N, 22.910°E] (*praedeubeli–scanicus biozones*), and Vilkaviškis-131 [54.764°N, 22.849°E] (*praedeubeli–deubeli biozones*) boreholes from the Lithuanian region of the Baltic Basin (Fig. 2), an area located near the equator during the late Wenlock and early Ludlow (Torsvik & Cocks 2013). Graptolite rhabdosomes were prepared from rock using hydrochloric acid and hydrofluoric acid solutions. In the absence of an available infrared camera, specimens were stripped of their outermost cortical layer by being placed in a combined solution of 15 mL of 65 % nitric acid, 15 mL distilled water, and 5 g of potassium chlorate for 5–7 days, rendering the specimens red-brown and translucent to make the sicular annuli more clearly visible. This procedure serves only to enhance visibility and does not damage specimens or affect annulus counts (Green 2001). Specimens were prepared and counted for sicular annuli if they possessed both an intact sicula and first theca. Species diagnoses were made for *Pristiograptus dubius frequens* Jaekel, *Pristiograptus virbalensis* Paškevičius, *Colonograptus praedeubeli* (Jaeger), and *Colonograptus deubeli* (Jaeger) based on descriptions by Urbanek *et al.* (2012), for *Pseudomonoclimacis dalejensis* (Bouček) based on descriptions of *Pseudomonoclimacis haupti* (Kühne) (e.g., Urbanek 1958), which was synonymised with *Ps. dalejensis* by Štorch *et al.* (2014), for *Uncinatograptus uncinatus* (Tullberg) based on descriptions by Urbanek (1958), and for *Saetograptus chimaera* (Barrande) based on descriptions by Walker (1953). Additionally, the genera *Bohemograptus*, *Lobograptus*, and *Neodiversograptus* were diagnosed according to descriptions by Urbanek (1963, 1970) and included in total counts of annuli but not identifiable to species in enough samples to warrant inclusion in individual species metrics (see Supplementary material). Mean counts of sicular annuli were plotted using PAST v.3.09 (Hammer *et al.* 2015). Additional plots were only made for individual species if they were present and identifiable to species in more than one sample to maintain consistency in taxonomic scale. Counts of annuli for each individual species were compared via Tukey's pairwise comparisons in PAST v.3.09 with a significance threshold of 95 % in any core sample where two or more species were represented by at least two specimens to determine any major divergences in mean counts of annuli between species in the same environment. Per-species counts of annuli were also compared to total counts via linear regression to determine if total annulus counts were predictive of counts in any given species.

Boreholes were correlated by applying a graphical correlation approach using the troughs and peaks of the double-peaked Mulde excursion akin to that used by Spiridonov (2017), where the δ^{13}C curve was used as an independent source of correlation between cores and was an independent test of the veracity of correlations derived from recurrence plots and conodont abundance data. There, and also in the current application, maxima and minima of mid- to late Homerian δ^{13}C excursions were used in a simple graphic correlation procedure. Here, Viduklė-61 was used as a reference core, and all measurements of sicular annuli were projected to correlation lines and combined in a single data for use in all subsequent statistical analyses.

In order to test the environmental associations of sicular annuli, the average number of sicular annuli per sicula in a sample was compared with the combined model of fourth- and fifth-order sea level cycles, which are presumably driven by sea level fluctuations, and approximately correspond to the 400 Ka and 100–130 Ka Milankovitch cycles (Radzevičius *et al.* 2014, 2017). This model is created from the high resolution (~0.1 m) natural gamma ray log of the Viduklė-61 core (Radzevičius *et al.* 2014) and the extraction of statistically significant frequencies using phase-preserving Gaussian filtering (Radzevičius *et al.* 2017). The major pattern of sea level change is widely recognised to be of global significance and is associated with the positive late Homerian δ^{13}C excursions and major biotic perturbations (Cramer *et al.* 2011; Venckutė-Aleksienė *et al.* 2016; Spiridonov *et al.* 2017b).

The variability of average frequencies of annuli per sicula is strongly non-Gaussian. In ~18 % of samples annuli are completely absent. This creates a 'clipped' from below pattern – widespread in positive direction and sudden collapse of variability at zero. In order to mitigate this bias two approaches were employed: (1) ln(x = 1) transformation of original number of sicular annuli and later ordinary least square regression; (2) transformation of number of sicular annuli into the categorical binary variable – '0' if annuli are absent, and '1' if annuli are present. In the second approach the logistic regression generalised linear model with binomial error structure and logit link function was used. The regression analysis was performed in PAST v.3.09. The statistically significant positive relations would indicate positive association of the prevalence of annuli in high-stand (presumably warm and humid) conditions. Due to the lack of a cyclic model associated with the depths of the highest (youngest) five collected sicular annuli samples from the Ludlow (*scanicus* Biozone), those samples were not included in environmental comparisons, but were still used in analyses of within-sample similarity between species. While not commonly distinguished from one another on a global scale, the *praedeubeli* and *deubeli* graptolite biozones are herein identified as separate as they are useful and easily distinguishable within Uzbekistan (Koren' & Suyarkova 1994) and the Baltic Basin (Radzevičius 2006; Koren' & Suyarkova 2007).

2. Results

If present, annuli were always found at the boundary of the prosicula and metasicula, but showing no distinct pattern of appearance elsewhere. Species appearing in multiple samples were as follows: *Pristiograptus dubius frequens* Jaekel, *Pristiograptus virbalensis* Paškevičius, *Colonograptus praedeubeli* (Jaeger), *Colonograptus deubeli* (Jaeger), *Pseudomonoclimacis dalejensis* (Bouček), *Uncinatograptus uncinatus* (Tullberg), and *Saetograptus chimaera* (Barrande). However, both *S. chimaera* and *P. dalejensis* occur primarily in the five omitted samples from the *scanicus* Biozone, and so are mostly only informative for within-sample comparisons of counts of annuli between species. Additionally, the genera *Bohemograptus*, *Lobograptus*, and *Neodiversograptus* were found and included in average and total counts of annuli but not identifiable to species in enough samples to warrant inclusion in individual species metrics (see Supplementary material). In all cases where annuli were found, there was an annulus observed at the boundary of the prosicula and metasicula as described by Urbanek (1958).

The beginning of the sicular annuli dataset approximately corresponds to the upper *nassa* Biozone (middle of the Ho2 stage

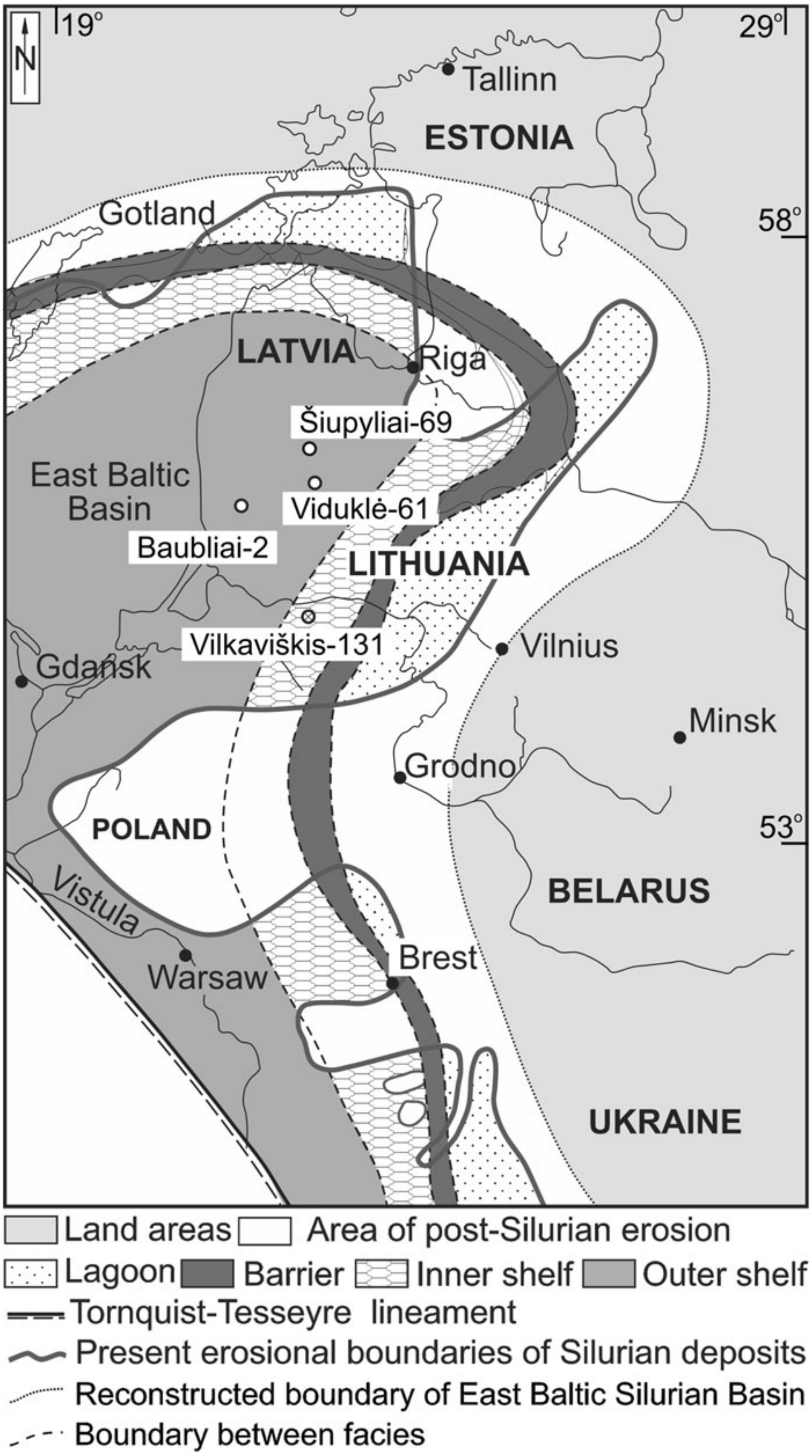

Figure 2 Facies map of the Baltic Silurian Basin during the *nassa* graptolite Biozone (after Einasto *et al.* 1986) and location of boreholes.

slice) of the Homerian, and ends with the lower *scanicus* Biozone (Go1 stage slice) of the early Gorstian (Cramer *et al.* 2011).

The counts collected showed changes in overall mean sicular annuli in multiple distinct phases over the late Wenlock and early Ludlow (Fig. 3). Prior to the *nassa* Biozone, counts of annuli could not be collected from any of the studied Lithuanian boreholes. As such, precise estimates of average counts of annuli prior to the *nassa* Biozone cannot be determined. However, evidence from specimens of *Testograptus testis* from the *lundgreni* Biozone of the late Wenlock indicate that at least some pre-*nassa* monograptids possessed an annulus on the prosicula (Lenz & Melchin 2008), while there are no known reports of sicular annuli from the lone monograptid species *Pristiograptus dubius parvus* from the proceeding *parvus* Biozone. The following interval (*nassa* to late *praedeubeli* biozones) shows fluctuation of mean counts of annuli between 1 and 3, with some rare

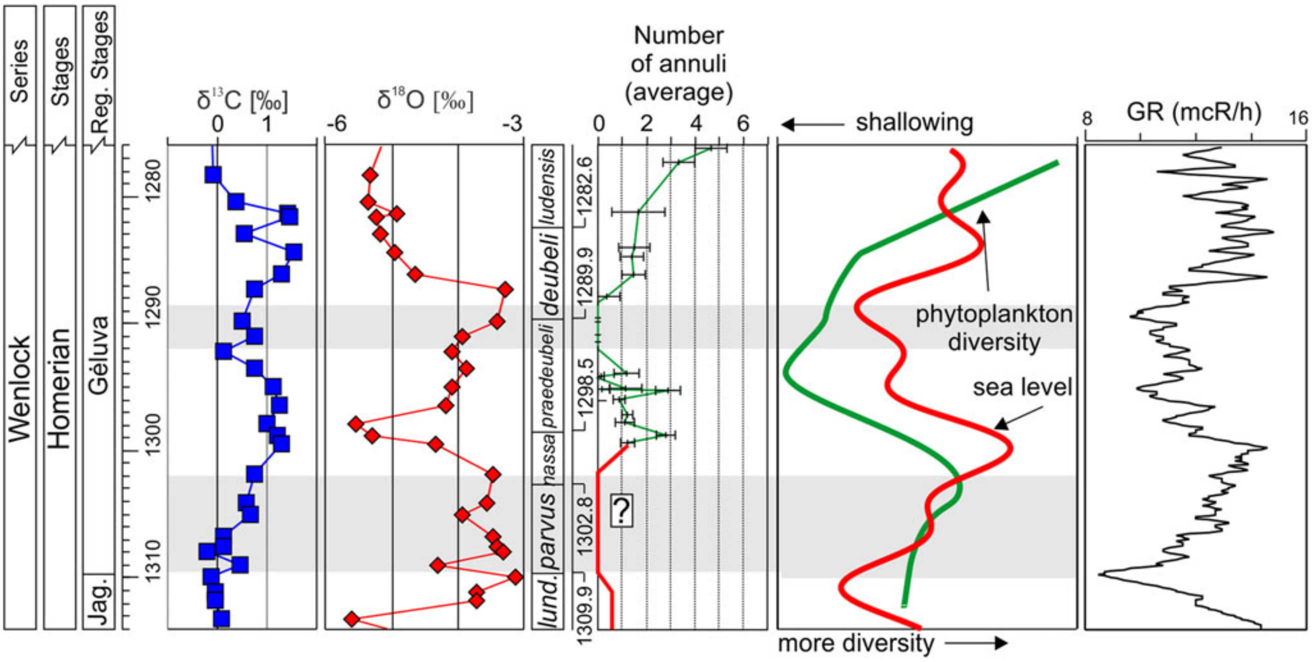

Figure 3 Homerian stable carbon and oxygen isotopic ratios in carbonates from Viduklė-61 (Martma *et al.* 2005), the trend in average frequencies of sicular annuli in graptolites, and filtered fourth- and fifth-order cycles in natural gamma, interpreted as representing sea level fluctuations, the generalised phytoplankton diversity trend (Venckutė-Aleksienė *et al.* 2016; Radzevičius *et al.* 2017), and gamma ray (GR) data from Radzevičius *et al.* (2014). The filtered fourth- and fifth-order sea level model, gamma ray, isotopic data, and phytoplankton diversity trends are derived from analyses of the Viduklė-61 core. The graptolite sicular annuli data were combined using a graphic correlation dataset projected on to the composite standard (Vidulkė-61 core). Intervals with extremely rare or no sicular rings are shown with grey bars. The section marked in red in and below the *nassa* Biozone was not included within the study range and is based on the lack of reporting of sicular annuli in *Pristiograptus dubius parvus* from other works, and the reporting of some singular annulus occurrences in *Testograptus testis* in the *lundgreni* Biozone (Lenz & Melchin 2008), both unconfirmed in the geographical context of this study.

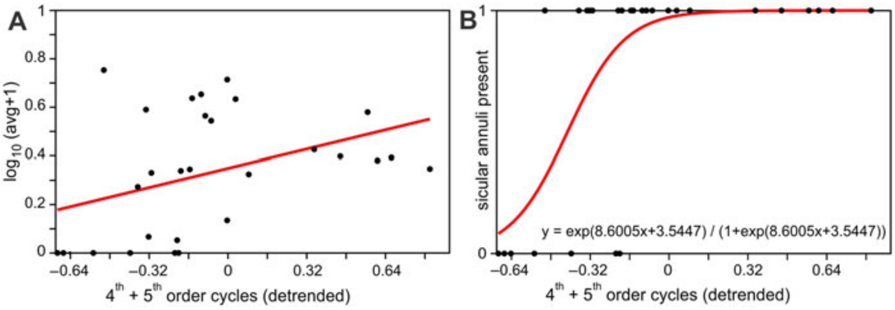

Figure 4 (A) Ordinary least squares regression of average log number of monograptid sicular annuli per specimen in a sample against the combined model of fourth- and fifth-order sea level cycles (a(slope) = 0.24; b(intercept) = 0.34; $r = 0.39$, $P = 0.03$, $n = 28$); (B) logistic regression of presences ('1') or absences ('0') of sicular annuli in graptolite specimens in samples against the combined model of fourth- and fifth-order sea level cycles ($G = 14.49$; $P(\text{slope} = 0) = 0.0001$; $n = 28$).

specimens lacking annuli. This is followed by an interval spanning the upper *praedeubeli* and lower *deubeli* biozones showing the disappearance of sicular annuli in conjunction with major excursions in fourth- and fifth-order filtered gamma ray logs, phytoplankton diversity, and $\delta^{18}O$ and $\delta^{13}C$ stable isotope curves. Counts of annuli then rebound in the latter half of the *deubeli* Biozone. The remainder of the Wenlock and early Ludlow are characterised by elevated counts of annuli and generally increasing within-sample variability in the same species which show few or no annuli in the *praedeubeli–deubeli* interval, with counts as high as seven or eight in some specimens in the upper *nilssoni* and *scanicus* biozones (Fig. 3).

The least square regression of log transformed average sicular annuli numbers per sicula per sample show statistically significant (at $P < 0.05$) relation with the sea level cycles, represented by fourth- and fifth-order cycle gamma ray values (Fig. 4a). This conclusion is supported by the logistic regression of absence or presence of sicular annuli in graptolite samples with the sea level cycles (Fig. 4b). The positive connection between presence of annuli and the high-stand conditions here is even more apparent and statistically highly significant ($P < 0.001$). The intervals which are typified by graptolite sicula without annuli fall completely into the regressive parts of sea level cycles (where standardised fourth- and fifth-order cycle values are <0). Least square regression also showed a statistically significant (at $P < 0.05$) negative correlation between average counts of annuli and $\delta^{13}C$ values despite the latter proxy being of rather moderate resolution.

For all but one core sample there were no significant between-species differences in mean counts of annuli, that lone exception being in the Šiupyliai-69 core at a depth of 951.2 m between samples of *Saetograptus chimaera* and *Pristiograptus dubius frequens* ($P < 0.001$). The discrepancy at this depth is large between the two species, with *S. chimaera* having a mean annulus count of 2.18 ± 0.78 and *P. dubius frequens* having a mean annulus count of 5.71 ± 0.66. However, that sample represents the only

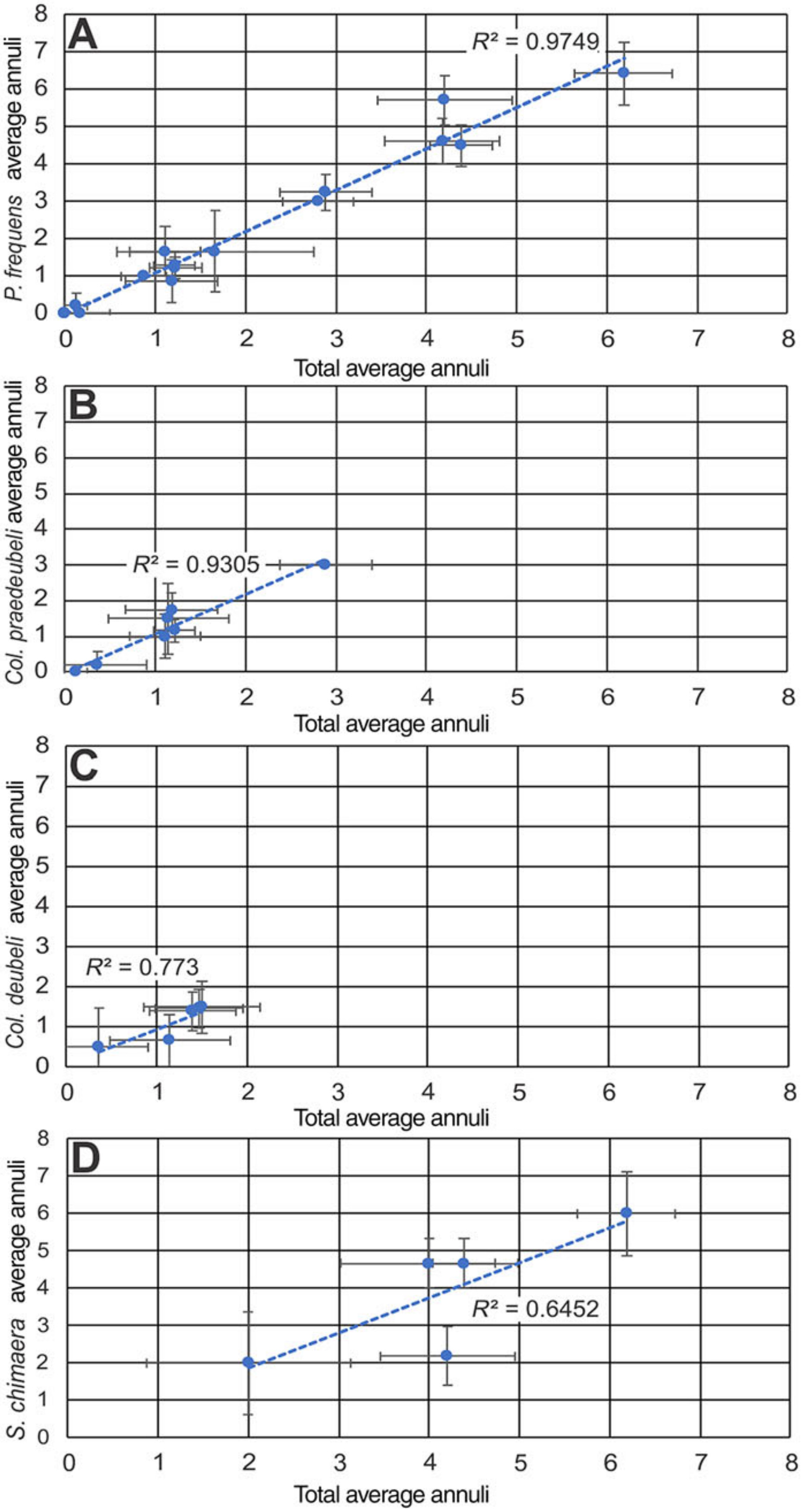

Figure 5 Ordinary least squares regression of mean counts of annuli per sample between an individual monograptid species and the remainder of species within the same samples. Tested species are (A) *Pristiograptus dubius frequens* ($P < 0.001$), (B) *Colonograptus praedeubeli* ($P < 0.001$), (C) *Colonograptus deubeli* ($P < 0.05$), and (D) *Saetograptus chimaera* ($P < 0.1$).

significant departure in sicular annuli means between *S. chimaera* and *P. dubius frequens*. Furthermore, comparison via linear regression (Fig. 5) showed significant correlation between total counts of annuli and counts from each of *P. dubius frequens* (r^2: 0.9749, $P < 0.001$), *Colonograptus praedeubeli* (r^2: 0.9305, $P < 0.001$), *Colonograptus deubeli* (r^2: 0.773, P: 0.05), and *S. chimaera* (r^2: 0.6542, P: 0.1). These results indicate that there is no correlation between counts of annuli and taxonomy.

3. Discussion

From the curve of mean sicular annuli through the late Wenlock (Fig. 3) it is clear that there is significant fluctuation in sicular annuli between the *praedeubeli* and *ludensis* graptolite biozones. Given the concurrent fluctuations in counts of annuli between species and lack of significant difference between mean counts of annuli in different species (Fig. 5), it is apparent that the variation in counts of annuli is not taxonomically significant. These findings imply dependence of counts of annuli on extrinsic environmental factors, indicating that the variation in the trait is ecophenotypic. As there are no reported cases of prosicular annulus absence in the presence of metasicular annuli, it is highly unlikely that the inclusion of prosicular annuli would confound the results. If prosicular annuli were to be formed independently of environmental conditions promoting metasicular annulus growth, they should bias the results towards a false-negative signal in the correlation between annulus counts and environmental factors, particularly in the comparisons between environmental conditions and annulus presence and absence. This bias is overcome where measured, even in the presence–absence results (Fig. 5b), indicating that the environmental conditions promoting the development of metasicular annuli are also relevant to the development of the prosicular annulus.

While the beginning of the *parvus* interval is accompanied by stable isotope and gamma ray excursions associated with the aftermath of the early part of the Mulde event both in the Viduklė-61 core and elsewhere in the Baltic Basin (Radzevičius *et al.* 2014, 2017, 2019; Venckutė-Aleksienė *et al.* 2016), the diversity of sampled localities and species analysed for counts of annuli is too low in the *parvus* Biozone to allow for any inferences of environmental correlation.

With sicular annuli likely ecologically controlled in number, local environmental data represent the best opportunity to explain their fluctuation. The correlations between counts of annuli and fourth- and fifth-order gamma ray logs indicate a positively correlated relationship between annuli and sea level. The fourth- and fifth-order cycles are derived from the natural gamma ray curve, which reflects the amount of radioactive isotopes of potassium, uranium, and thorium. The uranium shows affinity with clayey rocks and especially organics, thus indirectly showing the amount of preserved organic matter (Fig. 4). The combined fourth- and fifth-order cycles show periodic trends at the regional scale by reducing local noise, allowing for correlation with the regional scale graptolite data composited from multiple sites in the Baltic Basin. The close relationship between natural gamma values and the preserved carbon was previously clearly found in integrated studies of the Silurian Baltic Basin (Gelūnaitė & Spiridonov 2015; Cichon-Pupieni *et al.* 2020; Spiridonov *et al.* 2020). Moreover, no bentonites, which may affect gamma ray logs if present, have been recorded from *nassa–scanicus* biozones of the studied cores (Kiipli *et al.* 2008). The sedimentary and sea level cycles are congruent with the statistically estimated phytoplankton diversity grand fluctuations (Venckutė-Aleksienė *et al.* 2016), which suggest causal connection of high-stands, higher overall biological productivity in warmer eutrophic conditions as revealed by natural gamma curves, and the higher diversity of phytoplankton. The phytoplankton diversity fluctuations can be considered indicative of changes in primary productivity, as there is a general positive correlation between phytoplankton diversity and productivity (Irigoien *et al.* 2004), particularly where primary productivity is not already very high (Vallina *et al.* 2014), as is the case during the late Homerian. The low-stands in the Silurian Baltic Basin are associated with development of reef and carbonate factories during the late Homerian post-Mulde interval (Calner 2005), mid-Ludfordian Lau Event (Spiridonov *et al.* 2017a), and the recently recognised early Pridoli Šilalė Event (Spiridonov *et al.* 2020). For example, during the Šilalė Event, a significant ≈5 ° C drop in sea water temperatures (Žigaitė *et al.* 2010) was associated with the development of carbonate reefs (Kaminskas *et al.* 2015), and drop in gamma ray values, as well as amount of preserved organic carbon (proxy for productivity), and orders of magnitude decrease in abundance of nektobenthic carnivores–conodonts (Spiridonov *et al.* 2020). All these patterns point to the prevalence of decreased productivity in the water column and, thus, oligotrophy during cooling events and concurrent sea level regressions. This is particularly relevant due to the presence of annuli in specimens of *Colonograptus praedeubeli* from the low-palaeolatitude Canadian High Arctic (Lenz & Kozłowska-Dawidziuk 1998) and the apparent absence of annuli in contemporaneous high-palaeolatitude material from Bolivia (Maletz *et al.* 2003), indicating that the formation of annuli may have been unique to tropical monograptids. Moreover, the low-stand at the end of the *lundgreni* Zone and beginning of the *parvus* Zone was associated with the extreme dominance of very small plankton, which also confirms the dominance of oligotrophic and low-productivity conditions at low-stands/lower values of natural gamma curves in the Baltic Basin (Spiridonov *et al.* 2017b). Only one genus (*Leiosphaeridia*) was studied for variation in size by Spiridonov *et al.* (2017b), due to it possessing a simple spherical cyst shape, which eases calculations. Although just a part of the overall assemblage, *Leiosphaeridia* absolutely dominated the microphytoplankton communities, constituting approximately 85 % of all preserved individual organic microfossils (19,091 out of 22,338 counted individuals; reported in Venckutė-Aleksienė *et al.* 2016). Therefore, the conclusions on the size dynamics of the genus should, at first approximation, correctly represent states of whole communities.

Nowhere is the association of inferred sea level and productivity with counts of annuli more pronounced than during the *praedeubeli–deubeli* interval wherein all monograptid species entirely lack annuli, an interval concurrent with major excursions in fourth- and fifth-order gamma ray and stable isotope records (Fig. 4), and with a cooling event induced from data from Gotland from the same interval (Jepsson & Calner 2003). While the interval of zero annuli does not tightly co-occur with the nadir of phytoplankton diversity, it does closely align with the nadir of the fourth- and fifth-order gamma ray curve and generally comparatively low phytoplankton diversity. These combined observations indicate that the interval of zero annuli coincided with very low primary productivity.

These patterns represent a correlation between palaeoclimate and graptolite ecophenotypy, wherein higher sea levels (and likely higher primary productivity) are associated with higher counts of annuli, and low-sea-level regimes are associated with few or no annuli.

Though control of the trait's expression is extrinsic, origination of sicular annuli and their plasticity appears more likely to be evolutionary than a product of environmental factors. Given the extreme paucity of taxa at the time of the origination of sicular annuli, and the apparent resultant radiation of all future monograptids from that stem (Whittingham *et al.* 2020), it is fair to interpret that sicular annuli arose once in *Pristiograptus dubius frequens*, and that the plasticity of their number was homologous and plesiomorphic in later monograptids. The plasticity of sicular annuli and the conditions controlling their number appear to have been inherited in all measured descendant clades of *P. dubius frequens*, as shown by the presence and fluctuation of annuli in *Pristiograptus*, *Colonograptus*, *Saetograptus*, *Uncinatograptus*, *Pseudomonoclimacis*, *Bohemograptus*, *Lobograptus*, and *Neodiversograptus* (Appendix 1). This is a phenomenon that has been observed in a variety of animal groups

(Scheiner & Lyman 1989; Cheetham *et al.* 1995; Nussey *et al.* 2005; Pelletier *et al.* 2007). The evolution of plasticity in various morphological and behavioural traits has been documented as an apparent adaptive response to significant environmental disturbances in the modern biota across multiple clades (Grottoli *et al.* 2006; Nicotra *et al.* 2010), though the same has not yet been observed in the fossil record of graptolites. While the precedent set by the modern data indicates that significant disturbances such as those seen in the late Wenlock could influence the adaptive evolution of plastic traits, the extreme evolutionary bottlenecking of monograptids in the aftermath of the *lundgreni* extinction event could also have easily resulted in the fixation of nonadaptive traits. It therefore remains unclear as to whether sicular annuli and their plasticity were a functional, adaptive response to environmental disturbance, or simply an accident borne of random sorting.

As graptolites are understood to have been primary consumers (Berry & Wilde 1990; Underwood 1993; Cooper *et al.* 2012), it is likely that the formation of annuli was the result of a cascading effect of sea level changes on primary productivity, influencing nutrient availability for monograptids.

If counts of annuli were, at least in part, controlled by primary productivity as indicated, phytoplankton blooms may have contributed to increased annulus construction. In a low-latitude, tropical marine setting like the late Silurian Baltic Basin (Torsvik & Cocks 2013), large phytoplankton blooms are standard by-products of upwelling caused by monsoons (Brock *et al.* 1991; Tudhope *et al.* 1996; Tiwari & Rao 2004) and tropical storms (Chen *et al.* 2003; Roman *et al.* 2005; Lugo-Fernández & Gravois 2010; Gittings *et al.* 2018). Monsoon seasons are understood to increase in intensity and variability with temperature (Goswami *et al.* 2006; Sharmila *et al.* 2015) and are significantly subdued under cooler, dryer conditions (Prell & Kutzbach 1987). Likewise, the frequency of intense tropical cyclones is positively tied to high sea-surface temperatures (Yeh *et al.* 2010; Yan *et al.* 2016), with cooler, dryer conditions being associated with reduced tropical cyclone intensity (Hobgood & Cerveny 1988), aligning with the patterns observed in mean counts of annuli (Fig. 3). In mid- and high latitudes, storm events and storm-related upwelling are also projected to increase in frequency with increasing sea levels and sea-surface temperatures (Francis & Vavrus 2012; Mathis *et al.* 2012; Pickart *et al.* 2013; Tebaldi *et al.* 2012). These processes may then serve as potential drivers of increased annulus counts. As estimates of graptolite sicula growth are on the scale of a few weeks to a few months (Rigby & Dilly 1993), storm events are the more likely candidates to instigate annulus growth multiple times over the development of a sicula, as storm-related upwelling events may occur multiple times per month (Pickart *et al.* 2013). If this hypothesis is true, storm-related upwelling events would have either been directly responsible for the formation of sicular annuli, or would at least have significantly increased the likelihood of annulus formation. Some tempestites have been recorded from the upper Homerian and Gorstian of Estonia (Nestor *et al.* 2001), supporting the idea that storm action may have contributed to the formation of sicular annuli, and further recording of tempestites from periods of high annulus counts in Lithuania would help strengthen this hypothesis. In this way, mean counts of annuli may serve as a potential proxy for storm event frequency in a given locality.

4. Conclusion

Our results paint a comprehensive picture of the origination and variation in sicular annuli in upper Wenlock and lower Ludlow monograptids. The ecophenotypic nature of the plasticity in the trait is borne out by the lack of statistically significant differences between mean counts of annuli between all species from the same time intervals and by the correlation between total counts and species-specific counts. That plasticity appears to be borne out of the extreme evolutionary bottlenecking of the aftermath of the *lundgreni* extinction event. The construction of annuli is likely a product of the effects of sea level change cascading through changes in primary productivity. Upwelling events, possibly as a result of more intensified and/or more frequent tropical cyclones, would have further encouraged increases of primary productivity, driving increased annulus construction. Overall, our findings show the presence of an easily measured ecophenotypic character that may provide further insight into the changing climate of the mid- to late Silurian.

5. Supplementary material

Supplementary material is available online at https://doi.org/10.1017/S1755691021000402.

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