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The late Aeronian graptolite *sedgwickii* Event, associated positive carbon isotope excursion and facies changes in the Prague Synform (Barrandian area, Bohemia)

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Abstract – Study of the lower Silurian black shale succession of the Prague Synform has enabled detailed insight into graptolite faunal dynamics and diversity trends from the mid-Aeronian diversity maximum through to the late Aeronian crisis. Graptolite diversity decreased from 33 taxa in the *Lituigraptus convolutus* Biozone to 17 taxa in the upper part of the *Stimulograptus sedgwickii* Biozone and newly erected *Lituigraptus rastrum* Biozone. The graptolite assemblages of the latter biozones exhibit low species richness along with high dominance. Many graptolite species that became extinct in the early part of the *sedgwickii* Zone were promptly replaced by new forms. In the later part of the *sedgwickii* Zone, however, replacement of extinct species by new forms considerably decelerated. The increased rate of graptolite extinction recorded in the *convolutus–sedgwickii* biozone boundary beds coincided with subtle changes in black shale lithologies and a positive shift in $\delta^{13}C_{org}$ (of 2.2 ‰) compared to baseline values. Sea-level drawdown can be inferred from siltstones and/or temporary nondeposition in the middle *sedgwickii* Zone. This level also sees total organic carbon (TOC) fluctuations and a strong positive $\delta^{13}C_{org}$ excursion with a peak shift of at least 7 ‰. The *sedgwickii* Event exhibits substantial reorganization of the graptolite fauna, its taxonomic impoverishment and concomitant increase in species dominance rather than a sudden collapse of the pre-extinction assemblage. Associated changes in lithology, TOC and the pronounced $\delta^{13}C_{org}$ excursion suggest a relatively extended and probably multi-phase period of stressed conditions that affected the pelagic realm inhabited by graptolites in the course of the late Aeronian interval.

Keywords: graptolites, Silurian, extinction, species richness, community evenness, carbon isotope record.

1. Introduction

The timing and magnitude of graptolite bioevents have been the subject of numerous studies since the pioneering work by Koren' (1987), which for the first time considered diversity dynamics in relation to important global physical events. Loydell (1994, 1998) discussed causal relationships between sea-level drawdowns and graptolite extinctions. Melchin, Koren' & Štorch (1998) revealed similar patterns in their summary of global Silurian graptolite faunal dynamics.

Although most studies have been focused on the Late Ordovician graptolite extinction and the subsequent early Silurian recovery and radiation (Koren', 1991*a*; Melchin & Mitchell, 1991; Finney *et al.* 1999; Chen *et al.* 2005; Štorch *et al.* 2011) or the mid-Homerian crisis (Jaeger, 1991; Koren', 1991*b*; Lenz, 1993; Urbanek, 1993), a number of other critical intervals were identified by Koren' (1993), Urbanek (1993), Loydell (1994), Melchin (1994), Štorch (1995) and Melchin, Koren' & Štorch (1998).

It has been recognized for a long time (Bouček, 1953) that a distinct changeover and temporary impoverishment of graptolite fauna took place in late Aeronian time. Štorch (1995) placed this graptolite mass extinction at the top of the *Lituigraptus convolutus* Biozone and named it the *convolutus* Event. Subsequently, Melchin, Koren' & Štorch (1998) examined data from the principal graptolite-bearing successions worldwide and concluded that the extinction reached its peak in the subsequent *Stimulograptus sedgwickii* Zone, with minimum diversity attained in the upper part of the zone.

Widespread evidence for the late Aeronian sea-level drawdown, recognized already by Leggett *et al.* (1991) and Johnson (1996) was summarized by Loydell (1998). He correlated sedimentary successions from various palaeoplates and depositional settings by means of the then published graptolite records and showed that sediments indicating better oxygenation, higher input of siliciclastic material or carbonate deposition in otherwise siliciclastic successions were deposited during the *sedgwickii* graptolite Zone. The coincidence between lowered sea-level, a positive $\delta^{13}C$ excursion and graptolite extinction in the upper Aeronian *sedgwickii* Zone has been further discussed by Loydell (2007). Graptolite data, however, did not allow for higher resolution intrazonal correlation. The

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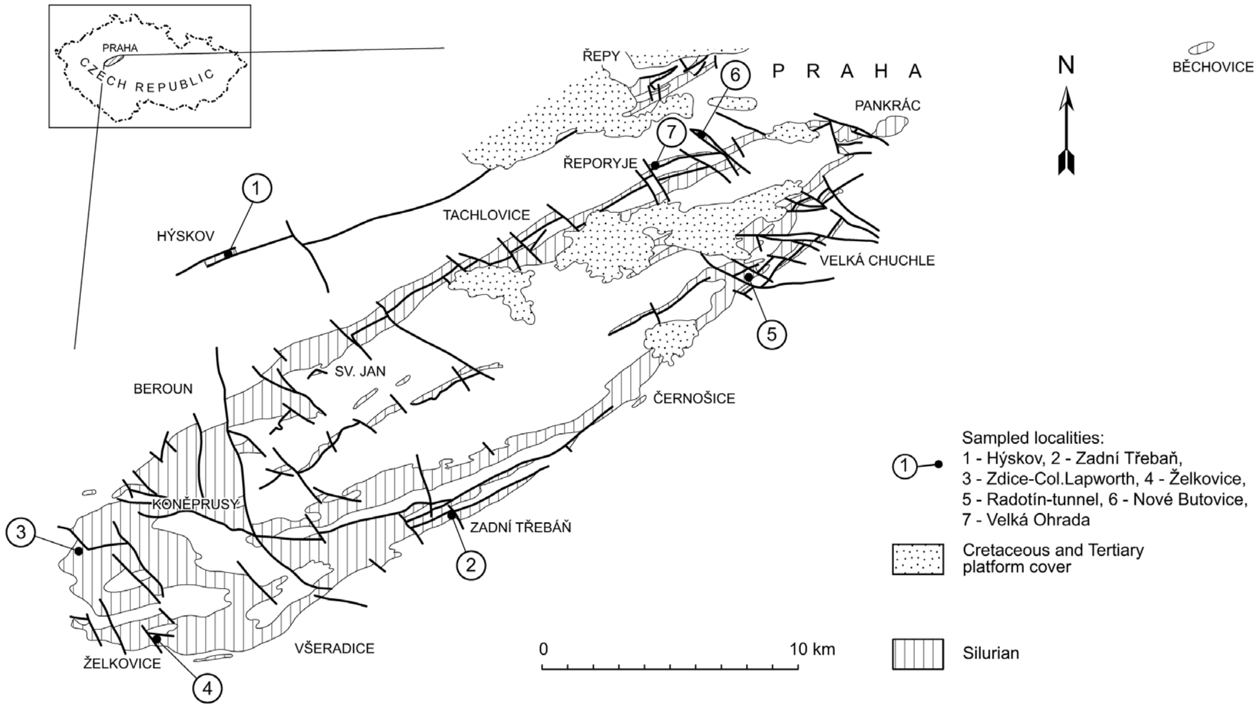

Figure 1. Location of the upper Aeronian sections in the Silurian outcrop area of the Prague Synform.

question remained as to whether the sea-level fell owing to a single or multiple eustatic event(s) and whether its major phase took place in the early, middle or even late part of the *sedgwickii* Zone. Since then, further sedimentological evidence of the sea-level fall has been found and more details of graptolite faunal dynamics combined with carbon isotope data have allowed for more precise dating and correlation of this turbulent period.

In the Prague Synform of the Barrandian area, the upper Aeronian strata are assigned to the upper part of the Želkovice Formation, which is dominated by black graptolitic shales (Kříž, 1975; Chlupáč *et al.* 1998). The interval between the middle Aeronian *L. convolutus* Biozone and lowermost Telychian *Rastrites linnaei* Biozone has been little known and little exposed so far. No section spanned the whole interval and both new and historical localities (Bouček, 1930, 1953; Štorch, 2001; P. Štorch, unpub. Ph.D. thesis, Czech Geological Survey, Prague, 1991) comprised either limited strata adjacent to basalt sills or heavily weathered shales with poorly preserved graptolites. A complete succession was made temporarily accessible, however, in the highway tunnel north of Radotín (Štorch *et al.* 2009) and provided a unique opportunity for detailed and multidisciplinary studies. Unweathered Llandovery strata, composed of black shales rich in stratigraphically important graptolites, have also yielded excellent material for total organic carbon (TOC) and carbon isotope analyses. Some parts of the late Aeronian–early Telychian succession are rich in pyrite and undergo rapid decomposition in outcrops; hence the rarity of surface exposures and the particular significance of the subsurface section used as a key reference in this paper.

We have exploited all data recovered from the Radotín tunnel and other present and past localities in different parts of the Prague Synform (Figs 1, 2) for quantitative assessment and detailed study of the *sedgwickii* Event, improving precision of its biostratigraphical correlation, and relative timing of the associated positive carbon isotope excursion and lithological changes.

2. Methodology

A series of 33 bulk samples, each with a mass of 4–5 kg, was collected from a 7 m thick succession comprising the *Pribylograptus leptotheca*, *Lituigraptus convolutus*, *Stimulograptus sedgwickii*, *Lituigraptus rastrum* and lower *Rastrites linnaei* biozones (zones in the following text), exposed in a gallery of the Radotín tunnel. For technical reasons, the succession was sampled at slightly irregular intervals concentrated around the supposed level of graptolite extinction and carbon isotope excursion in the *sedgwickii* Zone (see Fig. 3 for sampling levels). Bulk samples were split in the laboratory and all determinable graptolite rhabdosomes (4,000 specimens, excluding small fragments) were employed in calculations.

Basic biodiversity indices were calculated from graptolite quantitative data collected from the Radotín samples to evaluate the faunal and ecological changes within the studied stratigraphic interval. First of all, rarefaction curves were computed for all samples to investigate the effect of sample size upon species counts. Only samples having the rarefaction curves distinctly flattening out for the larger number of specimens were included in further analysis. This limited dataset was tested for correlation between species counts and

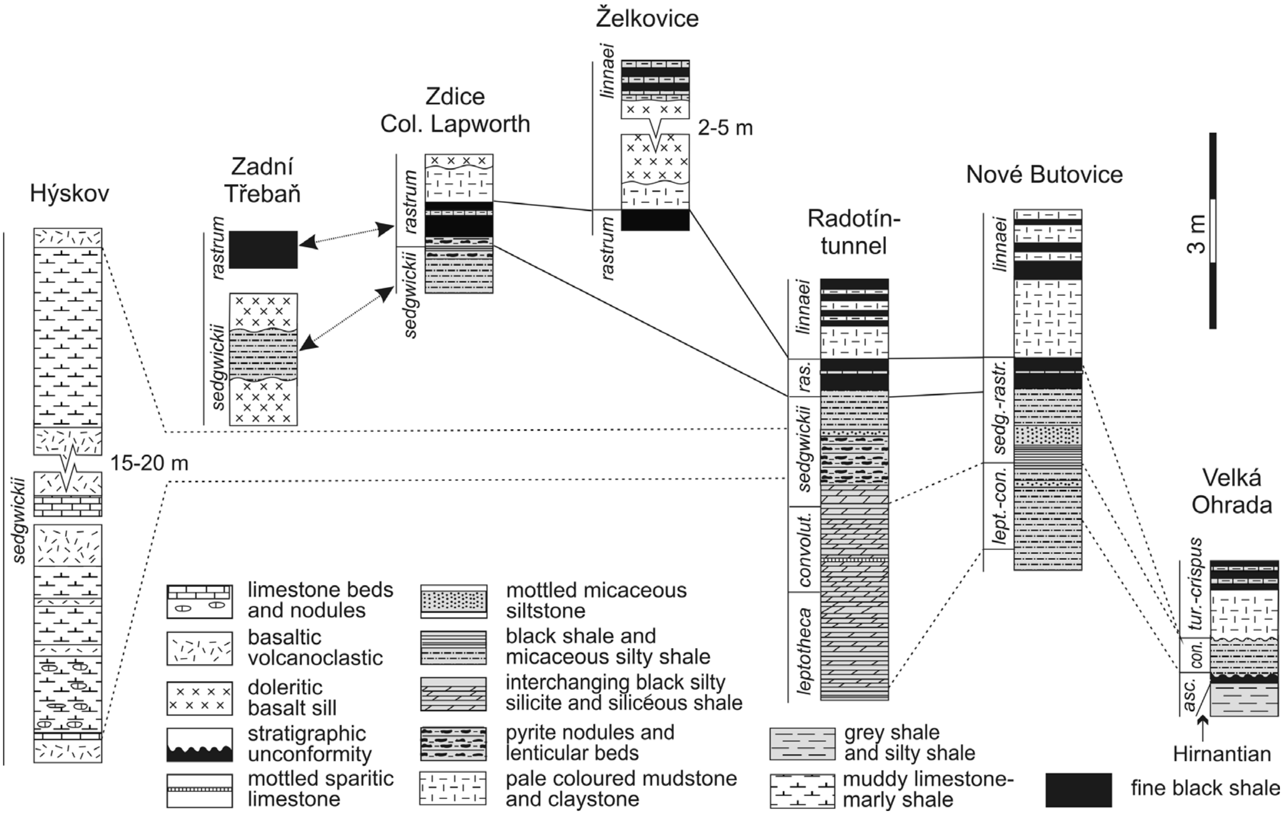

Figure 2. Correlation chart of the upper Aeronian localities in the Prague Synform: biostratigraphy and lithology.

sample size. Owing to the fact that it is not possible to presume generally the linearity of the anticipated relationship (i.e. species counts and sample size), the commonly used Pearson's correlation coefficient could not be used to assess the degree of correlation. For this reason two other correlation coefficients (Spearman's and Kendall's correlation coefficients) were used for the analysis. To characterize species richness across the studied interval we calculated Menhinick's and Margalef's richness indices and compared these data with rarefaction analysis. Dominance and Berger–Parker indices were also calculated for all samples to evaluate the evenness of the studied graptolite assemblages. Dominance was calculated using $\Sigma(n_i/n)^2$ where n_i is number of individuals of taxon i and n is sample size. The Berger–Parker index is the number of individuals of the most common taxon divided by sample size. Correlations between species richness indices and evenness indices were evaluated using Spearman's and Kendall's correlation coefficients. Another of the goals was ascertaining the time trends of all of the above-mentioned biodiversity indices; these were calculated. The statistical significance of these trends was analysed by the Mann–Kendall test. This statistical method is a non-parametric test for the detection of a trend in a time series and has been widely used in environmental science because it is simple, robust and can cope with missing values and values below a detection limit. The relationship between the above-mentioned species biodiversity indices and the stratigraphical position of samples was analysed to evaluate faunal and ecological changes in the studied interval. Most statistical calculations were undertaken using the software package Past, ver. 2.08b (Hammer, Harper & Ryan, 2001).

All 33 samples from the Radotín tunnel section were analysed for organic carbon isotopes and TOC. Entirely fresh hand specimens were cut and rock powder was prepared from a few grams of fresh sample. A few milligrams of rock powder were taken for TOC and total carbon isotope analyses. Before analyses, rock powders were decarbonatized with 10 % HCl at 40 °C for several hours, then washed and dried. About 20 mg of rock powder were used for TOC and about 10 mg for isotope analyses. Samples were combusted in a Fisons 1108 elemental analyser coupled on-line to a Finnigan Mat 251 mass spectrometer via a ConFlo interface. As reference material, NBS 22 (Gulf oil, with δ^{13}C value −29.75 ‰) and acetanilid (Analytical Microanalysis, UK) were measured. Accuracy and precision were controlled by replicate measurements of laboratory standards and were better than ± 0.1 ‰ (1 σ) for total carbon isotope analyses and better than ± 0.02 % (1 σ) for TOC content.

Biostratigraphical data from the Radotín tunnel were supplemented by extensive collections from large blocks dumped outside the tunnel. The latter served for further study on graptolite taxonomy and assemblages. Published and unpublished data from all other coeval sections in the Barrandian area available to the authors in the course of the last 30 years and the museum collections of B. Bouček have also been examined.

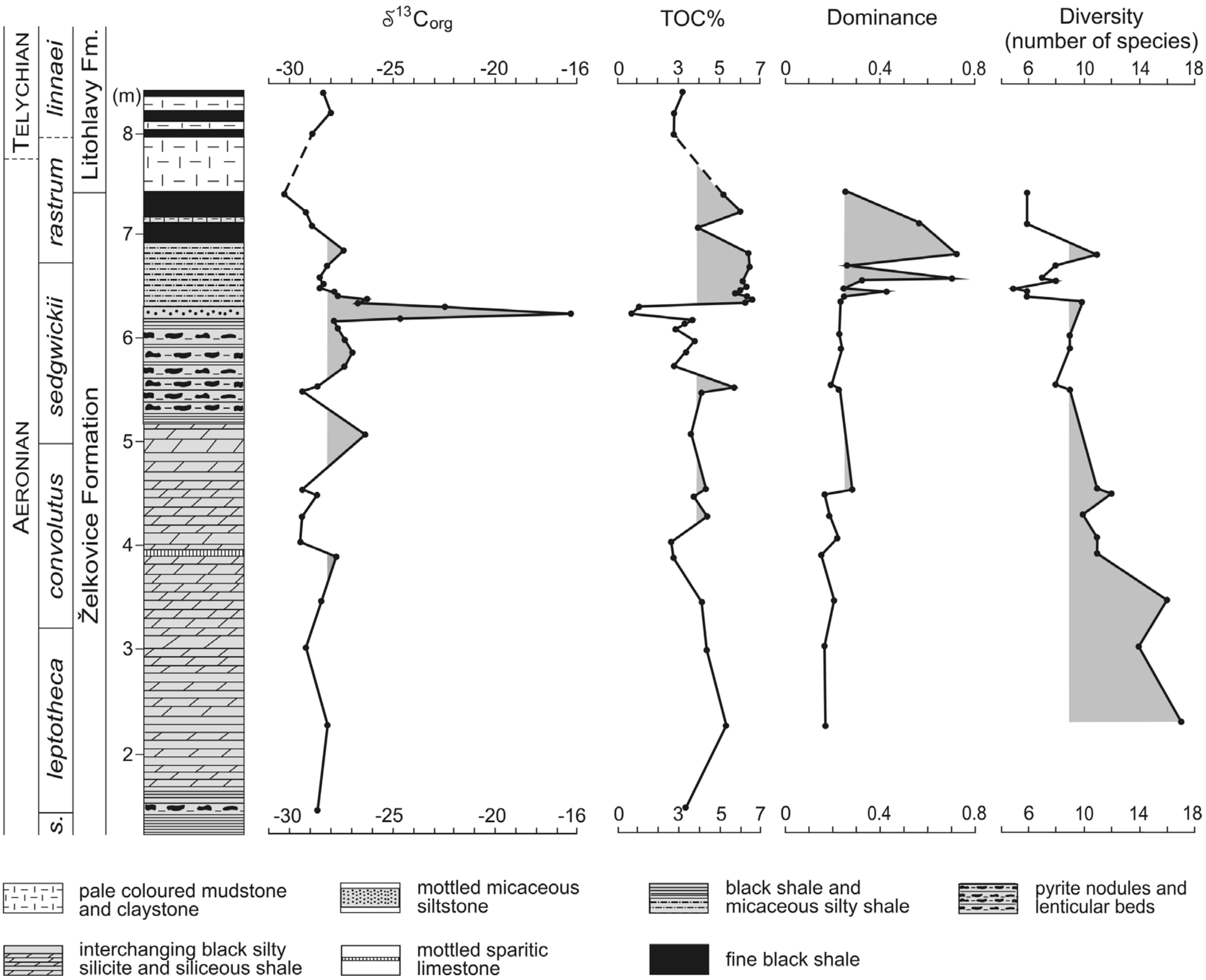

Figure 3. Radotín tunnel section: lithological column, lithostratigraphical units, chronostratigraphy based upon graptolite biozones, $\delta^{13}C_{org}$ and TOC profiles, and graptolite dominance and species diversity counted for respective samples (sampling levels). Dominance is calculated using $\Sigma(n_i/n)^2$ (n_i is number of individuals of taxon i). Values higher than the median value are highlighted by grey shaded fields.

Illustrated specimens from the first author's collection are housed in the Czech Geological Survey and bear the designation PŠ.

3. Localities

In the Barrandian area, natural exposures of upper Aeronian shales are very rare and of limited extent in comparison with the common exposures and subcrops of the solid, weathering resistent siliceous black shales and silicites of the middle Aeronian. The soft, clayey and micaceous upper Aeronian black shales are rich in pyrite and undergo rapid decomposition under surface or near-surface conditions. Thus, available sections (Figs 1, 2) are either within the weathering-resistant contact aureoles of neighbouring basalt sills or temporarily exposed by deep excavations or subsurface construction works.

3.a. Radotín tunnel

The sedimentary succession temporarily exposed in the highway tunnel (Fig. 4) north of Radotín, near Prague provided unique material for detailed and multidisciplinary studies. The unweathered Llandovery black shale succession, rich in well-preserved graptolites, also yielded excellent samples for TOC and carbon isotope analyses; hence this subsurface section is of particular significance. The tunnel also provided robust evidence of the middle and upper Aeronian and lower Telychian successions, including the *sedgwickii* Event. The lower part of the *sedgwickii* Zone and *convolutus–sedgwickii* zone boundary beds were studied for the first time in this section.

3.b. Zdice – Barrande's Colony Lapworth

A shallow test-pit in a forested slope between Holý vrch Hill and Smutný Hill east of Zdice

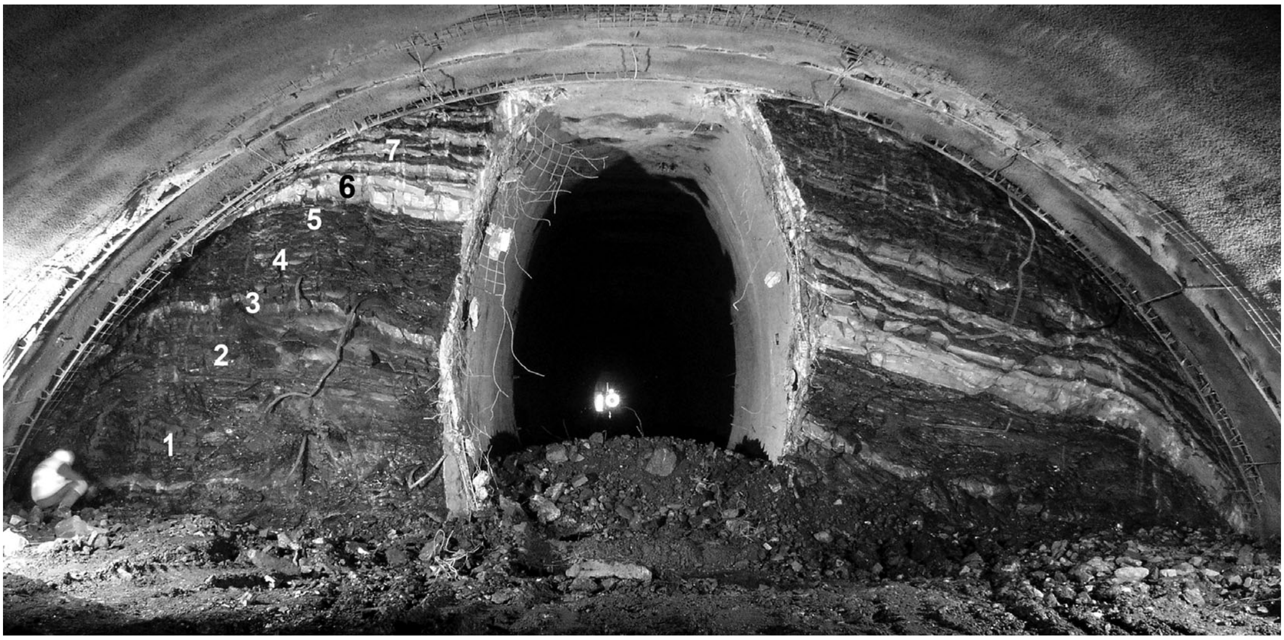

Figure 4. Middle Aeronian through to lowermost Telychian sedimentary rocks exposed in the face of the Radotín tunnel. No. 1 designates silty silicites and siliceous shales of the *convolutus* Zone, no. 2 points to pyrite-rich black shale of the lower *sedgwickii* Zone and no. 3 to a grey mottled silty bed in the middle part of the *sedgwickii* Zone. Micaceous black shale of the upper *sedgwickii* Zone is marked by no. 4. The black clayey shale (no. 5) immediately below the pale-coloured basal mudstone yielded graptolites of the *rastrum* Zone. The massive bed of pale-coloured, mottled carbonate mudstone, without graptolites, forms the base of the Litohlavy Fm. (no. 6). Lowermost Telychian graptolites of the *linnaei* Zone appear in the black claystone intercalations (no. 7) just above the basal mudstone. Photo by Jakub Bohátka.

(*c.* N 49° 54′ 22.3″, E 13° 59′ 56.0″) exposed a 2 m thick succession comprising micaceous black shale of the upper *sedgwickii* Zone, fine black shale of the *rastrum* Zone and yellowish-green mudstone without graptolites. The moderately weathered upper Aeronian sedimentary rocks are underlain and overlain by basalt sills.

3.c. Zadní Třebaň

Black micaceous shales, *c.* 1 m thick, are sandwiched between two doleritic basalt sills on the rocky slope west of Zadní Třebaň railway station (N 49° 55′ 05.2″, E 14° 11′ 53.9″) and belong to the upper part of the *sedgwickii* Zone. A shallow test-pit excavated in the upper part of the same forested slope (N 49° 55′ 02.2″, E 14° 11′ 50.3″) exposed black shale with graptolites assigned to the newly erected *rastrum* Zone.

3.d. Želkovice

A test-pit excavated for B. Bouček in the 1940s (see Bouček, 1953) and subcrops examined by P. Štorch in the field south of Želkovice village (N 49° 52′ 33.1″, E 14° 02′ 20.1″) exposed black clayey shales of the uppermost *sedgwickii* and *rastrum* zones that are topped by pale-coloured mudstone, barren of graptolites and further separated by a basalt sill from the overlying succession with graptolites of the *linnaei* Zone.

3.e. Nové Butovice

Large building excavations in the Prague-Nové Butovice district (N 50° 02′ 50,5″; E 14° 20′ 29.0″) exposed a continuous sedimentary succession ranging from the upper Hirnantian through to the lower Telychian (see also Štorch, 2006, fig. 5). Most graptolites were poorly preserved in weathered upper Aeronian micaceous and clayey shales. The first silty bed was recorded high in the *convolutus* Zone, but a major siltstone bed, 0.3 m thick, occurs within the *sedgwickii* Zone.

3.f. Velká Ohrada

Pipeline excavations north of Řeporyje (N 50° 02′ 19.6″, E 14° 18′ 57.5″) provided a temporary exposure of uppermost Hirnantian through to upper Telychian strata (Štorch, 2006, fig. 6). Two stratigraphical unconformities have been recorded in the early Silurian black shale succession. The second break in sedimentation separated condensed micaceous laminites of the *convolutus* Zone from the overlying Aeronian/Telychian boundary mudstone. The *sedgwickii* and *rastrum* zones are both missing.

3.g. Hýskov

A series of test-pits (N 50° 00′ 13.8″, E 14° 04′ 20.1″) runs through middle Llandovery basaltic volcaniclastic rocks, interbedded with tuffaceous shales and limestones, in a separate block preserved in a tectonized zone along the Prague Fault, *c.* 5 km NW of the nearest outcrop area of coeval black shale strata (Štorch, 2001). The local fauna, which is dominated by brachiopods (Havlíček, 1977), trilobites (Šnajdr, 1978) and dendroid graptolites (Kraft, 1982), provides evidence for dysoxic and oxic bottom conditions, unique to the middle Llandovery succession of Central Europe. Graptoloid graptolites (Štorch, 2001), all referable to the lower *sedgwickii* Zone, are subordinate.

4. Results

4.a. Late Aeronian graptolite fauna and biostratigraphy

4.a.1. Stimulograptus sedgwickii *Biozone*

The *sedgwickii* Zone comprises an interval from the lowest occurrence of the zonal index graptolite to the lowest occurrence of *Lituigraptus rastrum* (Richter) (Fig. 5d). It is 1.7 m thick in the Radotín tunnel section and *c.* 1.1 m thick in the Velká Ohrada 1 section. The Zadní Třebaň and Zdice sections preserved only the upper part of the biozone, which corresponds roughly in thickness to that measured in the Radotín tunnel section (Fig. 2). Also the Llandovery volcanic–carbonate succession exposed by trenches near Hýskov (Štorch, 2001) yielded graptolites typical of the lower *sedgwickii* Zone assemblage encountered from the Radotín tunnel section, although the two sections differ in relative abundances of the taxa. The observed thickness of lime- and mudstones, excluding volcaniclastic rocks, is 6.5 m. See Figure 6 for the graptolite record combined from all available localities. At least two successive graptolite assemblages are recognized within the zone:

(a) In the lower part of the zone uncommon *Stimulograptus sedgwickii* (Portlock) (Fig. 5g) is usually associated with *Petalolithus clandestinus* Štorch (Fig. 5h), *Torquigraptus magnificus* (Přibyl & Münch) (Fig. 5g) and *Pristiograptus variabilis* (Perner). *Cephalograptus extrema* Bouček & Přibyl (Fig. 5b) is common in the Radotín tunnel section, whereas *Neolagarograptus tenuis* (Portlock) is common at Hýskov. *Normalograptus scalaris* (Hisinger), *Pseudorthograptus insectiformis* (Nicholson), *Pristiograptus regularis* (Törnquist), *Campograptus lobiferus* (McCoy), *Torquigraptus*? aff. *cerastus* (Hutt) and *Torquigraptus decipiens* (Törnquist) continued from the upper part of *Lituigraptus convolutus* Biozone. *Pribylograptus* cf. *leptotheca* (Lapworth), and '*Monograptus*' *limatulus* Törnquist also persisted into the lowermost part of the *sedgwickii* Zone. The thin-walled, slightly proximally tapering *Metaclimacograptus undulatus* (Kurck) is common but further proliferates above this interval. *Torquigraptus pulcherrimus* (Manck) (Fig. 5c), *Torquigraptus* aff. *linterni* (Williams *et al.*) and *Parapetalolithus praecedens* (Bouček & Přibyl) (Fig. 5f) appear in high levels of the lower *sedgwickii* Zone.

(b) The upper part of the *sedgwickii* Zone (note that it was formerly referred to the middle and even lower parts of the zone by Bouček, 1953 and Štorch, 1994) is characterized in Barrandian sections by abundant graptolites with moderate to low taxonomic diversity. *St. sedgwickii* becomes more abundant and is accompanied by repeated blooms of *Metacl. undulatus*. *Torquigraptus* aff. *linterni* also increases in abundance; *Comograptus barbatus* (Elles & Wood) (Fig. 5e) and *Pristiograptus pristinus* Přibyl made their first occurrences at the base of this interval. *T. magnificus* makes its highest occurrence in the middle part; *Nl. tenuis* disappeared well below the top of the *sedgwickii* Zone. *Pristiograptus variabilis* (Perner) and *P. pristinus* continued through to succeeding zones. *Parapet. praecedens* is widespread, whereas records of *Ceph. extrema* are limited to the Zdice and Želkovice sections. Other typical taxa, although uncommon, are *T. pulcherrimus* and *Com. barbatus*. The uppermost part of the *sedgwickii* Zone in the present redefined usage is marked by the incoming of *Torquigraptus involutus* Lapworth and *Spirograptus andrewsi* (Sherwin) (Fig. 5a).

The graptolite assemblage of the *sedgwickii* Zone was originally identified by Lapworth (1878) from the upper Birkhill Shale Formation of Dob's Linn, Scotland, and named after a junior synonym of *St. sedgwickii* (Portlock, 1843): *Monograptus spinigerus* (Nicholson, 1868). In the Barrandian area, a corresponding assemblage was identified by Bouček (1930) at Barrande's former locality, Colony Lapworth near Zdice (present Zdice section), and designated as the *Monograptus involutus* Zone. Subsequently, Bouček (1934) adopted *St. sedgwickii* as a zonal index fossil and provided a more detailed description of the zone and its graptolite assemblage (Bouček, 1953), based upon collections from Zdice, Želkovice, Libomyšl, Běleč and Zadní Třebaň. A distinctive graptolite assemblage, dominated by *Lituigraptus rastrum* (Richter), was reported from the upper part of Bouček's *sedgwickii* Zone by Bouček (1953) and Štorch (1994). This assemblage forms the basis of the *Lituigraptus rastrum* Biozone recognized in this paper.

4.a.2. Lituigraptus rastrum *Biozone*

The upper part of the Bohemian *sedgwickii* Zone in the sense of Bouček (1934, 1953) and Štorch (1994, 2006) is separated from the succeeding *Rastrites linnaei* Zone and lowest occurrences of *Spirograptus guerichi* Loydell, Štorch & Melchin by a barren mudstone in all Barrandian sections (see Kříž, 1975 and Štorch, 2006). The uppermost levels of their *sedgwickii* Zone have been already cited by Bouček (1953) as having a specific assemblage dominated by '*Rastrites*' *rastrum*. A new systematic revision of the graptolite fauna has revealed that *Stimulograptus halli* (Barrande) is present in this interval, which is thus correlatable, at least in part, with the *Stimulograptus halli* Zone used in the British Isles by Jones & Pugh (1916), Loydell (1991*a*, 1992) and Zalasiewicz *et al.* (2009). Owing to difficulties in distinguishing between incomplete specimens – mostly distal fragments – of the two

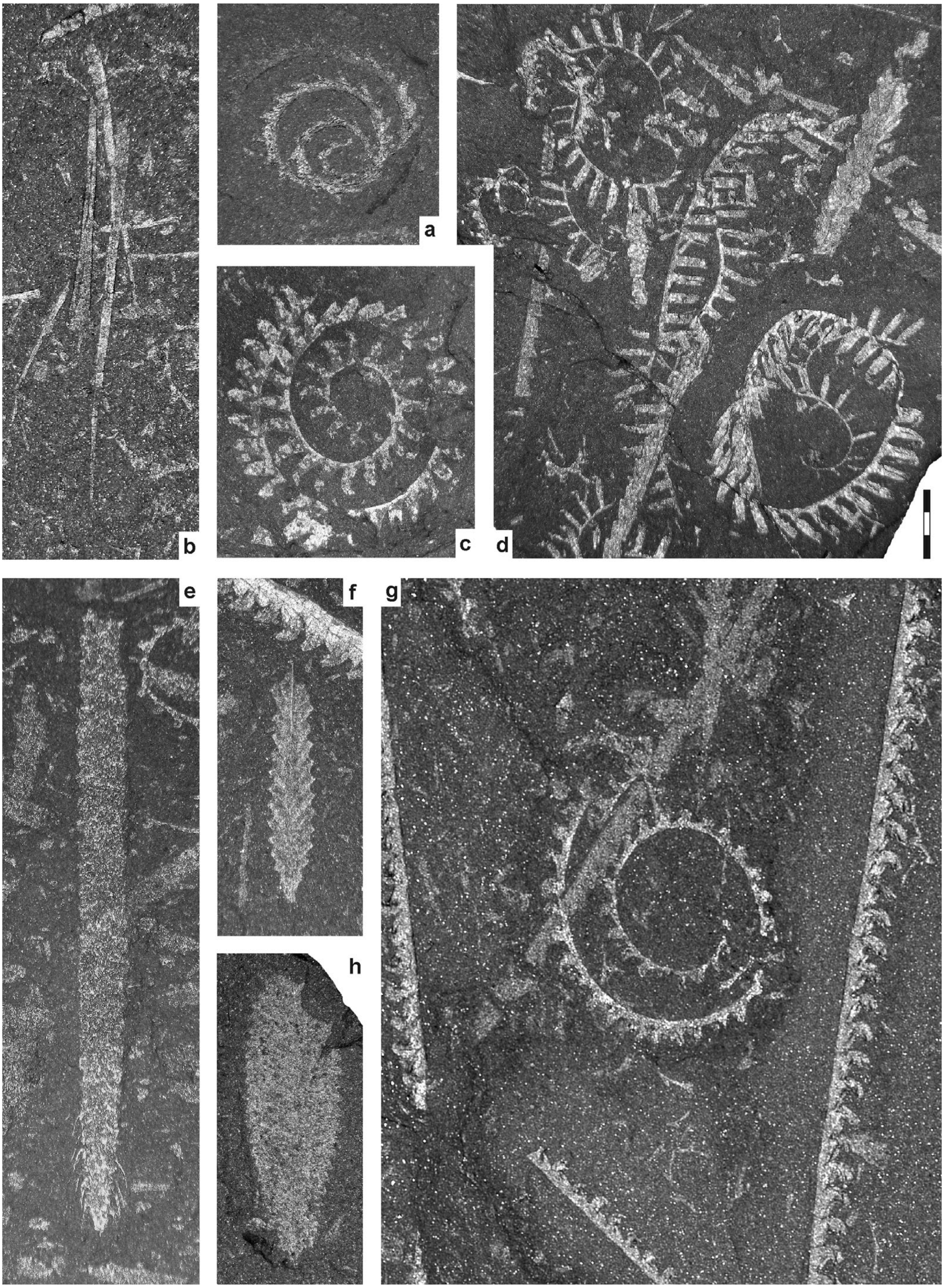

Figure 5. Selected upper Aeronian graptolites from the Prague Synform. (a) *Spirograptus andrewsi* (Sherwin), PŠ 1010, *rastrum* Zone, Radotín tunnel; (b) *Cephalograptus extrema* Bouček & Přibyl, PŠ 1009, lower *sedgwickii* Zone, Radotín tunnel; (c) *Torquigraptus pulcherrimus* (Manck), PŠ 1013, upper *sedgwickii* Zone, Zdice – Col. Lapworth; (d) *Lituigraptus rastrum* (Richter), PŠ 1008, *rastrum* Zone, Želkovice; (e) *Comograptus barbatus* (Elles & Wood), PŠ 1007, upper *sedgwickii* Zone, Zdice – Col. Lapworth; (f) *Parapetalolithus praecedens* (Bouček & Přibyl), PŠ 1014, upper *sedgwickii* Zone, Zadní Třebaň; (g) *Torquigraptus magnificus* (Přibyl & Münch) (centre) and *Stimulograptus sedgwickii* (Portlock) (right, left and below), PŠ 1011, middle *sedgwickii* Zone, Radotín tunnel; (h) *Petalolithus clandestinus* Štorch, PŠ 1012, lower *sedgwickii* Zone, Radotín tunnel. All specimens, scale bar represents 3 mm.

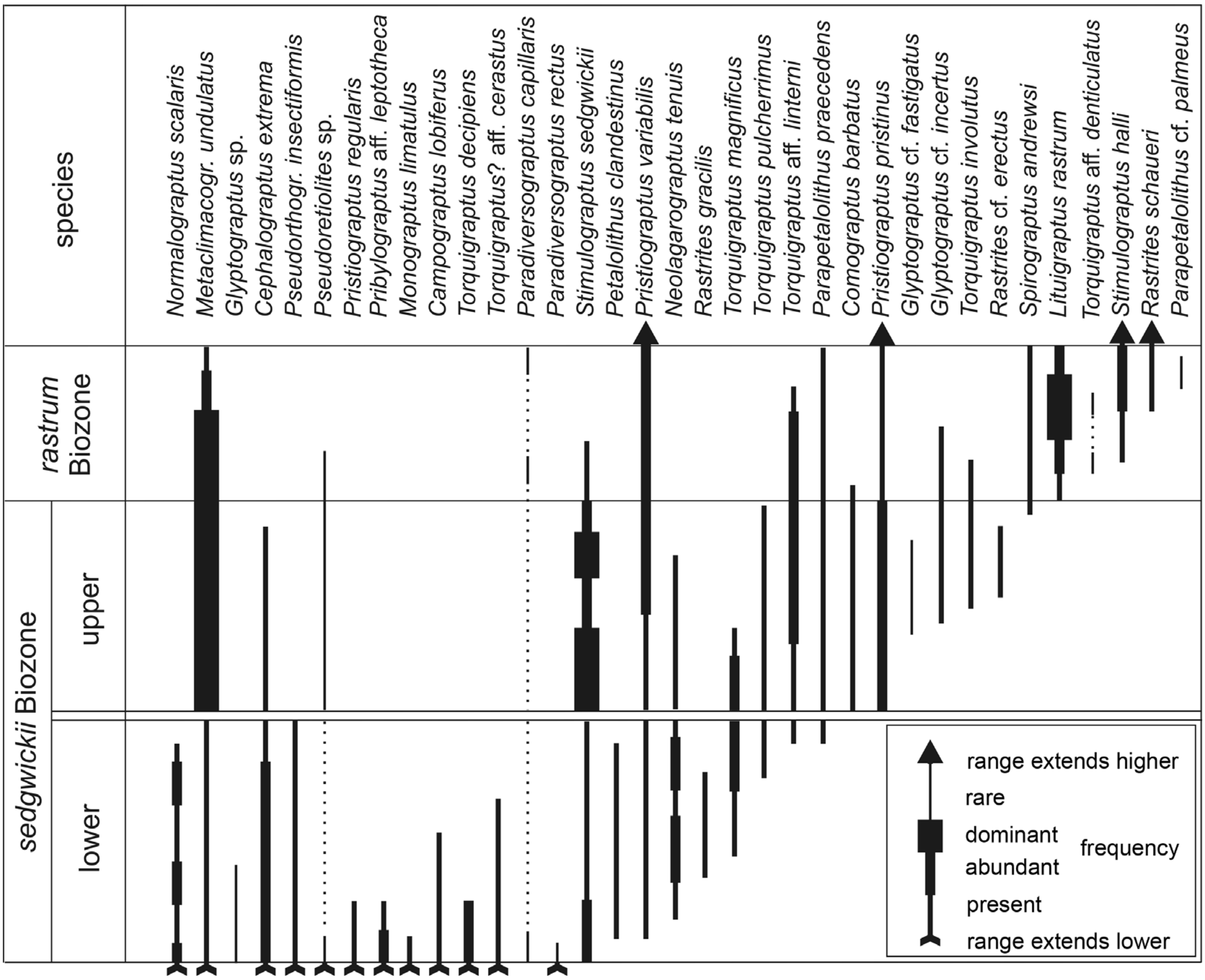

Figure 6. Composite range chart of the upper Aeronian graptolites recorded in the Prague Synform. In other areas the stratigraphic ranges of several taxa are either longer than shown (e.g. *N. scalaris*, *Metacl. undulatus* and *St. sedgwickii* records from Telychian succession of Wales; Loydell, 1993) or more restricted, such as '*M.*' *limatulus* and *Ceph. extrema* in British sections (Zalasiewicz *et al.* 2006). Break in graptolite ranges between informal lower and upper parts of the *sedgwickii* Zone indicates silty mudstone level, barren of determinable graptolites.

overlapping zonal index taxa (*St. sedgwickii* and *St. halli*), the question remained of how to separate formally the upper levels with a distinct graptolite assemblage from the underlying bulk of the *sedgwickii* Zone.

An alternative index graptolite was looked for. Instead of *St. halli*, the abundant and readily determinable *Lituigraptus rastrum* (Richter) (Fig. 5d) has been found to work well in practice in all relevant sections of the Barrandian area. The newly introduced *L. rastrum* Zone varies from 0.4 to 0.75 m thick in examined sections (Radotín tunnel, Nové Butovice, Želkovice, Karlík, Zdice, Zadní Třebaň).

The base of *L. rastrum* Zone, defined by the incoming of its abundant zonal index graptolite, roughly coincides with or pre-dates the lowest occurrence of *Stimulograptus halli* (Barrande) and slightly post-dates that of *S. andrewsi*. *Rastrites schaueri* Štorch & Loydell has its first occurrence in about the middle of the *rastrum* Zone. Several taxa, in particular *Glyptograptus* cf. *incertus* (Elles & Wood), *Com. barbatus* and *T. involutus* continued from the upper part of *sedgwickii* Zone to the lower part of *L. rastrum* Zone. *St. sedgwickii* itself and *T. involutus* also persisted into the *rastrum* Zone and *Parapet. praecedens* and *S. andrewsi* became more common. Other species not restricted to this zone are abundant *Metacl. undulatus*, *P. variabilis*, *P. pristinus* and *St. halli*.

4.b. Graptolite faunal dynamics

The Middle Aeronian *Pribylograptus leptotheca* and *Lituigraptus convolutus* zones exhibit ecologically well-balanced, high-diversity graptolite faunas with a particularly low degree of dominance and high values of evenness indices. Štorch (1998) described 33 species from a single locality of the *L. convolutus* Zone at Tmaň near Beroun. The baseline extinction rate accelerated and diversity declined across the *convolutus*/*sedgwickii* zonal boundary (*Rivagraptus*, *Neodiplograptus* and most species of *Campograptus* and *Rastrites* became extinct). Some of the surviving taxa disappeared in the subsequent earliest part of the *sedgwickii* Zone (‘*Monograptus*’ *limatulus* group, *Pribylograptus*).

The early part of the *sedgwickii* Zone saw a rapid turnover of graptolite taxa (Fig. 6). *Campograptus* gave origin to *Stimulograptus sedgwickii*, the lowest occurrence of which defines the formal base of this zone. Torquigraptids proliferated as *Torquigraptus decipiens* and *T.*? aff. *cerastus* were replaced by *T. magnificus*, *T. pulcherrimus* and *T.* aff. *linterni*. *Normalograptus* (*N. scalaris*), the last representatives of ancorate *Petalolithus* (*Pet. clandestinus*) and those of the *Rastrites peregrinus* lineage (*R. gracilis* Přibyl) are still important elements of this assemblage. The unancorate *Parapetalolithus* (*Parapet. praecedens*) first appears in the uppermost part of this interval. Graptolite diversity decreased to 23 species if counted for the whole lower *sedgwickii* Zone. Diversity recorded for individual sampling levels dropped still more significantly. A low degree of dominance indicates persisting stable conditions whereas conspicuously low graptolite abundance, generally lower but fluctuating TOC and high pyrite content indicate changing environmental conditions. A siltstone bed encountered in the upper middle part of the *sedgwickii* Zone in the Radotín tunnel and Nové Butovice sections occurs at the same level as a further change in the graptolite fauna.

Above this bed, in the upper part of the *sedgwickii* Zone, graptolites become abundant, but the assemblages are commonly dominated by two species (*St. sedgwickii* and *Metacl. undulatus*) both persisting from the lower part of the *sedgwickii* Zone. Extinction and speciation rates are low in this interval (Fig. 6) and overall diversity declined further to 17 species.

Through much of the *Lituigraptus rastrum* Zone the assemblages are dominated by one or two species (*Metacl. undulatus* and *L. rastrum*). Dominance increased still further while overall diversity remained at the minimum of 17 species (Fig. 6). The graptolite crisis known as the *sedgwickii* Event (Melchin, Koren’ & Štorch, 1998) persisted through this level.

Barren mudstones, which separate the black shale of the *rastrum* Zone from that of the *linnaei* Zone of the lowermost Telychian (Figs 2, 3, 4), hide the subsequent recovery interval in the Barrandian area. Graptolite assemblages sub- and suprajacent to the barren mudstone, when correlated with coeval successions of Wales (after Loydell, 1991*a*) and Spain (current research), suggest that the boundary interval of the *halli* and *guerichi* zones is barren of graptolites in the Barrandian area. Only four graptolite species were found both below and above the mudstone in the Radotín tunnel section. The first black shale intercalation above the mudstone hosts higher diversity and lower dominance assemblages, composed for the most part by likely descendants of the taxa recorded from the upper *sedgwickii* and *rastrum* zones. Surprisingly, a significant graptolite radiation probably commenced during the course of the more oxic sedimentation of this barren mudstone.

4.c. Biodiversity and time trend analyses

The effect of sample size upon species counts was investigated by rarefaction analysis for all samples from the Radotín section (Fig. 3). The analysis resulted in the need to reduce the dataset from 29 samples to 22 samples for subsequent biodiversity analyses (i.e. rarefaction curves flatten out well for these samples suggesting that further sampling would not increase the number of taxa substantially). The limited dataset contains two samples from the *leptotheca* Zone, six samples from the *convolutus* Zone, four samples from the lower *sedgwickii* Zone, seven samples from the upper *sedgwickii* Zone and three samples from the *rastrum* Zone. Tests of these 22 graptolite samples revealed no statistically significant correlation between species number and sample size in both used correlation coefficients (Spearman’s and Kendall’s).

To characterize species richness across the studied interval we compared the number of observed graptolite species in each sample and calculated Menhinick’s and Margalef’s richness indices. All of these data indicate that the graptolite species diversity is generally decreasing through the Radotín section (Fig. 7a, c). The analysis of time trends in all above-mentioned values (number of graptolite species found as well as in Menhinick’s and Margalef’s richness indices) across the whole studied stratigraphical interval (i.e. from *leptotheca* to *rastrum* zones) showed a statistically significant trend (p-values for all Mann–Kendall statistics are much lower than critical p-values for the 0.01 significance level). These results fit well with the general trend in number of graptolite species recorded in the Barrandian area in individual graptolite zones (Fig. 7d). The number of graptolite species in each of the five graptolite zones observed in the Radotín section as well as estimation of graptolite species diversity based on rarefaction analysis revealed the same decreasing trend from the *convolutus* to upper *sedgwickii* zones (Fig. 7d). However, statistical tests-based quantitative data from the Radotín section revealed statistically significant differences in the total number of graptolite species only between the *leptotheca*, *convolutus* and lower *sedgwickii* zones on the one hand and upper *sedgwickii* and *rastrum* zones on the other, even though the species richness of the *convolutus* Zone seems to be the highest (Fig. 7d). Estimations of graptolite species diversity based on values of Menhinick’s and Margalef’s richness indices for individual graptolite zones revealed a similar trend. Also in this case, a statistically significant change in the total biodiversity in the studied graptolite zones was revealed between the lower and upper *sedgwickii* Zone (Fig. 7e). On the other hand, evaluation of time trends of species richness indices for all samples from the *leptotheca* to lower *sedgwickii* zones (12 samples) by the Mann–Kendall test revealed a statistically significant decreasing trend for the Margalef’s richness index ($p < 0.05$) and number of graptolite species found ($p < 0.01$). No statistically significant trend in

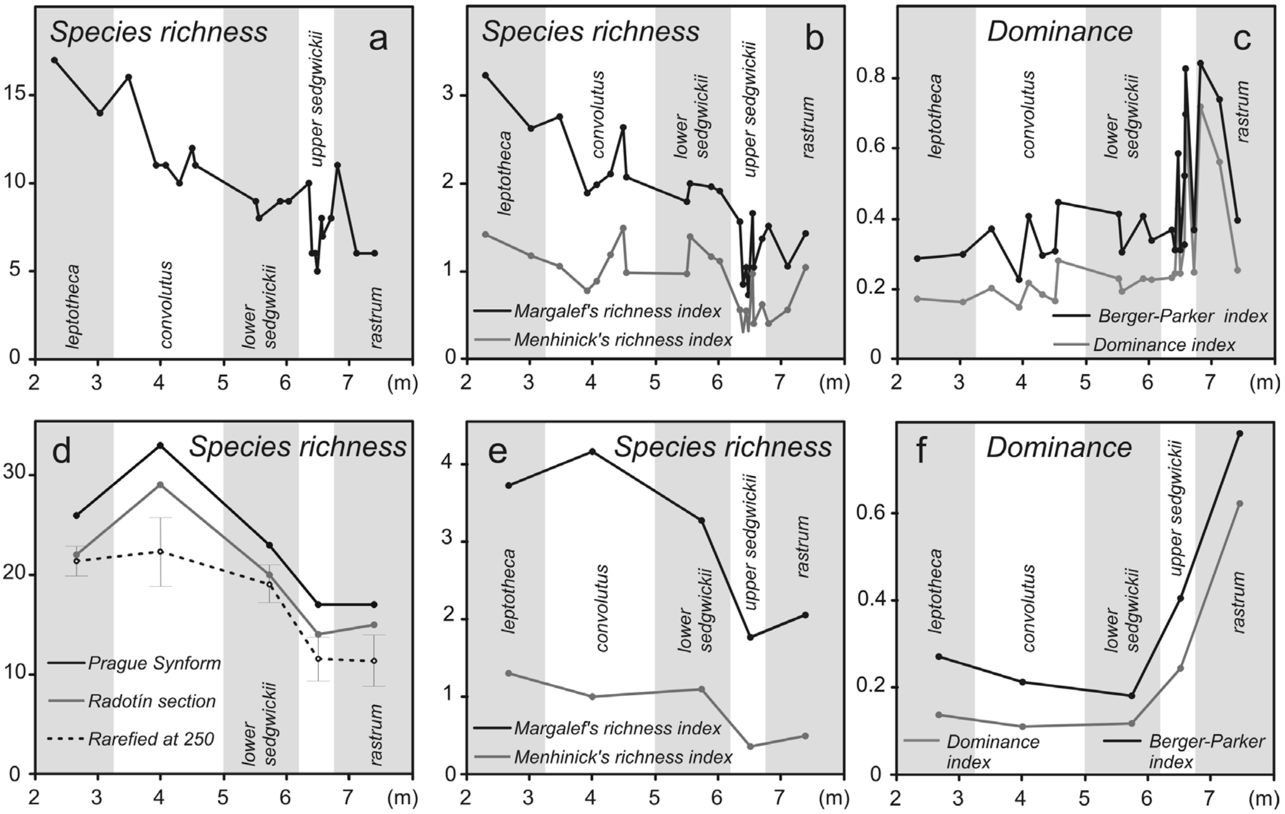

Figure 7. Species richness and community evenness indices calculated for individual samples (a–c) from the Radotín tunnel section and for cumulative samples uniting all samples within a particular graptolite zone (d–f). Species richness is expressed as number of individual species in each sample (a, d), and is estimated by Menhinick's and Margalef's richness indices (b, e). Species diversity at 250 occurrences (based on rarefaction analysis) is also shown for cumulative samples (d, e). Evenness is expressed by simple dominance and Berger–Parker indices.

species richness indices was found for data from the upper *sedgwickii* and *rastrum* zones. Taken together our analyses show a statistically significant decreasing trend in graptolite species diversity from the *leptotheca* to lower *sedgwickii* zones and subsequent distinct decrease in graptolite species diversity between the lower and upper parts of the *sedgwickii* Zone (Fig. 7a, b, d, e). Analyses of changes in graptolite species diversity inferred from summary data (i.e. from total number of graptolite species being present in each zone) are biased to some extent by the very likely different time duration of the graptolite zones.

Analysis of evenness of graptolite communities also revealed a distinct trend. Both the dominance and Berger–Parker indices show an increasing distinct trend in dominance within graptolite assemblages across the studied interval (Fig. 7c). Analysis using the Mann–Kendall statistics showed a statistically significant increasing trend in the both these indices ($p < 0.01$) through the Radotín section (Fig. 7c). A more detailed view shows that values of both the dominance and Berger–Parker indices have quite different dispersion for data from the *leptotheca* to lower *sedgwickii* zones on the one hand and for data from the upper *sedgwickii* and *rastrum* zones on the other. In the first stratigraphical interval both the dominance and Berger–Parker indices vary only slightly. On the other hand, both indices increased dramatically (three times) in the upper *sedgwickii* and *rastrum* zones (Fig. 7c). The distinct increase of both the dominance and Berger–Parker indices in the latter stratigraphical interval is also observable in the summary data calculated for the studied graptolite zones (Fig. 7f). Correlation analysis using Spearman's and Kendall's coefficients between species richness indices and evenness indices revealed statistically significant negative correlations ($p < 0.01$) between dominance on the one hand and all species richness indices (number of observed graptolite species in each sample and calculated Menhinick's and Margalef's richness indices) on the other. Taken together, the analysis of evenness has shown that graptolite assemblages that are richer in species have significantly higher evenness. The graptolite assemblages of the *leptotheca* to lower *sedgwickii* zones had very low dominance in contrast with those of the upper *sedgwickii* and *rastrum* zones. Very high variability and generally high values of dominance are typical for the graptolite assemblages of the upper *sedgwickii* and *rastrum* zones (Fig. 7c, f).

4.d. Sedimentary signatures of the *sedgwickii* Event

The Radotín tunnel section exhibits its first significant change in sedimentation in the lowermost *sedgwickii* Zone (Fig. 3). It is associated with a considerable, but not abrupt impoverishment of the graptolite assemblage for several important graptolite clades. Siliceous black shales of the *convolutus* Zone are replaced by pyrite-rich, graptolite-poor shale with lower TOC (*c.* 3 %). Uncommon graptolites refer this relatively thick level to the lower part of the *sedgwickii* Zone. It is overlain by a heavily bioturbated micaceous siltstone without any determinable graptolites, which, in turn, is succeeded by organic-rich (TOC *c.* 6 %), finely laminated micaceous black shale with an abundant, but still lower diversity, graptolite fauna. Differences between the graptolite assemblage below and above the siltstone and the abrupt change in grain size and TOC suggest that an interval of nondeposition and/or erosion may be coupled with the deposition of the siltstone bed. Organic-rich micaceous black shales above the siltstone bed are assigned to the upper part of the *sedgwickii* Zone. The stratigraphical ranges of numerous graptolite species span the interval. Hence a short duration of the potential stratigraphical break, still within upper middle part of the *sedgwickii* Zone, can be inferred.

The lower part of the *sedgwickii* Zone is preserved in the Hýskov section and was deposited under considerably shallower and better-oxygenated bottom conditions than the otherwise black shale dominated Llandovery succession of the Prague Synform. Marly shales and limestones, including grainstones with coated grains, host rich and diverse benthic faunas (Štorch, 2001).

The sedimentary record indicates incipient sea-level drawdown in the early part of the *sedgwickii* Zone, which culminated abruptly in about the middle of the zone. A high content of early diagenetic pyrite preserved in concretions and planar bioturbation fillings as well as lower TOC in the lower part of the *sedgwickii* Zone in the Radotín tunnel are consistent with temporarily disrupted anoxia as inferred from the model discussed by Schieber (2003).

In the Velká Ohrada section, the stratigraphical break is of much greater duration and late Aeronian sedimentary rocks are missing entirely. In a large east-central part of the Prague Synform, late Hirnantian siltstones are overlain directly by the pale-coloured mudstones of the basal Telychian (Štorch, 2006).

4.e. Carbon isotope excursion and its biostratigraphic dating

Carbon isotope sampling began at the base of the *leptotheca* Zone of the Želkovice Formation, about 6 m below the base of the Telychian Litohlavy Formation. The last sample was collected about 1 m above the base of the latter formation (Fig. 3). In total 33 samples were analysed for $\delta^{13}C_{org}$ and TOC content in the Radotín tunnel section. Both of these vary through the interval studied but statistical analysis revealed no significant trend. The first positive shift in $\delta^{13}C_{org}$ appears at 5.10 m, at the base of the *sedgwickii* Zone. Around the level of 6.2 m, in the middle of the *sedgwickii* Zone, $\delta^{13}C_{org}$ values rapidly increase whereas TOC values decrease (Fig. 3). Correlation analysis does not support a significant statistical relationship between $\delta^{13}C_{org}$ and TOC values. Both limbs of the $\delta^{13}C_{org}$ excursion are within strata with a relatively high organic content and minor silt content. Samples from the middle of the siltstone (6.24 m) exhibit extremely high $\delta^{13}C_{org}$ values (−14.31 to −18.12 ‰), which must be considered, however, with reservation. The TOC values of these two samples are considerably lower (0.6 %) than TOC values of other samples from the *sedgwickii* Zone (average value is about 4.8 %). In addition the siltstone derived probably from a shallower environment could primarily contain small amounts of carbonate carbon. For these reasons, partial opening of the organic carbon isotope system of these samples during diagenesis cannot be dismissed. Some part of the $\delta^{13}C$ excursion may not be preserved in the Radotín tunnel section owing to a possible stratigraphical break associated with the siltstone. $\delta^{13}C$ returns to its baseline values in the *rastrum* Zone. Maximum TOC values (up to 7 %) occur just above the siltstone and remain high in the *rastrum* Zone.

4.f. The Aeronian/Telychian boundary

A prominent, pale-coloured calcareous mudstone/claystone bed, the base of which marks the base of the Litohlavy Formation, separates the black shale with a *L. rastrum* Zone assemblage from the overlying black shale level with *S. guerichi* and *Rastrites linnaei* Barrande in all sections. The graptolite faunas of the two separate levels are readily recognizable since only a few species span the two levels (*St. halli*, *R. schaueri*, *P. pristinus* and *P. variabilis*). The black shale above the pale mudstone sees the incoming of *R. linnaei*, *S. guerichi*, *Torquigraptus planus* (Barrande), *Torquigraptus obtusus* (Schauer), *Glyptograptus fastigatus* Haberfelner, *Glyptograptus auritus* Bjerreskov, *Parapetalolithus elongatus* Bouček & Přibyl, *Parapetalolithus palmeus* (Barrande) and *Pseudoplegmatograptus* sp. *Glyptograptus* cf. *incertus*, *Parapet. praecedens*, *Ceph. extrema*, *S. andrewsi* and *L. rastrum* have all vanished from the fossil record. Considering the break in graptolite faunal composition and omission of some age-diagnostic taxa (e.g. *Paradiversograptus runcinatus* Lapworth), slow sedimentation must be considered likely for the graptolite-barren mudstone. It appears to correspond to both the upper part of the *halli* Zone *sensu* Loydell (1991*a*) and the *Paradiversograptus runcinatus* Sub-zone recognized by Loydell in the lowermost part of *S. guerichi* Zone in Wales and subsequently by Gutiérrez-Marco & Štorch (1998) in the lowermost part of *R. linnaei* Zone in the Western Iberian Cordillera of Spain.

The degree of diachroneity of the base of the barren mudstone is negligible in the Prague Synform. It overlies black shale with a *L. rastrum* zonal assemblage in all localities except Velká Ohrada (Fig. 2) where the succession is interrupted by a regional break in sedimentation (Štorch, 2006). The thickness of the mudstone bed, however, varies from 0.5 m (e.g. Radotín tunnel) to 1.25 m at Nové Butovice. Kříž (1975) reported a thickness of 0.3–4.10 m from unspecified boreholes in the SW part of the Silurian synform. Apart from subordinate black shale intercalations with a *guerichi* or *linnaei* Zone graptolite fauna, the same pale-coloured mudstone sedimentation continued well into the *Spirograptus turriculatus* Zone as documented for example in the classical Litohlavy section (Štorch, 1991). The maximum value reported for the mudstone thickness by Kříž (1975) encompassed all of this succession including minor black shale intercalations. Prominent pale-coloured mudstone discussed by Kříž (1975) and Štorch (2006) gives evidence that oxic sedimentation predominated in the Barrandian area during post-*sedgwickii* Event recovery through to the early Telychian *utilis* extinction Event recognized by Loydell (1994). Apparent links to graptolite mass extinctions and positive carbon isotope excursions are missing. Repeated oxic bands in the subsequent Litohlavy Formation account for cyclic, probably climatic changes, which influenced sedimentation in the Barrandian area up to the base of late Telychian *Oktavites spiralis* Zone.

The *Parapetalolithus palmeus* and *Parapetalolithus hispanicus* subzones were recognized within the classical Bohemian *Rastrites linnaei* Zone by Bouček (1953). This graptolite fauna comes from black shale intercalations in the mudstone-dominated interval. The graptolite assemblages of the two subzones suggest that both are correlatable with only a limited, presumably upper, part of the standard lowermost Telychian *S. guerichi* Zone. Consequently, the base of Telychian Stage associated with the first appearance datum (FAD) of *S. guerichi* in graptolite-bearing successions worldwide, must be placed from a chronostratigraphical point of view in the barren mudstone bed, below the black shale intercalation with the lowest occurrence of *Spirograptus guerichi* (*Parapet. palmeus* Subzone) and, consequently, above the black shale with *L. rastrum* but without *S. guerichi* and *R. linnaei*.

4.g. Correlation with graptolite-rich upper Aeronian successions abroad

4.g.1. Thuringia

Schauer (1967, 1971) listed most of the graptolite species recorded in the present study (such as *Parapet. praecedens*, *Ceph. extrema*, *T. decipiens*, *St. sedgwickii*, rare *Com. barbatus* and *Nl. tenuis*) from his sections but detailed correlation with the upper Aeronian succession of the Barrandian area may be partly biased by taxonomy. Apparent differences from Barrandian sections include *R. hybridus* ranging from the uppermost *L. convolutus* Zone through to the *linnaei* Zone. Upper Aeronian sections of the Barrandian area yielded *Rastrites gracilis* Přibyl and *R.* cf. *erectus* Hutt instead. Note that incomplete *R. hybridus* affected by tectonic strain may be easily misidentified as *Rastrites peregrinus* Barrande, which is a typical element of the *convolutus* Zone. Schauer (1967) reported also *Monograptus circularis* Elles & Wood, albeit without description or illustration, which could be actually *T.* aff. *linterni* of Bohemian sections. *T. magnificus*, described and figured from the *sedgwickii* Zone of Thuringia by Přibyl & Münch (1943), was reported from the lower *convolutus* Zone by Schauer (1967) and *T. pulcherrimus* was missing altogether. *L. rastrum*, identified by Törnquist (1907) in Raitzhain and Grobsdorf, was recorded by Schauer (1967, 1971) in the upper *sedgwickii* Zone of his sections and thus tentatively correlates with the *L. rastrum* Zone of this paper and, at least in part, with the *St. halli* Zone of Loydell (1991*a*).

4.g.2. Denmark

In Bornholm, the black shale of the uppermost *convolutus* Zone with *Ceph. cometa* and *Ceph. extrema* is sharply overlain by 'light grey, argillaceous and silty mudstone' barren of graptolites but rich in pyritized planar burrows (Bjerreskov, 1975). This interval grades upwards into laminated shale becoming darker and intercalated with bands of 'nonfossiliferous green mudstone'. The graptolite assemblage of this dark, laminated shale with *Glyptograptus auritus* Bjerreskov, *Parapet. palmeus*, *Paradiversograptus runcinatus* and *S. guerichi* a.o. is correlatable with the basal Telychian lower *linnaei* and/or *guerichi* Zone. The upper Aeronian is represented by a light grey silty mudstone interval without graptolites and/or may even be partly missing owing to a possible break in sedimentation at the base of the silty mudstone.

4.g.3. Spain

In the Western Iberian Cordillera (Gutiérrez-Marco & Štorch, 1998) and Central Iberian Zone (Štorch *et al.* 1998), the lower Silurian Los Puertos and Criadero quartzites are regularly overlain by black micaceous shales of the *linnaei* Zone. Also, the middle Aeronian *convolutus* Zone may be locally developed as a black shale interval within the quartzite succession (Gutiérrez-Marco & Štorch, 1998) but the upper Aeronian is always represented by quartzites. In the relatively deeper-water Silurian of the Ossa Morena Zone, however, black shale sedimentation commenced in the *Akidograptus ascensus* Zone and continued through much of the Silurian (Jaeger & Robardet, 1979). Black shales of the *c.* 6 m thick *sedgwickii* Zone are overlain by a complete succession of the *halli* Zone, which (according to David Loydell, pers. comm. 2010) comprises a significant interval with *L. rastrum* in its middle part. Graptolite assemblages as well as faunal dynamics are closely similar to those in Bohemian sections and allow for intrazonal correlation. The lower part of the *sedgwickii* Zone is marked by a low-diversity and low-dominance graptolite fauna with *St. sedgwickii*, *Pet. clandestinus*, *Ceph. extrema* and *T. magnificus*. *Nl. tenuis* proliferates in the middle part of the zone, above a 5 cm thick band of rusty, pyrite-rich silty mudstone, and it is associated with *Com. barbatus* and other typical species, including *Parapet. praecedens*. Further correlation with Bohemian successions would be premature since the El Pintado section is under detailed study by D. K. Loydell, P. Štorch and J. C. Gutiérrez-Marco. No remarkable changes in lithology have been encountered from the *convolutus* Zone through to the base of the *halli* Zone except for the pyrite-rich mudstone band in the middle part of the *sedgwickii* Zone, which may be interpreted as a temporary disruption of the anoxic regime.

4.g.4. *Scotland*

Toghill (1968) assigned an 8.4 m thick interval of the Dob's Linn succession to the *sedgwickii* Zone; the lower part of this, however, is barren of graptolites. Graptolite-bearing black shales in the middle part of this interval have been further studied by Pannell, Clarkson & Zalasiewicz (2006) who identified *St. sedgwickii*, *Nl. tenuis* concentrated in several peaks of abundance, *N. scalaris*, pristiograptids, glyptograptids and petalolithids. Loydell (1991*b*) provided a range chart of the graptolites through the uppermost *sedgwickii* Zone and *halli* Zone at Dob's Linn, based on a re-examination of Toghill's collection. Williams *et al.* (2003) reported graptolite assemblages including *St. sedgwickii*, *P.* aff. *regularis*, *Torquigraptus linterni* Williams *et al.*, *T. magnificus*, *Streptograptus ansulosus* (Törnquist), *Rastrites* cf. *gracilis*, *Paradiversograptus capillaris* (Carruthers), *Ps. insectiformis*?, *Gl.* cf. *incertus* and some undetermined taxa from various Scottish localities and referred them to the upper *sedgwickii* Zone. Carbon isotope data acquired from the Dob's Linn section by Melchin & Holmden (2006) revealed a prominent carbon isotope excursion in the upper Aeronian. The relatively condensed section, limited resolution of biostratigraphical data and limited sampling density, however, did not allow for more detailed determination of the structure and biostratigraphical dating of the isotope curve at this particular level.

4.g.5. *England and Wales*

Moderately diverse graptolite assemblages of the *sedgwickii* Zone occur in the Howgill Fells (Rickards, 1970) and Lake District (Hutt, 1974). A substantial part of the zonal succession, however, is lacking a graptolite record since graptolite-bearing black shale is confined to several intercalations within predominantly barren mudstones. In the Lake District area (Hutt, 1974) *Nl. tenuis* is associated with the lowest occurrences of *St. sedgwickii*. Rickards (1976) noted that the first occurrences of *Nl. tenuis* are well above those of *St. sedgwickii*. Loydell (1991*a*, 1992, 1993) studied the latest Aeronian strata of mid-Wales and recognized the *Stimulograptus halli* Zone erected by Jones & Pugh (1916) between the *sedgwickii* Zone and early Telychian strata with *Spirograptus guerichi*. In the Barrandian area, the *L. rastrum* Zone is now recognized between the upper Aeronian *sedgwickii* Zone and lower Telychian *linnaei* Zone, at about the same level.

4.g.6. *Libya and Algeria*

Štorch & Massa (2006) reported *sedgwickii* Zone assemblages with *St. sedgwickii*, *Glyptograptus* aff. *incertus*, *Metaclimacograptus hughesi*, *P. regularis*, *P.* cf. *renaudi* and *P.* cf. *pristinus* from the western Murzuq Basin and Al Qarqaf Arch of Libya. *Pet. clandestinus*, *P. regularis* and *Nl. tenuis* were taken as indices of the lower part of the biozone at Al Qarqaf Arch. A similar association was recognized by Štorch & Massa (2003) from a drill core in the Ghadāmis Basin (north-central Libya). *Pet. clandestinus* has also been found in the Algerian Eastern Tassili-n Ajjer (referred to *Petalolithus* cf. *wuxiensis* by Štorch & Massa, 2003). No significant graptolite data are available for the remaining part of the upper Aeronian in North Africa.

4.g.7. *Canada, Nova Scotia*

Graptolite-bearing black shales developed in the Lower Ross Brook Formation of the Arisaig Group were assigned to the lower part of the *sedgwickii* Zone by Melchin (2007). The graptolite assemblage, comprising metaclimacograptids, *N. scalaris*, *Pet. clandestinus*, *P. regularis*, *Camp. lobiferus* and *Nl. tenuis*, was referred to the *Neolagarograptus tenuis* Subzone. The black shale succession grades upwards into grey silty shale, which, according to Melchin (2007), still belongs in the *sedgwickii* Zone. The *c.* 160 m thick, shallowing up succession is topped by oxic strata with lowermost Telychian brachiopods. Subsequent carbon isotope analyses revealed three positive shifts of $\delta^{13}C_{org}$ (Melchin *et al.* 2011) in the upper Aeronian sedimentary succession, which corresponds with the *sedgwickii* and presumably also *halli* (or *rastrum*) zones. The middle peak of this three-fold $\delta^{13}C_{org}$ excursion reaches up to −25.5 ‰. Each of the peaks is associated with a phase of shallowing in the Nova Scotia succession (Melchin *et al.* 2011). Despite somewhat different sea-level histories, the Barrandian area and Nova Scotia exhibit roughly corresponding stratigraphical levels and a remarkably similar three-fold pattern to the carbon isotope excursion. Also the graptolite assemblage assigned by Melchin to the lower *sedgwickii* Zone (*Nl. tenuis* Subzone) is particularly remarkable for its palaeobiogeographical affinities to Gondwanan graptolite faunas (Melchin, 2007).

4.g.8. *Canada, Arctic Islands*

The upper Aeronian of Cornwallis Island is marked by an interval of thinly laminated and even rippled dolostones in a generally black shale dominated lower Silurian succession. The same interval sees a prominent positive $\delta^{13}C_{org}$ excursion, which Melchin & Holmden (2006) dated by graptolites to the lower *sedgwickii*

Zone. The lower *sedgwickii* Zone of Melchin & Holmden (2006), however, represents the bulk of the *sedgwickii* Zone of this paper since the upper *sedgwickii* Zone of Melchin & Holmden is within strata between the lowest occurrence of *St. halli* and the lowest occurrence of the lowermost Telychian *Spirograptus guerichi*, and thus correlates with the *halli* Zone of Loydell (1991*a*) or *rastrum* Zone of this paper. Although the isotope and sedimentary record account for a single massive event comprising all of the *sedgwickii* Zone, the limited stratigraphical resolution of published graptolite data and limited sampling density may have obscured the more complex nature of this critical interval. Published graptolite records do not allow for precise biostratigraphical control in the Arctic Canadian sections at this particular level, but particularly high TOC values and the falling $\delta^{13}C_{org}$ recorded in strata just above the peak of the late Aeronian positive excursion closely resemble the trends observed in the Radotín tunnel section (Fig. 3).

5. Discussion

Upper Aeronian successions in the Prague Synform and the eight other regions discussed above show a substantial decrease of graptolite diversity and rapid demise of many prolific middle Aeronian taxa. Loydell (2007), considering his data from Wales (Loydell, 1993) and Dob's Linn of Scotland (Loydell, 1991*b*), supposed that graptolite diversity dropped to minimum values in the *sedgwickii* Zone, whereas Melchin *et al.* (1998) draw the minimum diversity values in their upper *sedgwickii* Zone, which actually correlates with the *halli* Zone of Loydell (1991*a*) and *rastrum* Zone of this paper. Our data were sampled with higher stratigraphic resolution and suggest that faunal change started near to top of the *convolutus* Zone. The diversity decline culminated during the upper *sedgwickii* Zone (*s.s.*) and low diversity was maintained into the *rastrum* Zone. It must be considered that graptolite-bearing black shale referred to the *rastrum* Zone in the Prague Synform is the equivalent of a minor, presumably lower and/or middle part of the *halli* Zone of Wales. The post-extinction recovery interval and incipient adaptive radiation after the *sedgwickii* Event are hidden in the Bohemian succession within the graptolite-barren calcareous mudstone. This is probably why the increasing graptolite diversity reported by Loydell (1991*b*, 2007) from the *halli* Zone has not been found in the Prague Synform.

Published data from the Welsh *halli* Zone (Loydell, 1991*a*, 1992, 1993) suggest that the species present, their relative abundances and evenness of graptolite communities show considerable similarities to the Bohemian succession. Up to 80 % of graptolite rhabdosomes from bulk samples of the uppermost *sedgwickii* and lower *rastrum* zones in Radotín tunnel section belong to *Metacl. undulatus*. The same species predominated, although less dramatically, in Wales (32.8 % in the *halli* Zone; Loydell, 1993, p. 151). *Stimulograptus sedgwickii* and/or *St. halli* are also abundant in both areas. On the other hand, abundance peaks of *Nl. tenuis*, recorded by Pannell, Clarkson & Zalasiewicz (2006) in the *sedgwickii* Zone at Dob's Linn, are absent in the Prague Synform.

Within the Prague Synform specific relative abundances of graptolite taxa have been observed in mixed graptolite-shelly fauna of a rather shallow and oxygenated lime-rich succession of the lower *sedgwickii* Zone at Hýskov (Štorch, 2001). There, *Ceph. extrema* is absent whereas *Pet. clandestinus* and *Nl. tenuis* are equally as common as *T. magnificus* and *N. scalaris*. The role of water depth, oxygenation and food resources in composition of the graptolite fauna remains obscure until depositional settings are well defined in further, stratigraphically and palaeogeographically relevant sections.

The graptolite crisis named the *sedgwickii* Event coincides with sedimentary signatures of changing environment. Anoxia weakened after the end of the *convolutus* Zone alongside an increasing rate of graptolite species extinction. TOC values decreased along with substantial increase of early diagenetic pyrite preserved in planar bioturbation fillings, concretions and lenticular beds. A high content of early diagenetic pyrite coupled with lower TOC is consistent with temporarily disrupted anoxia according to the model advocated by Schieber (2003). Graptolite abundance dropped to a minimum but species richness decreased less dramatically owing to rapid replacement of the extinct species.

The middle part of the *sedgwickii* Zone is characterized by dominant silty material and intensive bioturbation. The difference between the graptolite fauna below and above the siltstone bed suggests the possibility of a distinct break in sedimentation associated with this level even though no unconformity has been detected and both the base and top of the siltstone are gradual rather than sharp. This level presumably represents the minimum sea-level and a sequence boundary recognized by Štorch (2006). It is also correlatable with an apparent gap in sedimentation recorded in several sections in the Prague Synform (Fig. 3 and Štorch, 2006). The middle–late Aeronian gap in sedimentation encountered by Kaljo & Maartma (2000) and Kaljo *et al.* (2003) in platform sections of Estonia may have been associated with the same eustatic event, although high-resolution $\delta^{13}C_{org}$ and graptolite data are missing. The graptolite fauna from the black shale subjacent to the siltstone matches the assemblage recorded in the shallow-water, carbonate-dominated succession of the *sedgwickii* Zone of the Hýskov section (Fig. 2). Štorch (2001) explained those shallow-water limestones and volcaniclastic rocks in an otherwise black shale dominated succession of the Prague Synform as resulting from rapid growth of a local submarine volcano simultaneously with late Aeronian sea-level drawdown.

Black shales above the siltstone bed are still silty and coarsely micaceous. Graptolites became abundant, although species richness has decreased to a minimum and evenness values are also strongly decreased. TOC reached particularly high values (6–7 %) above the siltstone (Fig. 3). Low species richness and low evenness of the assemblage combined with high TOC may be attributed to unfavourable conditions established by extensive algal/bacterial blooming. The organic fraction is dominated, apart from fragments of graptolite rhabdosomes, by amorphous organic matter of presumably algal origin. It is possible that algal blooms have been triggered by increased input of nutrients from windblown dust during a dry period of the glacial cycle envisaged by Melchin & Holmden (2006) and Loydell (2007). A similar proliferation of amorphous organic matter was recorded above the *lundgreni* Event by Lenz *et al.* (2006) at Cornwallis Island, Arctic Canada. There is no apparent relationship between increased carbon burial and isotope composition in the Radotín tunnel section. There is no statistically significant relationship between $\delta^{13}C_{org}$ and TOC values. Considerably high TOC values in black silty shale of the upper *sedgwickii* Zone clearly post-dated the major mid-*sedgwickii* Zone $\delta^{13}C_{org}$ excursion (Fig. 3). Low TOC in mottled siltstone with the maximum positive shift of $\delta^{13}C_{org}$ is likely to reflect early oxidation of the organic matter.

High TOC values combined with low species richness and low evenness of the graptolite community in the upper *sedgwickii* Zone are consistent with substantial change in both absolute and probably also relative abundance of different primary producers. Different groups of palynomorphs and macroalgae may have different carbon isotope compositions and thus bearing on $\delta^{13}C$ values (Lécuyer & Paris, 1997).

Carbon isotope curves based on data from Dob's Linn and Cape Manning (Cornwallis Island, Arctic Canada) exhibit a prominent positive excursion in $\delta^{13}C_{org}$ and $\delta^{13}C_{carb}$ in the *sedgwickii* Zone (Melchin & Holmden, 2006). The carbon isotope record seems to be more complex, however, than that outlined by Melchin and Holmden. In the Radotín tunnel section, the first positive shift in $\delta^{13}C_{org}$ appeared in the *convolutes*–*sedgwickii* zone boundary beds, but for technical reasons only one sample could be taken from this interval (Fig. 3). A major positive shift in $\delta^{13}C_{org}$ values (*c.* 7 ‰) followed in the middle part of the *sedgwickii* Zone and largely coincided with a silty incursion. Then $\delta^{13}C_{org}$ remained above baseline value through the upper *sedgwickii* Zone and after another minor positive shift dropped down to more negative values in the course of the *rastrum* Zone. Recent sampling of the far less condensed succession in NE Nova Scotia, Canada has shown a similar $\delta^{13}C_{org}$ pattern. Three positive shifts of $\delta^{13}C_{org}$ noted by Melchin *et al.* (2011) were dated by graptolites to the *sedgwickii* and presumably also *halli* (or *rastrum*) zones. The middle peak of this three-fold $\delta^{13}C_{org}$ excursion is the most prominent one and the peaks are associated with phases of shallowing (Melchin *et al.* 2011). Despite somewhat different palaeogeographical settings, the Prague Synform and Nova Scotia exhibit roughly corresponding stratigraphy and a similar three-fold pattern to the late Aeronian positive $\delta^{13}C_{org}$ excursion.

The late Aeronian sedimentary record preserved in the Prague Synform matches the conception of glacio-eustatically driven changes in Silurian sea-level advocated by Loydell (1998, 2007). The positive $\delta^{13}C_{org}$ excursion is correlative with changes in sedimentation, widespread unconformities and glacial deposits in South America recognized by Grahn & Caputo (1992), Díaz-Martínez & Grahn (2007) and Díaz-Martínez *et al.* (2011).

A basin-wide interval of graptolite-barren calcareous mudstone with an organic carbon content of less than 0.1 % separates the low-diversity uppermost Aeronian fauna of the *rastrum* Zone from the considerably richer assemblage of the *Spirograptus guerichi* Zone in the next black shale. Not only the post-extinction recovery interval, but also the Aeronian/Telychian boundary lie hidden with the graptolite-barren sedimentary rock. Although the GSSP is formally placed between the last appearance datum (LAD) of the brachiopod *Eocoelia intermedia* and FAD of *E. curtisi*, in practice the *guerichi* graptolite Zone is commonly used as the base of the Telychian (e.g. Zalasiewicz *et al.* 2009; Loydell, 2012).

6. Conclusions

(1) The upper Aeronian *Stimulograptus sedgwickii* Biozone of Bouček (1953) and Štorch (1994, 2006) is informally subdivided into lower and upper parts. A new *Lituigraptus rastrum* Biozone is recognized in the upper part of the former *sedgwickii* Zone. The new biozone correlates, in part, with the *Stimulograptus halli* Zone of Loydell (1991*a*) and Zalasiewicz *et al.* (2009). Along with significant refinement of the late Aeronian biostratigraphy, the Radotín tunnel section gave access to a critical interval, which is either oxic and graptolite-barren or absent owing to nondeposition in most other Czech and foreign sections.

(2) Good graptolite control has enabled biostratigraphical correlation and dating of the late Aeronian *sedgwickii* Event of Melchin, Koren' & Štorch (1998), including coeval sedimentary changes and carbon isotope signatures, with a particularly high resolution, previously unavailable at this level. A detailed, quantitative study of graptolite faunal dynamics, coupled with the sedimentary record and $\delta^{13}C_{org}$ data, has provided evidence for the complex and step-wise nature of the late Aeronian graptolite crisis, which extended through the whole *sedgwickii* Zone and well into the *rastrum* Zone. Our results suggest that the rapid increase in the extinction rate of graptolite species started near the end of the *convolutus* Zone and initially was partly balanced by an increased rate of graptolite speciation and/or immigration. This phase coincides with an initial positive shift in $\delta^{13}C_{org}$ values and weakened anoxia in the early *sedgwickii* Zone. Incursion of silty material and a strong $\delta^{13}C_{org}$ positive excursion

suggest that major sea-level drawdown coincided with the middle part of the *sedgwickii* Zone. Environmental perturbations mirrored by the biotic crisis, however, progressed further into the late *sedgwickii* and *rastrum* zones as indicated by minimum species richness and decreasing evenness of the graptolite community. A major drop in evenness post-dated falling species richness but correlates with an abrupt increase in TOC values. A new, although minor, positive shift in $\delta^{13}C_{org}$ values appeared as high as in the lowermost part of the *rastrum* Zone. The resulting carbon isotope curve resembles the multiple, three-fold pattern of the late Aeronian excursion recorded in Nova Scotia by Melchin *et al.* (2011).

(3) The combined biotic, sedimentary, carbon isotope and TOC record of the upper Aeronian succession of the Prague Synform indicates multiple sea-level drawdowns, culminating late in the middle *sedgwickii* Zone, which is consistent with the glacio-eustatic models proposed by Caputo (1998), Loydell (1998) and Melchin & Holmden (2006).

(4) Mature, ecologically well-balanced, high-diversity graptolite assemblages reappear in the lowermost Telychian *linnaei* (or *guerichi*) Zone in the Prague Synform. The recovery interval is obscured, along with the Aeronian/Telychian boundary itself, in the graptolite-barren oxic mudstone that separates the black shales of the *rastrum* and *linnaei* zones.

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References

BJERRESKOV, M. 1975. Llandoverian and Wenlockian graptolites from Bornholm. *Fossils and Strata* **8**, 1–94.

BOUČEK, B. 1930. O stratigrafických poměrech pásma eα “kolonie Lapworth” u Zdic. *Časopis Národního Muzea* **104**, 88–97.

BOUČEK, B. 1934. Bemerkungen zur Stratigraphie des böhmischen Gotlandien und seinen Faziesverhältnissen. *Zentralblatt für Geologie und Paläontologie, Abt. B* **11**, 477–94.

BOUČEK, B. 1953. Biostratigraphy, development and correlation of the Želkovice and Motol Beds of the Silurian of Bohemia. *Sborník Ústředního ústavu geologického, Oddil Paleontologický* **20**, 421–84.

CAPUTO, M. V. 1998. Ordovician–Silurian glaciations and global sea-level changes. In *Silurian Cycles: Linkages of Dynamic Processes in the Atmosphere and Oceans* (eds E. Landing & M. E. Johnson), pp. 15–25. New York State Museum Bulletin no. 491.

CHEN, X., MELCHIN, M. J., SHEETS, H. D., MITCHELL, C. E. & FAN, J.-X. 2005. Patterns and processes of latest Ordovician graptolite extinction and recovery based on data from South China. *Journal of Paleontology* **79**, 842–61.

CHLUPÁČ, I., HAVLÍČEK, V., KŘÍŽ, J., KUKAL, Z. & ŠTORCH, P. 1998. *Palaeozoic of the Barrandian (Cambrian to Devonian)*. Prague: Czech Geological Survey, 183 pp.

DÍAZ-MARTÍNEZ, E. & GRAHN, Y. 2007. Early Silurian glaciation along the western margin of Gondwana (Peru, Bolivia and northern Argentina): palaeogeographic and dynamic setting. *Palaeogeography, Palaeoclimatology, Palaeoecology* **245**, 62–81.

DÍAZ-MARTÍNEZ, E., VAVRDOVÁ, M., ISAACSON, P. & GRAHN, C. Y. 2011. Early Silurian vs. Late Ordovician glaciation in South America. In *Ordovician of the World* (eds J. C. Gutiérrez-Marco, I. Rábano & D. García-Bellido), pp. 371–8. Cuadernos del Museo Geominero 14. Madrid: Instituto Geológico y Minero de España.

FINNEY, S. C., BERRY, W. B. N., COOPER, J. D., RIPPERDAN, R. L., SWEET, W. C., JACOBSEN, S. R., SOUFIANE, A., ACHAB, A. & NOBLE, P. J. 1999. Late Ordovician mass extinction: a new perspective from stratigraphic sections in central Nevada. *Geology* **27**, 215–18.

GRAHN, Y. & CAPUTO, M. V. 1992. Early Silurian glaciations in Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* **99**, 1–15.

GUTIÉRREZ-MARCO, J. C. & ŠTORCH, P. 1998. Graptolite biostratigraphy of the lower Silurian (Llandovery) shelf deposits of the Western Iberian Cordillera, Spain. *Geological Magazine* **135**, 71–92.

HAMMER, Ø., HARPER, D. A. T., & RYAN, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* **4**(1), 9 pp.

HAVLÍČEK, V. 1977. Brachiopods of the Order Orthida in Czechoslovakia. *Rozpravy Ústředního Ústavu geologického* **44**, 1–327.

HUTT, J. E. 1974. The Llandovery graptolites of the English Lake District. Part 1. *Monograph of the Palaeontographical Society* **128**(540), 1–56.

JAEGER, H. 1991. Neue Standard-Graptolithenzonenfolge nach der “Grossen Krise” an der Wenlock/Ludlow Grenze (Silur). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **182**, 303–54.

JAEGER, H. & ROBARDET, M. 1979. Le Silurien et le Devonien basal dans le Nord de la Province de Séville (Espagne). *Géobios* **12**, 687–714.

JOHNSON, M. E. 1996. Stable cratonic sequences and a standard for Silurian eustasy. In *Paleozoic Sequence Stratigraphy: Views From the North American Craton* (eds B. J. Witzke, G. A. Ludvigson & J. Day), pp. 203–11. Geological Society of America Special Paper, no. 306.

JONES, O. T. & PUGH, W. J. 1916. The geology of the district around Machynlleth and the Llyfnant Valley. *Quarterly Journal of the Geological Society of London* **71**, 343–85.

KALJO, D. & MARTMA, T. 2000. Carbon isotopic composition of Llandovery rocks (East Baltic Silurian) with environmental interpretation. *Proceedings of the Estonian Academy of Sciences, Geology* **49**, 267–83.

KALJO, D., MARTMA, T., MÄNNIK, P. & VIIRA, V. 2003. Implications of Gondwana glaciations in the Baltic late Ordovician and Silurian and a carbon isotopic test of environmental cyclicity. *Bulletin de la Société Géologique de France* **174**, 59–66.

KOREN’, T. N. 1987. Graptolite dynamics in Silurian and Devonian time. *Bulletin of the Geological Society of Denmark* **35**, 149–59.

KOREN’, T. N. 1991*a*. Evolutionary crisis of the Ashgill graptolites. In *Advances in Ordovician Geology* (eds C. R. Barnes & S. H. Williams), pp. 157–64. Geological Survey of Canada, Paper 90–9.

Koren’, T. N. 1991*b*. The *lundgreni* extinction event in central Asia and its bearing on graptolite biochronology within the Homerian. *Proceedings of the Estonian Academy of Science, Geology* **40**, 74–8.

Koren’, T. N. 1993. Main event levels in the evolution of the Ludlow graptolites. *Stratigraphy, Geological Correlation* **1**, 44–52 [in Russian].

Kraft, J. 1982. Dendroid graptolites of Llandoverian age from Hýskov near Beroun (Barrandian). *Sborník Geologických věd, Paleontologie* **25**, 83–95.

Kříž, J. 1975. Revision of the Lower Silurian stratigraphy in central Bohemia. *Věstník Ústředního Ústavu Geologického* **50**, 275–83.

Lapworth, C. 1878. The Moffat Series. *Quarterly Journal of the Geological Society of London* **34**, 240–346.

Lécuyer, C. & Paris, F. 1997. Variability in the δ^{13}C of lower Palaeozoic palynomorphs: implications for the interpretation of ancient marine sediments. *Chemical Geology* **138**, 161–70.

Leggett, J. K., McKerrow, W. S., Cocks, L. R. M. & Rickards, R. B. 1981. Periodicity in the early Palaeozoic marine realm. *Journal of the Geological Society, London* **138**, 139–56.

Lenz, A. C. 1993. Late Wenlock-Ludlow (Silurian) graptolite extinction, evolution, and biostratigraphy: perspectives from Arctic Canada. *Canadian Journal of Earth Sciences* **30**, 491–8.

Lenz, A. C., Noble, P. J., Masiak, M., Poulson, S. R. & Kozlowska, A. 2006. The lundgreni Extinction Event: integration of paleontological and geochemical data from Arctic Canada. *GFF* **128**, 153–8.

Loydell, D. K. 1991*a*. The biostratigraphy and formational relationships of the upper Aeronian and lower Telychian (Llandovery, Silurian) formations of western mid-Wales. *Geological Journal* **26**, 209–44.

Loydell, D. K. 1991*b*. Dob’s Linn – the type locality of the Telychian (Upper Llandovery) *Rastrites maximus* Biozone? *Newsletters on Stratigraphy* **25**, 155–61.

Loydell, D. K. 1992. Upper Aeronian and lower Telychian (Llandovery) graptolites from western Mid-Wales, Part 1. *Monograph of the Palaeontographical Society* **146**(589), 1–55.

Loydell, D. K. 1993. Upper Aeronian and lower Telychian (Llandovery) graptolites from western Mid-Wales, Part 2. *Monograph of the Palaeontographical Society* **147**(592), 55–180.

Loydell, D. K. 1994. Early Telychian changes in graptoloid diversity and sea level. *Geological Journal* **29**, 355–68.

Loydell, D. K. 1998. Early Silurian sea-level changes. *Geological Magazine* **135**, 447–71.

Loydell, D. K. 2007. Early Silurian positive δ^{13}C excursions and their relationship to glaciations, sea-level changes and extinction events. *Geological Journal* **42**, 531–46.

Loydell, D. K. 2012. Graptolite biozone correlation charts. *Geological Magazine* **149**, 124–32.

Melchin, M. J. 1994. Graptolite extinction at the Llandovery-Wenlock boundary. *Lethaia* **27**, 285–90.

Melchin, M. J. 2007. Biostratigraphic and paleobiogeographic significance of some Aeronian (Lower Silurian) graptolites from the Arisaig Group, Nova Scotia, Canada. *Acta Palaeontologica Sinica* **46** (Suppl.), 311–9.

Melchin, M. J. & Holmden, C. 2006. Carbon isotope chemostratigraphy of the Llandovery in Arctic Canada: implications for global correlation and sea-level change. *GFF* **128**, 173–80.

Melchin, M. J., Koren’, T. N. & Štorch, P. 1998. Global diversity and survivorship patterns of Silurian graptoloids. In *Silurian Cycles: Linkages of Dynamic Processes in the Atmosphere and Oceans* (eds E. Landing & M. E. Johnson), pp. 165–82. New York State Museum Bulletin 491.

Melchin, M. J., MacRae, K.-D., Frýda, J., Štorch, P. & Bullock, P. 2011. A multiple carbon isotope excursion in the upper Aeronian *Stimulograptus sedgwickii* Biozone. In *Siluria Revisited: Programme and Abstracts, Meeting of the International Subcommission on Silurian Stratigraphy, Ludlow, England, July 10–15, 2011* (ed. D. Loydell), 46 pp.

Melchin, M. J. & Mitchell, C. E. 1991. Late Ordovician extinction in the Graptoloidea. In *Advances in Ordovician Geology* (eds C. R. Barnes & S. H. Williams), pp. 143–56. Geological Survey of Canada, Paper 90–9.

Nicholson, H. A. 1868. On the graptolites of the Coniston Flags; with notes on the British species of the genus Graptolites. *Quarterly Journal of the Geological Society of London* **24**, 521–45.

Pannell, C. L., Clarkson, E. N. K. & Zalasiewicz, J. 2006. Fine-scale biostratigraphy within the *Stimulograptus sedgwickii* Zone (Silurian: Llandovery) at Dob’s Linn, Southern Scotland. *Scottish Journal of Geology* **42**, 59–64.

Portlock, J. E. 1843. *Report on the Geology of the Country of Londonderry, and Parts of Tyrone and Fermanagh*. Dublin, London, 774 pp.

Přibyl, A. & Münch, A. 1943. Revise středoevropských zástupců rodu *Demirastrites* Eisel. *Rozpravy České Akademie věd a Umění, Třída II*, **51**(31), 1–29.

Rickards, R. B. 1970. The Llandovery (Silurian) graptolites of the Howgill Fells, Northern England. *Monograph of the Palaeontographical Society* **123**(524), 1–108.

Rickards, R. B. 1976. The sequence of Silurian graptolite zones in the British Isles. *Geological Journal* **11**, 153–88.

Schauer, M. 1967. Biostratigraphie und Taxionomie von *Rastrites* (Pterobranchia, Graptolithina) aus dem anstehenden Silur Ostthüringens und des Vogtlandes. *Freiberger Forschungshefte, Reihe C* **213**, 171–99.

Schauer, M. 1971. Biostratigraphie und Taxionomie des tieferen Silurs unter besonderer Berücksichtigung der tektonischen Deformation. *Freiberger Forschungshefte, Reihe C* **373**, 1–185.

Schieber, J. 2003. Simple gifts and buried treasures – implications of finding bioturbation and erosion surfaces in black shales. *The Sedimentary Record* **1**(2), 4–8.

Šnajdr, M. 1978. Llandoverian trilobites from Hýskov (Barrandian area). *Sborník geologických věd, Paleontologie* **21**, 7–47.

Štorch, P. 1994. Graptolite biostratigraphy of the Lower Silurian (Llandovery and Wenlock) of Bohemia. *Geological Journal* **29**, 137–65.

Štorch, P. 1995. Biotic crises and post-crisis recoveries recorded by Silurian planktonic graptolite faunas of the Barrandian area (Czech Republic). In *Evolution and Extinctions* (eds P. Čejchan, J. Hladil & P. Štorch), 59–70. *Geolines* **3**.

Štorch, P. 1998. Graptolites of the *Pribylograptus leptotheca* and *Lituigraptus convolutus* biozones of Tmaň (Silurian, Czech Republic). *Journal of the Czech Geological Society* **43**, 209–72.

Štorch, P. 2001. Graptolites, stratigraphy and depositional setting of the middle Llandovery (Silurian) volcanic-carbonate facies at Hýskov (Barrandian area, Czech

Republic). *Bulletin of the Czech Geological Survey* **76**, 55–76.

Štorch, P. 2006. Facies development, depositional settings and sequence stratigraphy across the Ordovician-Silurian boundary: a new perspective from the Barrandian area of the Czech Republic. *Geological Journal* **41**, 163–92.

Štorch, P., Černý, J., Bohátka, J. & Melichar, R. 2009. Ražba tunelů silničního obchvatu Prahy mezi Lochkovem a Radotínem – výsledky geologicko-paleontologického výzkumu. *Český Kras* **35**, 5–13 [In Czech with English résumé].

Štorch, P., Gutiérrez-Marco, J. C., Sarmiento, G. N. & Rábano, I. 1998. Upper Ordovician and Lower Silurian of Corral de Calatrava, southern part of the Central Iberian Zone. In *Proceedings of the Sixth International Graptolite Conference of the GWG (IPA) and the SW Iberia Field Meeting 1998 of the International Subcommission on Silurian Stratigraphy (ICS-IUGS)* (eds J. C. Gutiérrez-Marco & I. Rábano), pp. 319–25. *Temas Gológico-Mineros ITGE* **23**.

Štorch, P., & Massa, D. 2003. Biostratigraphy, correlation, environmental and biogeographic interpretation of the lower Silurian graptolite faunas of Libya. In *The Geology of Northwest Libya*, Vol. 1 (eds M. J. Salem & K. M. Oun), pp. 237–51.

Štorch, P. & Massa, D. 2006. The mid-Llandovery (Aeronian) graptolite fauna of western Murzuq Basin and Al Qarqaf Arch (south-western Libya). *Palaeontology* **49**, 83–112.

Štorch, P., Mitchell, C. E., Finney, S. C. & Melchin, M. J. 2011. Uppermost Ordovician (upper Katian–Hirnantian) graptolites of north-central Nevada, USA. *Bulletin of Geosciences* **86**, 301–86.

Toghill, P. 1968. The graptolite assemblages and zones of the Birkhill Shales (Lower Silurian) at Dob's Linn. *Palaeontology* **11**, 654–68.

Törnquist, S. L. 1907. Observations on the genus *Rastrites* and some allied species of *Monograptus*. *Lunds Universitets Arsskrifter, Afd. 2* **3**(5), 1–22.

Urbanek, A. 1993. Biotic crises in the history of upper Silurian graptoloids: a palaeobiological model. *Historical Biology* **7**, 29–50.

Williams, M., Zalasiewicz, J., Rushton, A. W. A., Loydell, D. K. & Barnes, R. P. 2003. A new, stratigraphically significant *Torquigraptus* species (Silurian graptolite) from the Southern Uplands Terrane. *Scottish Journal of Geology* **39**, 17–28.

Zalasiewicz, J. A., Taylor, L., Rushton, W. A., Loydell, D. K., Rickards, R. B. & Williams, M. 2009. Graptolites in British stratigraphy. *Geological Magazine* **146**, 785–850.