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The graptolite, conodont and sedimentary record through the late Ludlow Kozlowskii Event (Silurian) in the shale-dominated succession of Bohemia

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Abstract – The shale-dominated hemipelagic succession exposed in the southwestern part of the Prague Synform preserves the most complete Ludfordian graptolite record so far encountered from peri-Gondwanan Europe. Four graptolite biozones – the *Neocucullograptus inexpectatus*, *Nc. kozlowskii*, *Pseudomonoclimacis latilobus–Slovinograptus balticus* and *Pristiograptus fragmentalis* biozones – are recognized in the middle and late Ludfordian, between the *Bohemograptus tenuis* Biozone and the base of the Pridoli Series. Conodont occurrences are restricted to scattered limestone beds, but enable tentative integration of the graptolite and conodont biozonal schemes. Particular attention was paid to faunal and sedimentary changes and the carbon isotope record across the middle Ludfordian Kozlowskii extinction Event. The Kozlowskii Event caused the almost simultaneous extinction of graptolites with ventrally curved rhabdosomes. The genera *Bohemograptus*, *Polonograptus* and *Neocucullograptus*, along with *Pseudomonoclimacis dalejensis*, disappeared from the fossil record. The offshore conodont fauna recorded in the section was not strongly affected and similarly the pelagic orthocerids and nektonic *Ceratiocaris* passed unaffected through the extinction interval. The abundant and widespread pelagic myodocopid ostracod *Entomis*, however, became extinct. The late Ludfordian graptolite recovery gave origin to a novel fauna of Pridoli type from taxa that emerged or just reappeared above the Kozlowskii crisis. In Všeradice and elsewhere in the Prague Synform, the recovery, manifested by the appearance of *Pseudomonoclimacis latilobus* and *Slovinograptus balticus*, closely postdates the end of the isotope excursion but pre-dates the first appearance of the conodont index '*Ozarkodina*' *snajdri*. Here the graptolite recovery was delayed relative to the recovery of the benthic fauna. A canalized intraformational limestone conglomerate corresponds with a gap in the sedimentary record above the Kozlowskii extinction and just below the graptolite recovery. The benthic faunas from the conglomerate matrix and pebbles permit correlation with the shallower part of the basin indicating a distinct fall in sea-level. The present data demonstrate the coincidence of the graptolite crisis with benthic faunal change and eustatic fall in sea-level manifested by facies change and the carbon isotope excursion. *Polonograptus chlupaci* sp. nov., from the *Nc. kozlowskii* Biozone, is described and several other graptolite taxa are redescribed.

Keywords: graptolites, conodonts, Silurian, biostratigraphy, Kozlowskii Event, extinction, peri-Gondwana.

1. Introduction

The Silurian was long considered to have been a period with a relatively stable greenhouse climate, devoid of significant extinction events (see Holland, 1991 and Calner, 2008 for summary). This view of an 'idyllic Silurian' rapidly changed in the 1990s. Prominent extinction events were described among graptolites (Jaeger, 1991; Koren', 1993; Urbanek, 1993; Loydell, 1994; Štorch, 1995*a,b*; Melchin, Koren' & Štorch, 1998) and conodonts (Jeppsson, 1990, 1998; Jeppsson & Aldridge, 2000). Later studies on carbon isotopes revealed that some extinctions correlate approximately with positive carbon isotope excursions and may have resulted from extraordinary perturbations in the carbon-ocean cycle (Munnecke, Samtleben & Bickert, 2003; Lehnert *et al.* 2007*b*; Calner, 2008). In addition, oxygen isotopes suggest dramatic fluctuations in water temperature during the Silurian, indicating recurrent periods with an icehouse climate (Lehnert *et al.* 2007*a*; Calner, 2008; Eriksson & Calner, 2008). Various climatic and oceanographic models have been proposed to explain extinctions and changes in chemistry in the Silurian oceans (Jeppsson, 1990; Bickert *et al.* 1997; Samtleben, Munnecke & Bickert, 2000). Nevertheless, there is as yet no generally accepted explanation (see discussion in Loydell, Jeppsson & Aldridge, 2001 and Loydell, 2007). Particular debates have been devoted to high-resolution correlation. The correlation of graptolite extinctions in deeper water shale facies with those of conodonts in shallow water limestone facies, combined with correlation between different

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palaeogeographical settings, i.e. higher and lower latitudes, is a difficult exercise. The timing, extent and selectivity of extinction in benthic groups are still poorly known (Talent *et al*. 1993; Kříž, 1998, 1999*a*, 2010*a,b*; Manda & Kříž, 2006; Eriksson, Nilsson & Jeppsson, 2009). The question has been posed (Loydell, Jeppsson & Aldridge, 2001; Manda & Kříž, 2006; Loydell, 2007; Manda & Frýda, 2010): are extinctions in graptolites, conodonts and benthos coincident or do they represent separate events? Loydell (2007) presented evidence to indicate that the Wenlock graptolite and conodont extinction events are not coincident, but for some other events, so far no adequate evidence has been provided.

The middle Ludfordian change in marine faunas is an example of such an extinction event. The Kozlowskii Event is considered to be one of the most significant graptolite extinction events, and has been recorded from Baltica, central-Asian terranes and peri-Gondwanan Bohemia (Koren', 1993; Urbanek, 1993; Štorch, 1995*a,b*; Manda & Kříž, 2006). A conodont extinction event, known as the Lau Event in Baltica, Laurentia and East Gondwana (Australia), is roughly coincident with the Kozlowskii Event, but detailed comparison is lacking (Jeppsson, 1990; Eriksson & Calner, 2008). A positive carbon isotope excursion, the largest in the Phanerozoic, has been identified close to both the Lau conodont extinction Event (Samtleben, Munnecke & Bickert, 2000; Calner & Eriksson, 2006; Stricanne, Munnecke & Pross, 2006; Kaljo *et al*. 2007) and the Kozlowskii graptolite extinction (Lehnert *et al*. 2007*b*). In Bohemia, the Kozlowskii Event is associated with prominent extinctions among benthic faunas (Manda & Kříž, 2006). Oxygen isotopes suggest progressive cooling accompanying an icehouse period around the time of the extinction (for details see Lehnert *et al*. 2007*a*).

The Prague Synform (i.e. Barrandian area) of central Bohemia has long been considered a classic area for Silurian graptolite biostratigraphy and a reference area for correlation of the Early Palaeozoic of northwestern peri-Gondwana. Many graptolite biozones and index species were first distinguished and described from this area. The Llandovery, Wenlock and lower Ludlow sedimentary rock sequence, composed largely of graptolite-bearing shales, provides an ideal opportunity for detailed study of the graptolite succession (Bouček, 1953; Přibyl, 1983; Štorch, 1994, 2006 and further references therein). Similarly, the Pridoli succession, composed of limestones interbedded with shales, has yielded graptolite assemblages, permitting its division based upon graptolites (Přibyl, 1940; Kříž *et al*. 1986). In the limestone-dominated upper Ludlow strata of the Prague Synform, however, the graptolite biostratigraphy remained of rather poor resolution. The graptolite biozones established by Bouček (1936) and revised by Přibyl (1983) were defined inadequately and, in particular, there were no published descriptions of sections that had been measured and sampled in detail. Comparison between graptolite taxa based upon Bohemian type material preserved as internal moulds in skeletal limestones and specimens flattened in shales was inadequate and resulted in some confusion in stratigraphic correlation. Some of these graptolite taxa, described by Bouček (1931, 1936) and Přibyl (1943, 1983), are in need of revision.

The most detailed late Ludlow, Ludfordian, graptolite biozonal scheme was elaborated in Poland (Urbanek & Teller, 1997 and references therein) and partly applied in other parts of the Eastern European Platform (such as Podolia in Ukraine, Belarus and Latvia). Koren' & Sujarkova (1997, 2004) introduced a different biozonation in Central Asia. The graptolites collected from Kosov Quarry near Beroun (Štorch, 1995*a*) and from the present Všeradice section enable correlation with both the Eastern European Platform and Central Asia.

In this paper, the shale-dominated succession comprising the middle Ludfordian Kozlowskii Event and post-extinction recovery is described for the first time both from Bohemia and peri-Gondwana. The Všeradice section was exposed in trenches and measured and sampled bed by bed for graptolites. Isolated limestone beds were sampled for conodonts. The sedimentary succession was examined in detail and the carbon isotope record analysed in order to evaluate the depositional environment of the graptolite-bearing rocks and to recognize possible gaps in sedimentation. Scattered shelly faunas recovered from shales and some limestone beds enabled correlation between abundant benthic faunas of the limestone-dominated facies widespread in other Bohemian sections and the widely applicable graptolite biozones recognized herein.

2. Všeradice section

In the Prague Synform, the middle and upper Ludfordian succession usually comprises carbonate rocks with poorly preserved and rare graptolites (Bouček, 1936; Kříž, 1992). The relatively deeper water, oxygen-depleted hemipelagic shale facies, potentially rich in diverse graptolites, is restricted to the southwestern closure and southeastern flank of the Prague Synform. There are only a few poorly exposed sections in the shale-dominated area, usually insufficient for detailed investigations (Horný, 1955, 1960). The single exception is the section along the field track near Všeradice village. This area is regarded as the deepest preserved part of the basin infill (Horný, 1960; Kříž, 1991, 1992).

2.a. Location and previous research

The Všeradice section is located on a gentle, S-facing slope along a field track running NNW from the Bykoš–Všeradice road, NW from Všeradice village (Fig. 1). Rather discontinuous exposures and subcrops may be traced along the field track over a length of about 200 m. Close to the summit, bedrock becomes buried under

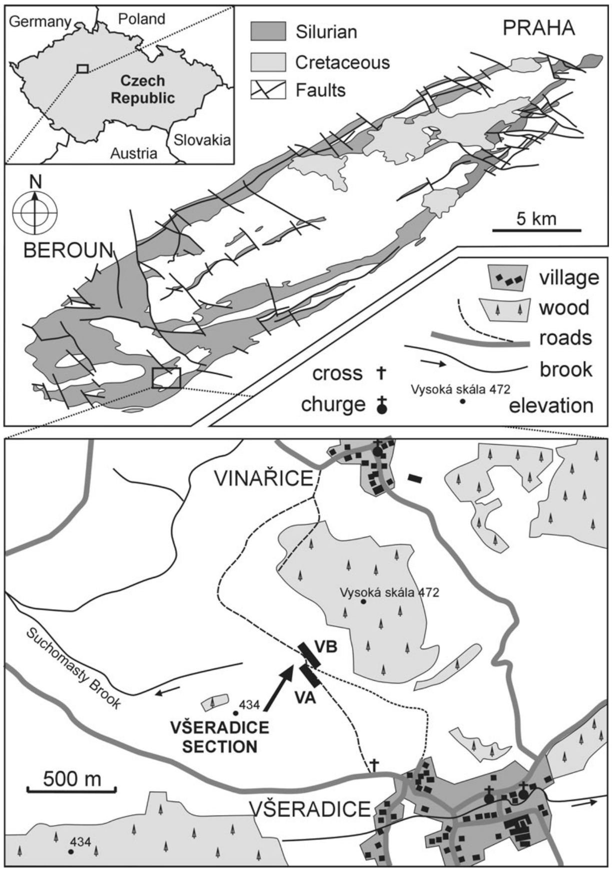

Figure 1. Position of the area studied within the Czech Republic. (a) Distribution of the Silurian rocks of the Prague Synform; and (b) detailed position of the Všeradice section on a topographic map.

thick drift deposits. The section represents the shale-dominated, relatively offshore facies of the Silurian succession in the Prague Synform, beginning with the middle Wenlock and terminating with the lower part of the Pridoli Series. Sedimentation here was little influenced by syn-sedimentary basalt volcanic activity, which left a significant record in most other Silurian sections of Bohemia (see e.g. Kříž *in* Chlupáč *et al.* 1998 for instance).

The first note on this important section was published by Horný (1960). Much later, Kříž (1992) presented a more detailed, but still incomplete log. His section started from marly shales high in the Homerian *Cyrtograptus lundgreni* Biozone and terminated with the middle Ludfordian intraformational conglomerate (bed no. 13 of this paper). Shale beds with the ostracod *Entomis migrans* and some bivalves, encountered just below the conglomerate, Kříž (1992) referred to the '*B. bohemicus tenuis* Interzone'. Kříž *et al.* (1993) and later Kozłowska-Dawidziuk, Lenz & Štorch (2001) examined the uppermost Wenlock (upper Homerian) part of the section with particular emphasis on the Lundgreni Event and post-extinction recovery. Piras (2006; unpub. Ph.D. thesis, Univ. degli Studi di Modena e Reggio Emilia, 2006) studied the lower Gorstian beds comprising the *Neodiversograptus nilssoni* and *Lobograptus progenitor* graptolite biozones. Budil, Collette & Manda (2010) studied the phyllocarid fauna from the lower Ludfordian.

In late 2008 and early 2009, excavations were conducted to expose the supposedly graptolite-rich, shale-dominated section through the upper Ludlow strata. Our data came from two up to 2.5 m deep trenches VA and VB, excavated on both sides of the field track (Fig. 1). Trench VA and the upper part of trench VB exposed a *c*. 24 m thick middle and upper Ludfordian succession up to the base of the Pridoli Series.

2.b. Material and methods

The shale-dominated Ludfordian was sampled for graptolites in a similar way to the late Homerian interval studied by Kozłowska-Dawidziuk, Lenz & Štorch (2001). Isolated limestone beds and tuffitic intercalations enabled division of the 24 m thick succession into 37 arbitrary units of different stratigraphic thickness (beds 1–37 in ascending order, see Fig. 2). Shaly beds were further subdivided into 10–60 cm thick sub-units. Each sub-unit was sampled bed by bed down the section and all of its fossil samples were placed in the same sample bag(s). The majority of these sampling intervals were about 30 cm thick. Many intervals were rich in graptolites; some others were poor or barren. Every graptolite, at least tentatively determinable, was collected from the rock volume of about 0.03 m^3. The lower part of the section exposed by trench VB (see Fig. 2) lacks the arbitrary subdivision, but fossils were collected in the same manner, in intervals (sub-units) of similar thickness. Only a few graptolites were found in the limestone and tuffitic beds.

The carbon isotope record of upper Silurian carbonates coming from deeper water environments of the Prague Basin has never been studied, in contrast to the carbonates from shallower environments (Lehnert *et al.* 2007*b*). The carbonates of the Všeradice section were sampled for determination of $\delta^{13}C_{carb}$ isotope evolution through the late Ludlow Kozlowskii Event. The isotopic composition of organic carbon from shales occurring between the carbonate beds was not studied owing to the relatively high degree of weathering. The carbon isotope sampling of the Všeradice section (Fig. 2) started about 8.5 m below the late Ludlow Kozlowskii Event. The highest sample was collected from lowermost Pridoli beds (about 2 m above the first appearance (FA) of *Neocolonograptus parultimus*). Fifteen samples were analysed for $\delta^{13}C$: 12 samples were taken from the Ludlow part of the section and 3 samples from the lowermost Pridoli. A few milligrams of rock powder (preferably micrite) were recovered with a dental drill from rock samples or polished slabs. Carbonate samples were decomposed in a vacuum by 100 % phosphoric acid at a temperature of 25 °C. The carbon and oxygen isotopic composition of the released CO_2 was measured with a Finnigan Mat 251 mass spectrometer. All values are reported in ‰ relative to V-PDB (Vienna Pee Dee Belemnite) by assigning a $\delta^{13}C$

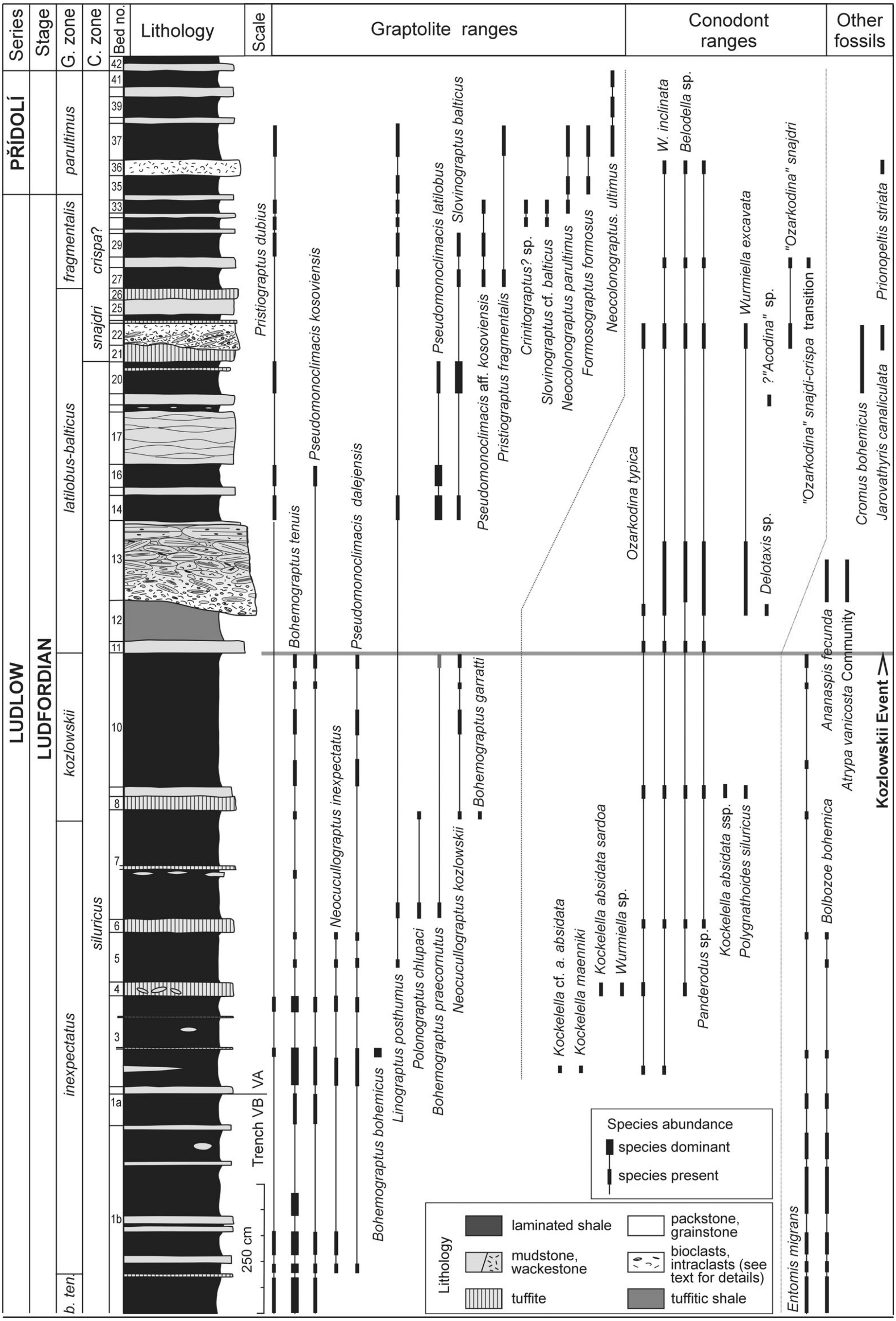

Figure 2. Chronostratigraphy and lithology of the Všeradice section. Ranges of graptolites, conodonts and selected other fossils are included.

value of +1.95 ‰ and a $\delta^{18}O$ value of 2.20 ‰ to NSB 19. Accuracy and precision were controlled by replicate measurements of laboratory standards and were better than ± 0.1 ‰ for both carbon and oxygen isotopes.

Conodont samples were collected from the majority of limestone beds and nodules uncovered in both trenches across the interval from Ludfordian to the lowermost Pridoli. A total of 28 samples of average weight between 3 and 5.5 kg was taken mostly from the entire thickness of each limestone bed (bulk samples). The rock was broken into approximately 5 cm sized pieces and processed using standard acid techniques with 10–15 % acetic acid. Residues were washed through calibrated double sieves of 2.24 mm (upper) and 90 µm (lower) meshes. Wet residues were washed with acetone and dried. Dried, relatively voluminous residues (of up to 250 ml), with a prevalence of pyrite, goethite and complex silicates (e.g. nagashimalite, macfallite) were concentrated using the heavy liquids diiodomethane (density 3.3 g/cm^3) and tribromomethane. Conodonts were obtained from only nine of the limestone beds; no conodonts were extracted from nodules. The conodont material was documented directly in aluminium cells using a Leica D160 digital camera and a Leica MZ7s stereomicroscope, and scanning electron microscope (SEM) images of selected conodont elements (coated with gold) were made by using a Cameca SX100 electron microscope.

Graptolites are housed in the collection of Petr Štorch in the Czech Geological Survey. Non-graptolite macrofauna is deposited in the collection of Štěpán Manda in the Czech Geological Survey (unnumbered specimens in locality collection, prefix SM Všeradice section). The conodont material is temporarily stored in the collection of Ladislav Slavík at the Institute of Geology, Academy of Sciences, Czech Republic and will be later deposited as a part of a larger collection in the National Museum, Prague.

2.c. Sedimentary succession, benthic fauna and depositional environment

The lower part of the section consists of light grey laminated calcareous shale (beds 1–10, *Bohemograptus tenuis–Neocucullograptus kozlowskii* biozones). Graptolites and pelagic ostracods (*Entomis migrans* Barrande, *Bolbozoe bohemica* Barrande) are the most common faunal elements, but their abundance is strongly variable. Pelagic orthocerids (*Parakionoceras originale* Barrande, *Michelinoceras michelini* Barrande, *Kopaninoceras* sp., *Arionoceras* sp.) and the phyllocarid *Ceratiocaris* sp. occur only in some beds. Flattened smooth atrypids are present occasionally, but on some bedding planes they occur abundantly. Bivalves are rather rare: *Cardiola docens* Barrande, *C.* aff. *docens* Barrande, *C.* cf. *pectinata* Barrande, *C.* aff. *foma* Barrande, *Butovicela migrans* (Barrande) and *Tenka aspirans* (Barrande). Shale bed no. 3 yielded the trilobite *Cromus beaumonti* Barrande. Up to 20 cm thick beds of grey argillitic, usually laminated, mudstones occur throughout this part of the section. Limestones contain occasional graptolites and cephalopods; in one case graptolites were found to be oriented by currents and wrapped around a cephalopod shell lying obliquely to the bedding plane – a so-called ‘comet’ (Ferretti & Kříž, 1995). Limestone nodules rich in pyrite, with a maximum diameter of 20 cm occur sporadically. Thin, 1–3 mm thick lenticular laminae of mudstone are common in the shales. Seven beds of yellow-grey, upward fining tuffites, 5 to 25 cm thick, were found in this part of the section. Rare trilobite debris (*Otarion* sp. and unidentified taxa) was found in some tuffites. In addition, tuffitic bed no. 4 contains close to its base small rounded intraclasts of rusty cephalopod packstone with small cephalopod fragments (*Michelinoceras michelini*, *Pseudocycloceras* sp., *Kopaninoceras* sp., *Ophioceras simplex* Barrande), common disarticulated bivalves (*Cardiola docens*) and rare rhynchonellid brachiopods.

The shale-dominated sequence suggests an offshore hemipelagic environment. Some light coloured laminae contain brachiopods and bivalves, which indicates the occasional activity of weak bottom currents ventilating the otherwise anoxic conditions close to the sea bottom. Deposition of shales was interrupted by that of tuffite layers, which also include skeletal fragments derived from shallow water environments (e.g. intraclasts of cephalopod limestone, trilobite fragments).

The shale-dominated sequence ends with a thin bed of fine-grained mud-wackestone overlain by bioturbated tuffitic shale (bed nos 11 and 12), but no body fossils were found.

The section continues with a large lens, up to 160 cm thick, formed of inverse graded intraformational conglomerate (bed no. 13). The matrix consists of coarse, light grey crinoidal grainstone, which passes upward into fine-grained wackestone (Fig. 3). Crinoid ossicles are abraded only in the lower part. Brachiopods are usually disarticulated, but well preserved including fine growth structures in shells. *Atrypa evenida* Havlíček is the most common: from 126 collected shells, 72 are ventral valves, 53 are dorsal valves, and only one shell is articulated (for a complete list of brachiopods see Kříž, 1992). Fragments of trilobites, *Ananaspis fecunda* (Barrande), proetids, odontopleurids, corals and gastropods are also present. Pebbles are usually rounded; their abundance and size (maximum diameter is about 25 cm) increase from the base of the bed upward. Pebbles include four lithological types that differ also in their fossil content: (1) small rounded pebbles of dark grey wackestone with cephalopods and the bivalve *Cheiopteria glabra* Goldfuss (which indicates a latest *Nc. kozlowskii* Biozone age; see Kříž, 1999*a*; Manda & Kříž, 2006); (2) rounded pebbles of brachiopod-trilobite wackestone with the trilobite *Ananaspis fecunda*; (3) small angular intraclasts of rusty fine-grained packstone with ostracods, the brachiopod *Atrypa* sp. and trilobite *A. fecunda*; (4) intraclasts that represent probably exhumed limestone nodules

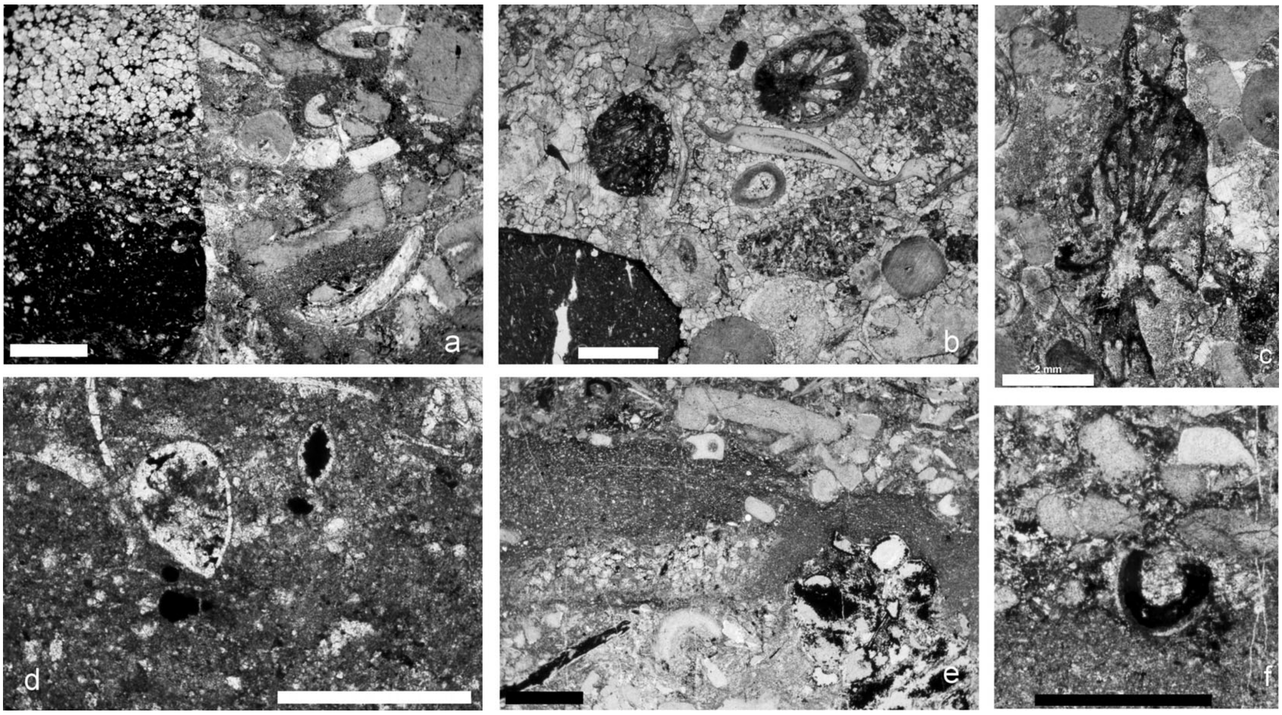

Figure 3. Microfacies of the carbonate gravity deposits from the Všeradice section. (a) Coarse-grained grainstone with an intraclast of dark grey mudstone with dolomite, bed no. 13. (b) Coarse-grained grainstone with crinoids, trilobites and rugose coral, small rounded intraclasts (wackestone with sponges and ostracod fragments and fine-grained wacke-grainstone), bed no. 13. (c) Partly pyritized rugose coral with partly damaged wall preserved in grainstone, bed no. 13. (d) An intraclast of mudstone with ostracods; smaller ostracod is filled with pyrite, bed no. 13. (e) Intraclastic crinoidal grainstone with cohesive intraclasts of shale and a fragment of tabulate coral, bed no. 22. (f) Detail of contact of matrix with cohesive intraclasts, bed no. 22. Scale bars 2 mm, in (d) 0.5 mm.

with *Entomis migrans* (i.e. *Saetograptus linearis–Nc. kozlowskii* Zone in age; see Kříž, 1999*a*). The conglomerates are overlain by an up to 10 cm thick bed of dark grey mudstone with some cracks on the upper bedding plane.

The intraformational conglomerate probably represents a canalized debris flow because it forms large lenses in the shale and shows clear inverse grading (e.g. Einsele, 2000, p. 214). The fauna preserved in the matrix of the conglomerate suggests transport from a nearby shallow water locality.

The overlying sedimentary succession comprises dark grey mudstones (particularly nodular) intercalated with dark grey laminated shale (bed nos 14–20, *Pseudomonoclimacis latilobus–Slovinograptus balticus* Biozone). The shale contains common graptolites and rare cephalopods (e.g. *Parakionoceras originale*, *Michelinoceras michelini*, *Arionoceras* sp.), phyllocarids (*Ceratiocaris* sp.) and a few benthic remains including scolecodonts, brachiopods (*Plectodonta* sp.), smooth ostracods and juvenile gastropods. Higher up a distinct tuffitic bed is present. The tuffite is locally eroded and filled with cross-stratified, rusty, upward fining grainstone with cohesive shale intraclasts (bed nos 21–22). The grainstone contains crinoids, trilobites, corals, ostracods, cephalopods and other fossils (see Table 1). This limestone is overlain by a thin bed of tuffite (bed no. 23) and, higher up, shale (bed no. 24). The succeeding strata comprise a mudstone bed overlain by a tuffitic bed (bed nos 25–26).

The sequence above the intraformational conglomerates was deposited at the margin of a bathymetric high, as indicated by the shales with benthic fauna and limestone beds. The skeletal limestone filling the depressions in the tuffite probably represents storm event deposits with cross-stratification, normal grading and shale intraclasts (see Fig. 3). Brachiopods are usually disarticulated and large brachiopods and trilobites are broken into small fragments (Table 1). The brachiopod assemblage is dominated by the shallow water brachiopod *Kirkidium* sp. accompanied by the rather deeper water *Jarovathyris canaliculata* (see Havlíček & Štorch, 1990); this suggests mixing of two distinct depth-related communities during transport.

The upper part of the studied section (beds 27–43, *Pristiograptus fragmentalis* and *Ne. parultimus–Ne. ultimus* biozones) is developed as calcareous shale and platy argillite mudstone, but the shale dominates. One thin bed (no. 36) of grey, upward fining crinoidal wackestone is present. It contains common, minute fragments of brachiopods (atrypids, orthids, leptaenids and strophomenids), trilobites (*Otarion* sp. and *Prionopeltis striata* Šnajdr) and disarticulated ostracods. Shale beds yielded graptolites and rare pelagic cephalopods. Bed no. 27 contains also pyritized shells of juvenile cephalopods and gastropods. A thin level with accumulations of the flattened atrypid *Lissatrypa* sp. was observed in mudstone bed no. 30.

This part of the succession was deposited during deepening, which corresponds with that interpreted in

Table 1. Fauna and selected taphonomic features recorded in limestone bed no. 22 (late Ludfordian, *Pseudomonoclimacis latilobus–Slovinograptus balticus* Biozone)

Species	S	D	A	C	P	
Lissatrypa postfumida	27	20	7	–	–	
Jarovathyris canaliculata	21	8	13	–	–	D
Tabulata indet.	15					S
Kirkidium sp.	14	14	–	–	–	S
Septatrypa aff. *verna*	11	5	6	–	–	
Atrypa sp.	10	9	1	–	–	S
Bryozoa indet.	9	–	–	–	–	S
Aulacoporida indet.	9	–	–	–	–	S
Rugosa indet. (slender form)	5	–	–	–	–	
Michelinoceras sp.	5	–	–	–	–	D
Janiomya aff. *flexa*	5	5	–	–	–	
Cromus aff. *bohemicus*	5	–	–	–	5	
Treptostomata indet.	3	–	–	–	–	S
Strophomenacea indet.	3	3	–	–	–	
Otarion sp.	3	–	–	3	–	
Orhoria sp.	3	3	–	–	–	
Navispira sp.	3	3	–	–	–	D
Euophalompterus sp.	3	–	–	–	–	S
Cryptophyllus copelandi	3	3	–	–	–	
Salopina sp.	2	2	–	–	–	
Ryckholtia cf. *ryckholti*	2	–	–	–	2	S
Rhynchonellidina indet.	2	2	–	–	–	
Resserella sp.	2	2	–	–	–	
Hyolithes sp.	2	–	–	–	–	
Arionoceras sp.	2	–	–	–	–	D
Pseudocycloceras sp.	1	–	–	–	–	
Plectodonta sp.	1	1	–	–	–	D
Platyceras sp.	1	–	–	–	–	
Orbiculoidea sp.	1	1	–	–	–	
Lyocelia sp.	1	–	1	–	–	
Lingulida indet.	1	1	–	–	–	
Isorthis aff. *tomyris*	1	1	–	–	–	S
Interproetus sp.	1	–	–	1	–	
Cheirurina indet.	1	–	–	1	–	
Harpetida indet.	1	–	–	1	–	
Decoroproetus sp.	1	–	–	1	–	
Ceratiocaris sp.	1	–	–	–	–	D
smooth ostracods	c	c	r	–	–	

Sample weight is *c*. 15 kg. Abbreviations: S – number of specimens; D and A – number of disarticulated/articulated specimens in brachiopods; C and P – numbers of cephalons/pygidia in trilobite remains. S and D mean deeper/shallow-water faunal elements, respectively. c – common; r – rare. This taphocoenosis is composed of two different faunas mixed together in a gravity flow deposit. The respective faunas originated from relatively shallow and deeper slope settings.

other coeval sections of the Prague Synform (Horný, 1955; Kříž *et al.* 1986; Kříž, 1991; Manda & Kříž, 2006). The sparse or absent benthic fauna suggests usually anoxic conditions at the bottom. Bed no. 36, of fine-grained skeletal limestone, probably reflects a storm event as indicated by its sharp base and upward fining. Rounded crinoid debris and small fragments of disarticulated atrypid brachiopods indicate a significant amount of transport.

2.d. Gaps in sedimentation and source area of conglomerates

The Všeradice section is located in the Western Segment (Kříž, 1992) of the Prague Synform. This is characterized by offshore hemipelagic sedimentation throughout the Silurian as indicated by the shale-dominated sequence ranging from the lowest Llandovery to the Ludlow (Horný, 1955, 1960). Common tuffite beds throughout the Ludlow succession indicate nearby volcanic activity and deposition of reworked volcaniclastic material. Tuffites in the upper *Ps. latilobus–Sl. balticus* Biozone are the youngest known manifestation of volcanic activity in the Silurian strata of the Prague Synform, although coeval basalt effusives are unknown. More limestones (wacke-mudstone and gravity deposits) appear in the middle and upper Ludfordian parts of the succession, which is consistent with basinward extension of shallow water sedimentation into the Western Segment of the synform (Horný, 1955, 1960). This proliferation of carbonates is correlatable with the latest Ludlow lowstand well documented in coeval limestone sequences elsewhere in the Prague Synform (Horný, 1955; Kříž, 1991; Kříž *in* Chlupáč *et al.* 1998; Manda & Kříž, 2006). Earlier lowstands (those in the late Wenlock and early Ludfordian) are not distinguishable in the sedimentary log in the Všeradice section and elsewhere in the Western Segment (Horný, 1955, 1960). Kříž (1991) suggested that intense subsidence occurred in this part of the basin in the Ludlow. However, a relatively thin sedimentary succession, including limestones of the uppermost Ludlow, probably indicates reduced accommodation space. Canalized debris-flow deposits indicate the appearance of nearby shallow water environments (although these are not preserved in the rock record) within the Western Segment, which was isolated from the main shallow platforms located further to the north. Although corresponding with the lowstand recorded in coeval limestone strata, eustatic sea-level oscillation cannot explain fully the appearance of this local shallow water area, i.e. a small-scale carbonate domain surrounded by shale deposition. The submarine high was most probably associated with local, synsedimentary uplift. Sea-level drawdown, associated with the middle Ludfordian Kozlowskii and/or Lau Event initiated only a debris flow from the neighbouring submarine high. Slopes were probably relatively steep, as suggested by the exhumed limestone nodules with ostracods in the debris flow. These nodules (but no surrounding matrix) contain fine framboidal dolomite, which directly documents the early diagenetic origin of the dolomite.

The stratigraphically significant shelly fauna preserved in the limestone debris flow (intraformational conglomerate), the lenticular cross-section of the conglomerate body and the much reduced thickness of the post-Kozlowskii Ludfordian indicate prominent erosion and a gap in sedimentation in the Všeradice section, when compared to coeval strata in the limestone-dominated sections of the Prague Synform.

The temporal and spatial extent of the gap connected with these canalized debris-flow deposits is evident from analysis of faunas in the matrix and pebbles (i.e. it spans the interval between the last appearance (LA) of *Nc. kozlowskii* until at least the FA of the index trilobite *A. fecunda*). However, allochthonous fauna from both intraclasts and matrix make correlation with coeval carbonate sequences of the Prague Synform possible (see discussion in Section 3).

2.e. Conodont fauna

The late Silurian conodont biozonation was developed by Walliser (1964), who included the conodont data from the Prague Synform into his first biozonal framework. Schönlaub (*in* Chlupáč, Kříž & Schönlaub, 1980 and *in* Kříž *et al*. 1986) furnished crucial conodont data from sections in the upper Ludlow and Pridoli of the Prague Synform and demonstrated taxon ranges. Schönlaub *in* Kříž *et al*. (1986) made an extensive summary of conodont faunas obtained from samples from numerous sections and localities that were sampled and studied by him or by previous authors. He recognized a succession of Walliser's biozones for the Ludlow and Pridoli: *Ancoradella ploeckensis*, *Polygnathoides siluricus*, *Pedavis latialatus*, '*Ozarkodina*' *snajdri*, '*Oz.*' *crispa* and '*Oz.*' *eosteinhornensis*. The Ludlow part of this biozonation is in use without large changes; the '*Oz.*' *eosteinhornensis sensu stricto* and '*Oz.*' *detorta* biozones suggested for the Pridoli by Jeppsson (1988) are problematic or inapplicable (see discussions in Carls, Slavík & Valenzuela-Ríos, 2007).

The conodont faunas of the Všeradice section (Fig. 4) are studied for the first time in this paper. The conodont sampling was successful only in one third of the samples, which yielded *c*. 350, mostly fragmented conodont elements. The conodont faunas are rather poor regarding taxonomic diversity and are of low abundance in general, with the exception of the intraformational conglomerate (bed no. 13) and grainstone bed no. 22 where the numbers of conodont elements exceed 80. A relatively rich conodont sample was obtained from bed no. 28 with more than 70 conodont elements. The composition of conodont faunas in all samples is well balanced and variable regarding the size of the elements; also the frequent presence of tiny, simple-cone elements suggests that assemblage composition was not strongly affected by hydrodynamic sorting of particles. The depositional characters of some carbonate layers (i.e. intraformational conglomerate, presence of intraclasts and grainstone fillings) described in the previous Sections suggests the likelihood of stratigraphical mixing of conodont elements, but evidence for conodont redeposition was not found.

The preservation of conodonts in samples is good. Apart from long-ranging simple cones (e.g. belodellids, *Panderodus*), the conodont material obtained enables recognition of the following conodont genera: *Delotaxis*, *Kockelella*, *Ozarkodina*, *Polygnathoides* and *Wurmiella*. Owing to fragmentation, some taxonomic assignments are only to generic level, but several stratigraphically important taxa were recognized and enabled delimitation of the *P. siluricus*, '*Oz.*' *snajdri* and '*Oz.*' *crispa* conodont biozones in the middle–upper Ludfordian (see Fig. 4). The stratigraphically lowest evidence for the *P. siluricus* Biozone is the presence of *Kockelella maenniki* Serpagli & Corradini in bed no. 2. This species, erected in Sardinia (Serpagli & Corradini, 1998, 1999), is confined to the lower–middle part of the *P. siluricus* Biozone. Representatives of the genus *Kockelella* were found also in beds nos 4 and 9. Following the reconstruction of the origin and phylogeny of the genus given by Serpagli & Corradini (1999), *Kockelella absidata sardoa* (see Serpagli & Corradini, 1999) found in bed no. 4 ranges into the lower *P. siluricus* Biozone; Pa elements of the long-ranging *Kockelella absidata* group were found in beds nos 2 and 9. The record of *K. absidata* ssp. together with *P. siluricus* points to the highest stratigraphical occurrence of the *K. absidata* group (Branson & Mehl, 1933). The distribution of several taxa of the genus *Kockelella* and their stratigraphic relations within the *P. siluricus* Biozone are shown in Slavík, Kříž & Carls (2010) from the Požáry section.

The interval from bed no. 11 to bed no. 19 yielded mostly representatives of the genus *Wurmiella* (*W. excavata excavata* (Branson & Mehl) and *Wurmiella inclinata* (Rhodes)), and *Ozarkodina typica* Branson & Mehl (= *Hindeodella confluens* Jeppsson). *Oz. typica* particularly shows high intra-specific variability as regards denticulation of the blade, variation in 'cockscomb' structure and proportions of the Pa element (length and width of the unit). The stratigraphical evaluation of the changing morphology of the Pa element of *Oz. typica*, however, requires more material with precise stratigraphical control. The *P. latialatus* Biozone could have been expected to be found within this interval, but there is no direct evidence for this biozone and there is also no proof that the coniform element of *Acodina*? sp. may truly belong to the apparatus of *Pedavis* Klapper & Philip.

The '*Oz.*' *snajdri* Biozone is directly documented by several Pa elements of the name-bearer taxon in bed no. 22. Transition Pa elements between '*Oz.*' *snajdri* and '*Oz.*' *crispa* were obtained from bed no. 28. The element shown in Figure 4r exhibits already a large undulated platform like that seen in typical '*Oz.*' *crispa*, but the termination of the blade within the platform is in question. The taxa overlap considerably stratigraphically; however, '*Oz.*' *snajdri* appears at a lower stratigraphical level in the Prague Synform (Walliser, 1964; Schönlaub *in* Chlupáč, Kříž & Schönlaub, 1980). Accordingly, the base of the '*Oz.*' *crispa* Biozone can be expected to lie close to this stratigraphical level. The generic name of these biozonally diagnostic taxa is placed in quotation marks because of the ambiguity over the generic assignment as explained in Murphy, Valenzuela-Ríos & Carls (2004). Bed no. 36 is the highest bed that yielded conodonts, although these are of no biostratigraphical value, the Pridoli age of this level being indicated by graptolites only.

2.f. Graptolite fauna

Graptolite rhabdosomes are uncommon in this hemipelagic, shale-dominated offshore succession, if compared to the rich early Silurian and even early Ludlow

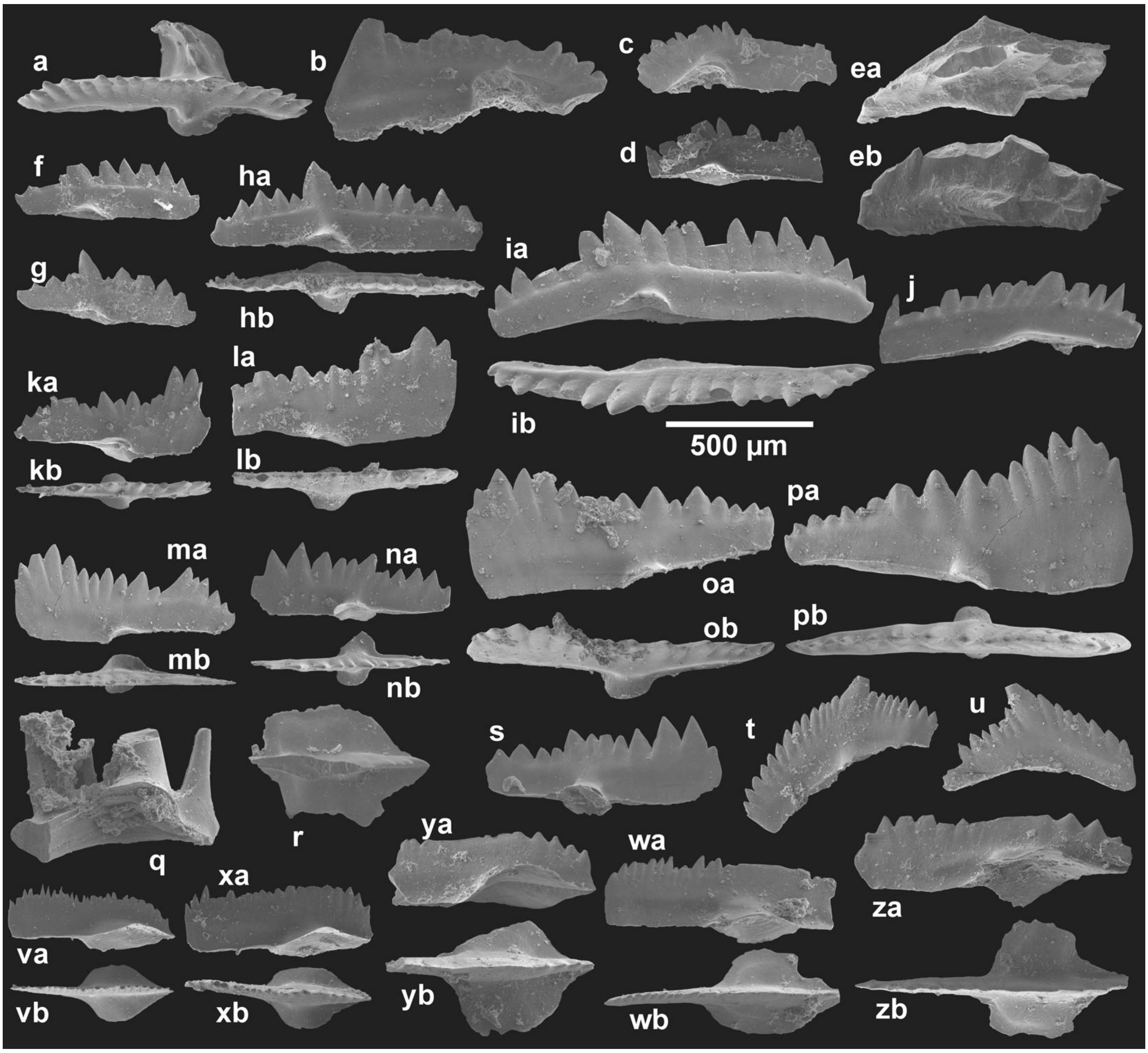

Figure 4. Conodonts from the Všeradice section (SEM images). All images are at the same magnification (scale bar represents 500 µm). (a) *Kockelella maenniki* Serpagli & Corradini, oral view of Pa element, bed no. 2. (b) *Kockelella* cf. *a. absidata*, lateral view of Pa element, bed no. 2. (c) *Kockelella absidata sardoa* Serpagli & Corradini, lateral view of Pa element, bed no. 4. (d) *Kockelella absidata* ssp., lateral view of Pa element, bed no. 9. (e) *Polygnathoides siluricus* Branson & Mehl, oral view (ea) and lateral view (eb) of incomplete Pa element from bed no. 9. (f) *Wurmiella inclinata* (Rhodes), lateral view of Pa element, bed no. 13. (g) *W. inclinata*, lateral view of Pa element from the base of bed no. 13. (h) *W. inclinata*, lateral view (ha) and oral view (hb) of Pa element from base of bed no. 13. (i) *Wurmiella excavata excavata* (Branson & Mehl), lateral view (ia) and oral view (ib) of Pa element from base of bed no. 13. (j) *W.* cf. *excavata*, lateral view of Pa element, bed no. 2. (k) *Ozarkodina typica*, lateral view (ka) and oral view (kb) of Pa element, bed no. 9. (l) *Ozarkodina typica* Branson & Mehl, lateral view (la) and oral view (lb) of Pa element from the base of bed no. 13. (m) *O. typica*, lateral view (ma) and oral view (mb) of Pa element from the base of bed no. 13. (n) *O.* cf. *typica*, lateral view (na) and oral view (nb) of Pa element, bed no. 22. (o) *Oz. typica*, lateral view (oa) and oral view (ob) of Pa element from the base of bed no. 13. (p) *Oz. typica*, lateral view (pa) and oral view (pb) of Pa element from the base of bed no. 13. (q) *Delotaxis* sp., lateral view of incomplete element from the base of bed no. 13. (r) '*Ozarkodina*' *snajdri–crispa* transition, oral view of incomplete Pa element, bed no. 28. (s) *Oz. typica*, lateral view of Pa element, bed no. 22. (t) '*Ozarkodina*' *snajdri* or *crispa*, lateral view of Pb element, bed no. 22. (u) *Oz. typica*, lateral view of Pb element from the base of bed no. 13. (v–z) '*Ozarkodina*' *snajdri* Walliser, lateral views (va–za) and oral views (vb–zb) of Pa elements from bed no. 22.

taphocenoses. Diversity is moderate to low. Twenty graptolite taxa have been identified from the middle and upper Ludfordian and lowest Pridoli. Despite the relative scarcity, however, graptolites are still playing a dominant role in the preserved pelagic macrofauna, being associated with myodocopid ostracods before the Kozlowskii Event. Shale beds with few graptolite rhabdosomes are rich in ostracods (accompanying cephalopods) and *vice versa*. The principal graptolite taxa are figured in Figures 5, 6 and 7. All biozones applied in this paper are interval zones defined as an interval between two biohorizons (see *International Stratigraphic Guide* edited by Salvador, 1994).

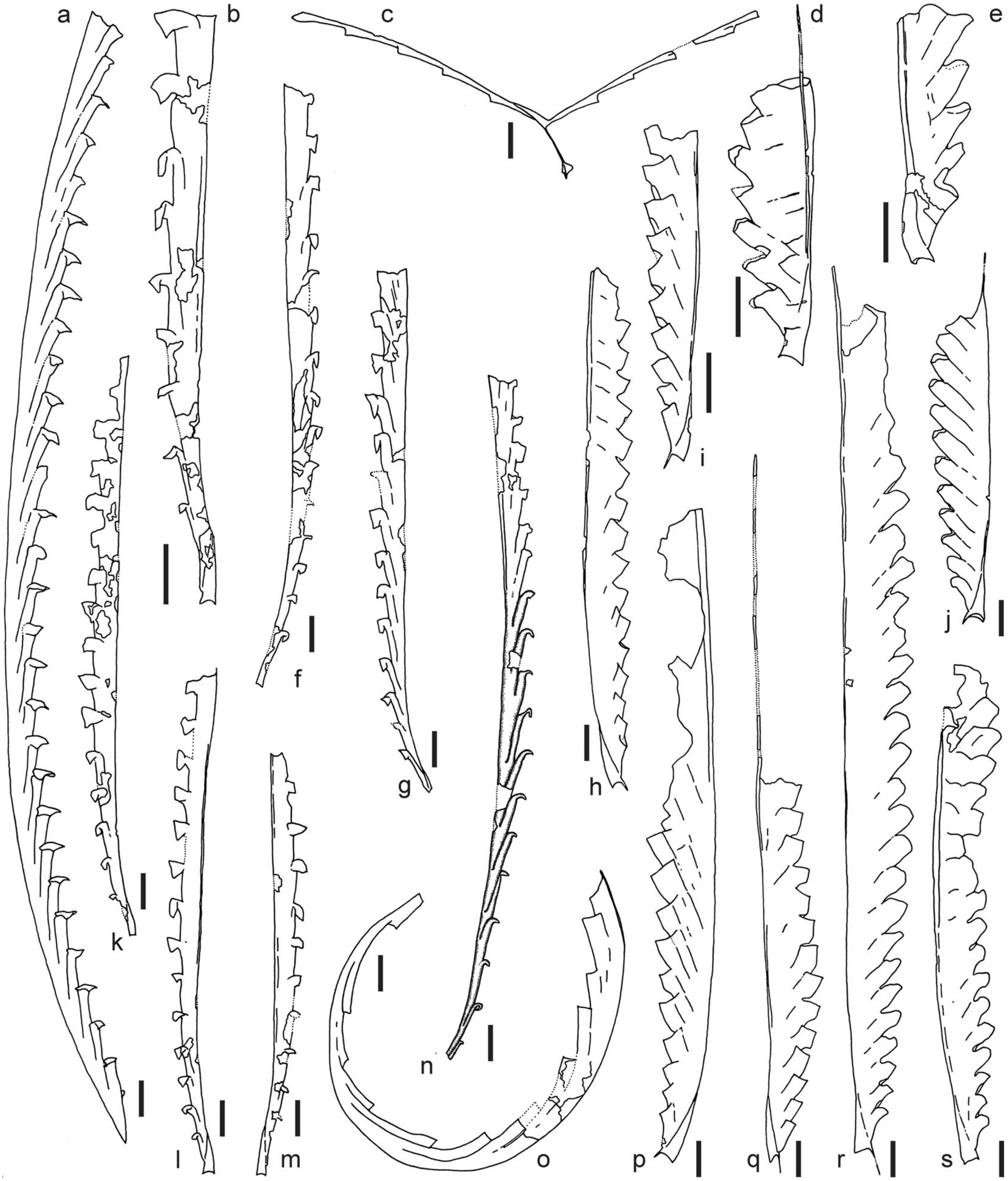

Figure 5. Middle and late Ludfordian graptolites from the Všeradice section. (a) *Neocucullograptus kozlowskii* Urbanek: PŠ 2028, upper part of bed no. 10; (b, f, g, k–n) *Slovinograptus balticus* (Teller): (b) PŠ 2020, (f) PŠ 2011, (g) PŠ 2018, (k) PŠ 2016, (l) PŠ 2017–1, (m) PŠ 2017–2, (n) PŠ 2015, bed no. 20; (c) *Linograptus posthumus* R. Richter: PŠ 2029, lowermost part of bed no. 7; (d, e, j, r, s) *Pseudomonoclimacis latilobus* (Tsegelnjuk): (d) PŠ 2004, (e) PŠ 2023, (j) PŠ 2001, (r) PŠ 2006, (s) PŠ 2003, (d, j, r, s) bed no. 14, (e) bed no. 20; (h) *Pristiograptus dubius* (Suess): PŠ 2024, bed no. 31; (i) *Pseudomonoclimacis kosoviensis* (Bouček): PŠ 2009, bed no. 16; (o) *Polonograptus chlupaci* sp. nov.: PŠ 2030, lowermost part of bed no. 7; (p) *Pristiograptus fragmentalis* (Bouček): PŠ 2031, bed no. 27; (q) *Pseudomonoclimacis dalejensis* (Bouček): PŠ 2027b, bed no. 10. Vertical scale bars represent 1 mm.

The lower part of the succession described in this paper was exposed in the upper part of the VA trench, on the western side of the field track. It is developed in the form of partly bleached, brownish calcareous shales with *Pristiograptus dubius* (Suess) *sensu lato*, *Pseudomonoclimacis kosoviensis* (Bouček) and *Bohemograptus tenuis* (Bouček), and referred to the uppermost part of the lower–middle

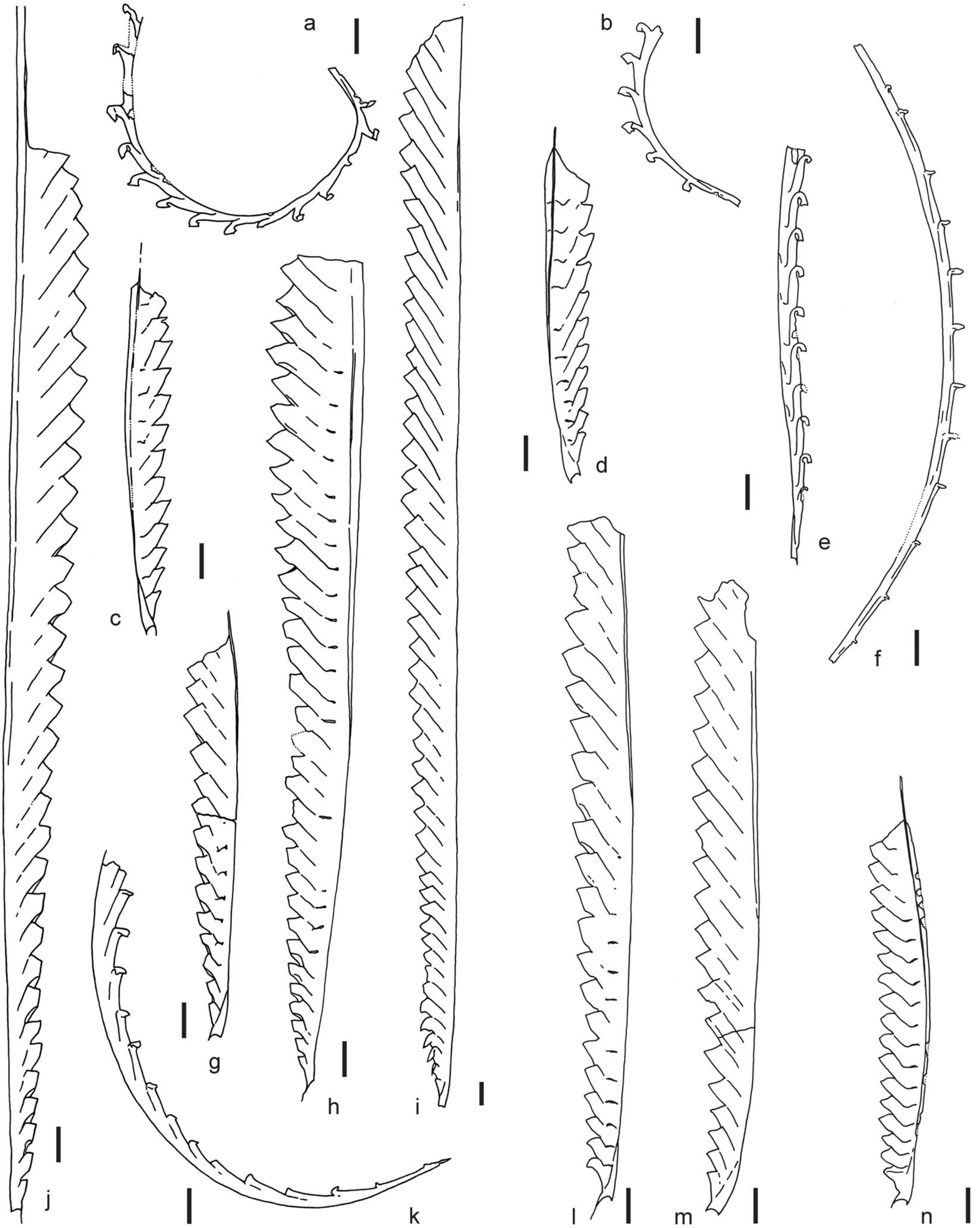

Figure 6. Middle and late Ludfordian and basal Pridoli graptolites from the Všeradice section. (a, b) *Formosograptus formosus* (Bouček): (a) PŠ 2025, (b) PŠ 2303, bed no. 37; (c, d) *Neocolonograptus parultimus* (Jaeger): (c) PŠ 2026, (d) PŠ 2302, bed no. 37; (e) *Slovinograptus* cf. *balticus* (Teller): PŠ 2307, bed no. 33; (f) *Crinitograptus*? sp.: PŠ 2308, bed no. 33; (g–j) *Pseudomonoclimacis kosoviensis* (Bouček): (g) PŠ 2244; (h) PŠ 2114, (i) PŠ 2101, (j) PŠ 2110a, lowermost part of section VB; (k) *Neocucullograptus inexpectatus* (Bouček) ssp.: PŠ 2100, lowermost part of the section designated VB; (l) *Pseudomonoclimacis* aff. *kosoviensis* (Bouček): PŠ 2304, bed no. 27; (m) *Pristiograptus fragmentalis* (Bouček): PŠ 2309, bed no. 27; (n) *Neocolonograptus ultimus* (Perner): PŠ 2310, bed no. 39. Vertical scale bars represent 1 mm.

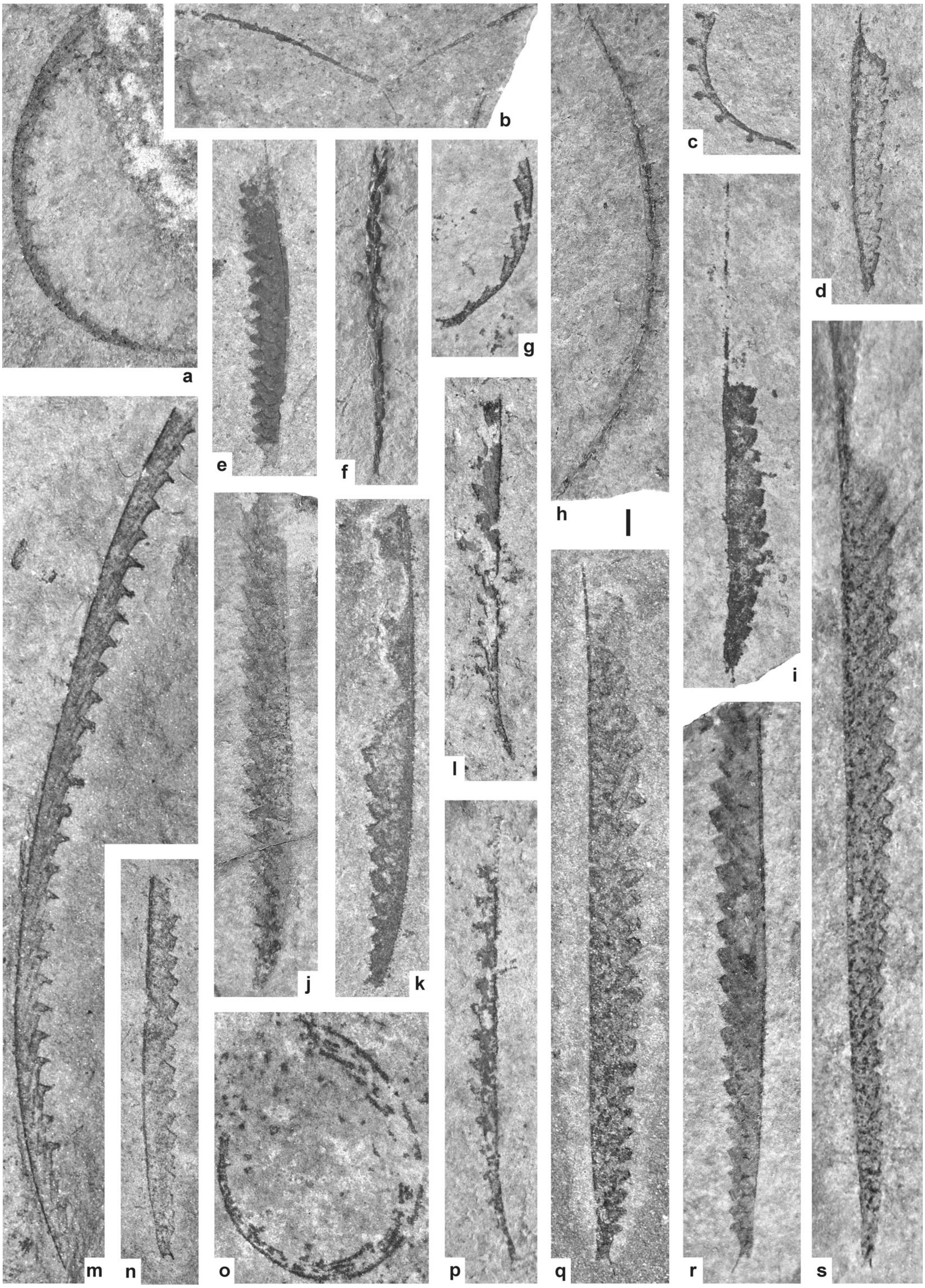

Figure 7. Middle and late Ludfordian and basal Pridoli graptolites from the Všeradice section. (a) *Neocucullograptus inexpectatus* (Bouček) ssp.: PŠ 2100, lowermost part of the section designated VB; (b) *Linograptus posthumus* R. Richter: PŠ 2029, lowermost part of bed no. 7; (c) *Formosograptus formosus* (Bouček): PŠ 2303, bed no. 37; (d) *Neocolonograptus parultimus* (Jaeger): PŠ 2302, bed

Ludfordian *B. tenuis* Biozone. The same lithology, but intercalated with several muddy limestone and tuffitic-carbonate beds, continues through the succeeding *Neocucullograptus inexpectatus* and *Neocucullograptus kozlowskii* biozones.

The lower part of the 8.7 m thick *Nc. inexpectatus* Biozone was exposed in the overlapping parts of the neighbouring trenches VB and VA. Small, long-ranging *P. dubius*, *Pseudomonoclimacis dalejensis* (Bouček), *B. tenuis*, large rhabdosomes of *Ps. kosoviensis* (Bouček) and the biozonal index species *Neocucullograptus inexpectatus* (Bouček) are common in the shale. Uncommon *Linograptus posthumus* (R. Richter), *Bohemograptus praecornutus* Urbanek and *Polonograptus chlupaci* sp. nov. have been collected from the upper part of the *inexpectatus* Biozone on the eastern side of the track, in the VA trench.

Higher in the VA trench *Nc. inexpectatus* is replaced by a more derived form, *Neocucullograptus kozlowskii* Urbanek, which is the index species of the next biozone. Apart from the different index graptolite, the 3.2 m thick *kozlowskii* Biozone contains an assemblage similar to that of the *inexpectatus* Biozone. *Polonograptus podoliensis* Přibyl, a prominent but uncommon element in the assemblage of the *Nc. kozlowskii* Biozone in Kosov Quarry near Beroun (Štorch, 1995*a*) and a few other sections (Přibyl, 1983), has not been recovered from the Všeradice section.

The continuous graptolite record and sedimentation were interrupted at the base of limestone bed no. 11 and graptolites reappeared only above the intraformational conglomerate (Figs 2, 3, bed no. 13).

The mass extinction of the middle Ludfordian graptolite fauna at the top of the *kozlowskii* Biozone has been described and discussed by Urbanek (1970, 1993). Although all graptolites with ventrally curved rhabdosomes (*Bohemograptus*, *Neocucullograptus* and *Polonograptus*) vanished, some generalists such as *Pristiograptus dubius*, *Linograptus posthumus* and *Pseudomonoclimacis kosoviensis* reappeared soon after the extinction, together with several newcomers of rather cryptic origin.

Graptolites appearing in the first shale intercalations within the limestone-dominated interval immediately above the intraformational conglomerates belong to a new, post-extinction assemblage of the *Ps. latilobus*–*Sl. balticus* Biozone. The assemblage, dominated by *Ps. latilobus* (Tsegelnjuk), comprises also *Sl. balticus* (Teller), *L. posthumus*, *Ps. kosoviensis* and a slender form of *P. dubius*.

Higher in the succession *Sl. balticus* has been replaced by the more slender, weakly S-shaped *Sl.* cf. *balticus* (Teller) accompanied by *Pseudomonoclimacis* aff. *kosoviensis*, *Crinitograptus*? sp. and the long-ranging *L. posthumus* and *P. dubius*. Rare finds of *Pristiograptus fragmentalis* (Bouček) in bed no. 27 enable recognition of a specific *P. fragmentalis* Biozone in the interval between the last joint occurrence of *Ps. latilobus* and *Sl. balticus* and the first occurrence of *Neocolonograptus parultimus* (Jaeger), the latter indicating the base of the Pridoli Series.

In the uppermost shale beds exposed in the trench (beds nos 35–41), *Ne. parultimus* is accompanied by *Neocolonograptus ultimus* (Perner), *Formosograptus formosus* (Bouček), *Crinitograptus*? sp., *L. posthumus*, the last *P. fragmentalis* and a slender form of *P. dubius*.

2.g. Carbon isotopes

The $\delta^{13}C_{carb}$ values from the Všeradice section range from –2 to +2 ‰, and in contrast to earlier studied sections of the Prague Basin (Lehnert *et al*. 2007*b*), no distinct positive $\delta^{13}C$ shift was observed above the level of the Kozlowskii Event. The lack of this $\delta^{13}C$ positive excursion as well as the relatively low $\delta^{13}C_{carb}$ values in the Všeradice section (frequently close to or just below zero) may suggest an absence of sedimentary record equivalent to beds with the high positive $\delta^{13}C$ values and/or a slight diagenetic overprint. A high content of organic carbon in the shale-dominated succession could cause a lowering of the $\delta^{13}C_{carb}$ values during diagenetic processes. The decomposition of organic matter yields isotopically light carbon, which can then be precipitated as carbonate, which pushes the $\delta^{13}C_{carb}$ values down in organic-rich carbonates. Because of that we cannot determine whether the measured low $\delta^{13}C$ values represent the primary isotopic composition of the studied micrites or values that have been slightly secondarily lowered by diagenetic overprint, or both. The only positive $\delta^{13}C$ values were recorded in an interval just above the late Ludlow Kozlowskii Event roughly to a level about 4.5 m below the FA of '*Ozarkodina*' *snajdri*. However, no distinct positive $\delta^{13}C$ shift was found in the carbonates from the Všeradice section (Fig. 8).

Previous studies (Lehnert *et al*. 2003, 2007*b*) revealed a distinct positive shift of the $\delta^{13}C_{carb}$ values from the carbonate platform of the Prague Basin. The most complete isotopic peak was recorded from the Kosov Section (Fig. 8) where the positive $\delta^{13}C$ shift

no. 37; (e) *Neocolonograptus ultimus* (Perner): PŠ 2310, bed no. 39; (f) *Slovinograptus* cf. *balticus* (Teller): PŠ 2307, bed no. 33; (g) *Bohemograptus tenuis* (Bouček): PŠ 2098, lowermost part of section VB; (h) *Crinitograptus*? sp.: PŠ 2308, bed no. 33; (i) *Pseudomonoclimacis dalejensis* (Bouček): PŠ 2027b, bed no. 10; (j, k) *Pristiograptus fragmentalis* (Bouček): (j) PŠ 2309, (k) PŠ 2031, bed no. 27; (l, p) *Slovinograptus balticus* (Teller): (l) PŠ 2018, (p) PŠ 2016, bed no. 20; (m) *Neocucullograptus kozlowskii* Urbanek: PŠ 2028, upper part of bed no. 10; (n) *Pristiograptus dubius* (Suess): PŠ 2024, bed no. 31; (o) *Polonograptus chlupaci* sp. nov.: PŠ 2030, lowermost part of bed no. 7; (q) *Pseudomonoclimacis latilobus* (Tsegelnjuk): PŠ 2006, bed no. 14; (r) *Pseudomonoclimacis* aff. *kosoviensis* (Bouček): PŠ 2304, bed no. 27; (s) *Pseudomonoclimacis kosoviensis* (Bouček): PŠ 2110a, lowermost part of section VB; All specimens × 5, vertical scale bar represents 1 mm.

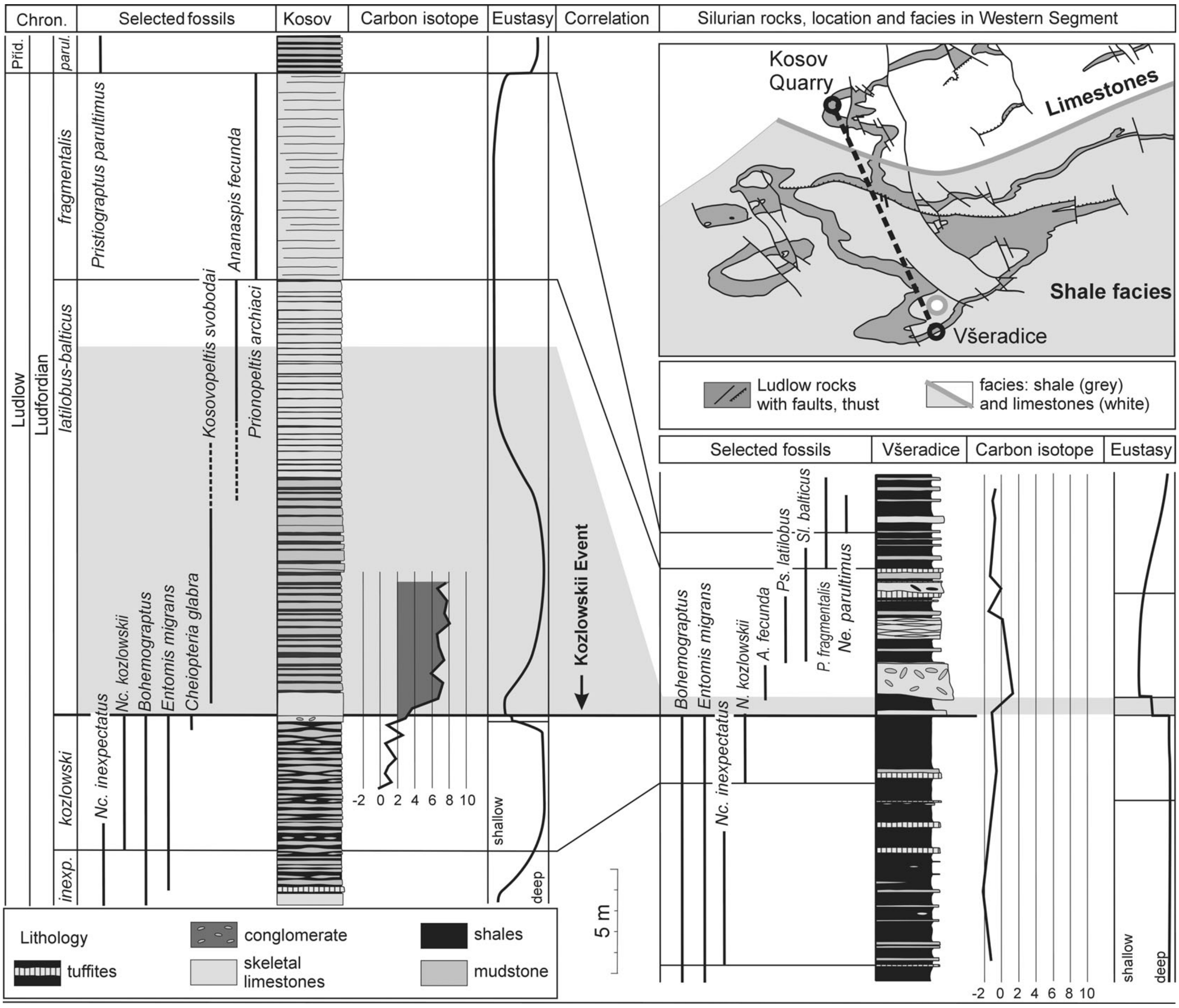

Figure 8. Correlation of the Všeradice section with a shallow water succession exposed in the New Kosov Quarry section showing lithology, ranges of selected fossils, relative eustatic oscillation and carbon isotope curve. Note that conodonts are not included because conodonts have not been studied in Kosov Quarry. The grey field indicates the interval of a sedimentary break in the Všeradice section. Data from Kosov Quarry are adopted from Kříž (1992) and Lehnert *et al.* (2007*b*).

starts at the level of the late Ludlow Kozlowskii Event (Fig. 8). The values in the subsequent part of the Kosov Section (between 6.7 and 8 ‰) show no indication of a decrease in δ^{13}C. Another, earlier studied section, the Mušlovka Quarry Section, clearly shows that this δ^{13}C positive excursion ends before the FA of ‘*Oz.*’ *snajdri*. The level of the late Ludlow Kozlowskii Event was confidently indicated biostratigraphically in the Všeradice section; however, determination of the FAD of ‘*Oz.*’ *snajdri* is less certain because only a few conodont elements of the latter conodont species were found. The true FA of ‘*Oz.*’ *snajdri* may thus be lower in the section than shown (Fig. 2).

In the Všeradice section, the level of the late Ludlow Kozlowskii Event is just below the intraformational conglomerate (bed no. 13), which probably corresponds to the prominent gap in the sedimentary record (Fig. 2). The absence of a distinct positive shift of the δ^{13}C values in the Všeradice section likely suggests an absence of sedimentary record equivalent to beds with the high positive δ^{13}C values in the Kosov Section (Fig. 8).

3. Graptolite biozones and correlation

Graptolite biozones are used as the primary correlation tool as the conodonts from the section are not sufficient to compose a precise zonal scheme. Whenever possible the shelly fauna and its potential for correlation are commented upon.

3.a. The *Bohemograptus tenuis* Biozone

Přibyl (1983) designated an interval between the demise of the saetograptids and the first occurrence of *Neocucullograptus inexpectatus* (Bouček) as the ‘*Pristiograptus longus*’ Biozone with, at its top, the *Bohemograptus bohemicus* Bed. '*Pristiograptus longus*' (Bouček) is considered herein to be a junior synonym of *Pristiograptus dubius* (Suess) *sensu lato*. *Bohemograptus bohemicus* (Barrande) is considerably outnumbered by its evolutionary offshoot *Bohemograptus tenuis* (Bouček) in this level. We prefer to define the entire interval between the last saetograptids and the first *Neocucullograptus* as the *Bohemograptus tenuis* Biozone. This interval is probably coeval with the *Bohemograptus bohemicus–Neolobograptus auriculatus* biozones erected by Teller (1969) and Urbanek (1970) in the subsurface Silurian rocks of Poland and further updated by Urbanek & Teller (1997). Holland & Palmer (1974) used the *B. tenuis* Biozone to designate strata with a monospecific bohemograptid fauna overlying the *Saetograptus leintwardinensis* Biozone in the Welsh Borderland (see *Bohemograptus* proliferation Zone in Zalasiewicz *et al*. 2009). The present *B. tenuis* Biozone is correlatable also with the *B. tenuis* Interzone sandwiched between the *S. linearis* and *Polonograptus podoliensis* biozones in Tien Shan, Kyrgyzstan (Koren' & Sujarkova, 2004). *Saetograptus linearis* is a biozonal index graptolite in Bohemia and *Polonograptus podoliensis* (Přibyl) is an important component in assemblages of the *Nc. inexpectatus* and *Nc. kozlowskii* biozones (Přibyl, 1983; Štorch, 1995*a*). Finally, in Bohemia the *B. tenuis* Biozone is used to name the interval between the late *S. leintwardinensis* Biozone mass extinction and the subsequent development of the new neocucullograptid and polonograptid fauna. The uppermost part of the *B. tenuis* Biozone, overlain by the FA of *Nc. inexpectatus*, is shown in the lowermost part of the section illustrated in Figure 2.

3.b. The *Neocucullograptus inexpectatus* Biozone

The *Nc. inexpectatus* Biozone of this paper corresponds to the lower part of the *Nc. inexpectatus* Biozone of Přibyl (1983). The stratigraphically lowest neocucullograptid rhabdosomes define the base of the biozone, whereas its top is defined by the FA of *Nc. kozlowskii*. Apart from *Nc. inexpectatus inexpectatus* (Bouček, 1931), Urbanek (1970) recognized the more advanced subspecies *Nc. inexpectatus supernus* that certainly occurs in the upper part of the biozone at Kosov Quarry (Štorch, 1995*a*). Preservation of the specimens found in the Všeradice section, however, is not good enough to enable separation of the two subspecies. Limestone nodules in tuffite bed no. 4 contain the conodont *Ozarkodina fundamentata* that indicates the *P. siluricus* Biozone. In addition, a bivalve assemblage with *Cardiola docens* occurs in the limestone nodules (bed no. 4). This bivalve assemblage is used in correlations of carbonate sequences in peri-Gondwanan Europe; it ranges from the *S. linearis* Biozone up to the *Nc. inexpectatus* Biozone (Kříž, 1998, 1999*a,b*, 2010*a,b*).

3.c. The *Neocucullograptus kozlowskii* Biozone

Přibyl (1983) did not recognize the *Neocucullograptus kozlowskii* Biozone in Bohemia; hence the upper part of his *Nc. inexpectatus* Biozone correlates with the *Nc. kozlowskii* Biozone *sensu* Štorch (1995*a*) and the present paper. The *Nc. kozlowskii* Biozone comprises an interval between the FA and LA of its name-giving species. The present conception of the *Nc. kozlowskii* Biozone matches well that introduced for the East European Platform by Urbanek (1970) and further elaborated by Urbanek & Teller (1997). The same neocucullograptid biozones are probably applicable in Podolia, although Tsegelnjuk (1976, 1981) did not use a *Nc. inexpectatus* Biozone. A limestone bed just above the base of the *Nc. kozlowskii* Biozone yielded the index conodont *Polygnathoides siluricus*. The direct correlation between the *Nc. kozlowskii* Biozone and upper part of the *P. siluricus* Biozone has been previously documented in Kosov Quarry only (Lehnert *et al*. 2007*b*). The upper limit of the *Nc. kozlowskii* Biozone is defined by the sudden extinction of the bohemograptid–polonograptid–neocucullograptid fauna, defined as the Kozlowskii Event by Urbanek (1993). Graptolite extinction and facies change indicating shallowing were identified also in Kosov Quarry near Beroun (Štorch, 1995*a,b*). There, however, graptolites are missing in the supposed post-extinction recovery interval.

Limestones and intraformational conglomerates that occur just above the graptolite extinction level in the Všeradice section suggest that the extinction coincides with the beginning of shallowing as suggested by Urbanek (1993) and Melchin, Koren' & Štorch (1998). Apart from graptolites, the ostracod *Entomis migrans* disappeared (similarly as elsewhere in the Prague Synform, see Manda & Kříž, 2006). This is a striking feature because this ostracod is a common component of pelagic faunas in peri-Gondwanan basins starting from the lower Ludfordian *S. linearis* Biozone (Siveter, Vannier & Palmer, 1991; Kříž, 1999*a*). *Bolbozoe* disappeared from shales in the *Nc. inexpectatus* Biozone. Note that no pelagic ostracods appeared during the post-extinction recovery. Pelagic orthocerids pass through the Kozlowskii extinction Event and *Parakionoceras*, *Kopaninoceras*, *Arionoceras* and *Michelinoceras* occur throughout the section. Conodonts found in limestone just above the Kozlowskii Event are the same as in the lowest *Nc. kozlowski* Biozone except for *P. siluricus*. This suggests that the deeper water conodont assemblage consists mainly of long-ranging taxa and that the extinction thus affected rather shallow water conodont faunas (see also Slavík, Kříž & Carls, 2010). This should be taken into account when correlating deeper water limestones.

Manda & Kříž (2006) concluded that the Kozlowskii Event correlates roughly with the conodont extinction known as the Lau Event (Jeppsson, 1993). However, no section with adequately combined graptolite and conodont records is known. Consequently, high-resolution correlation of the graptolite and conodont extinctions is doubtful. Moreover the Lau Event is not clearly manifested in the conodont faunas in the Prague Synform and its lower part is entirely missing in the sections (Slavík, Kříž & Carls, 2010).

In the Kosov Section the LA of *P. siluricus* (defining the Lau Event) is drawn below the LA of *Nc. inexpectatus* and *B. tenuis*. Conodonts are, however, rare in this section. The late Ludfordian carbon isotope excursion which is commonly ascribed to the Lau Event (Saltzman, 2001; Maartma *et al.* 2005; Lehnert *et al.* 2007*b*) started in the Kosov Section close to the level of the graptolite extinction.

3.d. The *Pseudomonoclimacis latilobus–Slovinograptus balticus* Biozone

The graptolite assemblage recovered from shaly intercalations within the post-*kozlowskii* limestone suite is dominated by the two biozonal index species, *Pseudomonoclimacis latilobus* (Tsegelnjuk, 1976) and *Slovinograptus balticus* (Teller, 1966), both widespread in the East European Platform (e.g. Tsegelnjuk, 1976; Paškevičius, 1979; Urbanek, 1997). Přibyl (1983) described these two species under the junior synonyms '*Saetograptus insignitus*' and '*Monograptus abhorrens*', respectively, from a temporary trench in Velký Vrch hill near Koněprusy. He recognized a distinctive '*S. insignitus*' Biozone also in Kosov Quarry and in a water supply gallery in Praha-Podolí. We are not surprised to find these graptolites in relatively more offshore facies in the Všeradice section. The *Ps. latilobus–Sl. balticus* Biozone of this paper is an interval between the last occurrence of *Nc. kozlowskii* at the base and last joint occurrence of *Ps. latilobus* and *Sl. balticus* at the top.

The intraformational conglomerate just below the lowest occurrences of *Ps. latilobus* and *Sl. balticus* contains trilobites and other shelly fossils of relatively inshore provenance corresponding with the former *Ananaspis fecunda* Horizon (Horný, 1955). Benthic fossils recovered from both matrix and pebbles of the conglomerate belong to the *Ananaspis fecunda–Cyrtia postera* Assemblage, which therefore pre-dated the *Ps. latilobus–Sl. balticus* graptolite assemblage. The relict graptolite fauna that survived the maximum lowstand (shallow water limestones with *Ananaspis fecunda* overlie deeper water shale and mudstone in the Kosov and Mořina areas) was subsequently joined by the new association of *Ps. latilobus* and *Sl. balticus*. Although in the Všeradice section the interval between the Kozlowskii extinction and the FA of *Ps. latilobus* is only about 2.5 m thick, in Kosov Quarry it comprises at least 10 m of strata. This indicates that the post-extinction interval with strongly impoverished or missing graptolites was remarkably long and the recovery of graptolites was delayed after the benthic faunal recovery. Finally, the limestone sequence with the *Ananaspis fecunda–Cyrtia postera* Assemblage (*A. fecunda* Horizon of Horný, 1955) developed across the basin, correlates with the *Ps. latilobus–Sl. balticus* Biozone as used here.

Pseudomonoclimacis latilobus and *Slovinograptus balticus* range together higher up the succession, close to the FA of *Neocolonograptus parultimus* (Jaeger), the biozonal index of the lowermost Pridoli. The graptolite assemblage of the present *Ps. latilobus–Sl. balticus* Biozone is quite similar to that of the homonymous zone applied by Urbanek (1997) in Poland. It is uncertain, however, how precisely the two *latilobus–balticus* biozones correlate. The index taxa of the three succeeding biozones, i.e. *Uncinatograptus acer* Tsegelnjuk, *Uncinatograptus protospineus* Urbanek and *Uncinatograptus spineus* Tsegelnjuk, which overlie the *Ps. latilobus–Sl. balticus* Biozone in Poland (Urbanek, 1997), are missing in the Všeradice section and elsewhere in peri-Gondwanan Europe. The lack of these biozones may be explained by the palaeogeographical isolation of peri-Gondwanan Europe in the latest Ludlow. In the Všeradice section, however, some gaps in sedimentation should be also considered since the 2.5 m between the LA of *Ps. latilobus* and the FA of *Ne. parultimus* corresponds with a *c.* 120 m thick sequence in Poland (see Urbanek, 1997, fig. 3). Přibyl (1983) recognized a monospecific '*Pristiograptus*' *fecundus* Biozone above his '*insignitus* Biozone' in Kosov Quarry and some other sections of the Prague Synform. '*Pristiograptus*' *fecundus* (Přibyl), which is probably a descendant of *Ps. latilobus*, has not been recovered from the Všeradice section.

Limestone bed no. 22, containing '*Oz.*' *snajdri* and other conodont taxa (Fig. 2), immediately overlies the last occurrence of *Ps. latilobus*. The FA of '*Oz.*' *snajdri* is therefore above the FA of *Ps. latilobus*.

3.e. The *Pristiograptus fragmentalis* Biozone

Instead of distinctive range biozones, we can apply only another interval biozone, named after the presumably long-ranging *Pristiograptus fragmentalis* (Bouček) and defined as an interval between the highest joint occurrence of *Ps. latilobus* and *Sl. balticus* and the FA of *Ne. parultimus*. *Pristiograptus fragmentalis* (Bouček, 1936) is a robust form having a weakly ventrally curved to almost straight proximal-most part of its rhabdosome and considerably overlapping, pristiograptid distal thecae. Our specimens (Figs 5p, 7j, k) are identical with forms figured by Kříž *et al.* (1986), Urbanek (1997, pl. 15, figs 5–6) and, in part, by Koren' & Sujarkova (1997, pl. 1, figs 1–6; text-fig. 7A–G).

The *Pristiograptus fragmentalis* Biozone is the uppermost graptolite biozone of the Ludlow in Bohemia (Bouček, 1936). Bouček (1936, p. 13) noted that *P. fragmentalis* occurs in cephalopod limestones with the trilobites *Cromus intercostatus* Barrande and *Cerauroides hawlei* (Barrande), below the FA of *Ne. ultimus* at the Lochkov locality. *Cr. intercostatus* and *C. hawlei* form part of the distinct *Denckmanites–Cromus* trilobite Assemblage established by Chlupáč

(1987). This assemblage is known only from a few sections near Lochkov village where it is restricted to a single thin bed. Šnajdr (1985) noted that the latter assemblage occurs 11–14 cm below the FA of *Ne. parultimus* in the Orthoceras Quarry Section. Kříž *et al.* (1986) reported *P. fragmentalis* from the uppermost Ludlow just below the FA of *Ne. parultimus* (in the Koledník and Karlštejn sections). New data from the Všeradice section suggest that the FA of *P. fragmentalis* in Bohemia falls immediately after the LA of *Ps. latilobus*.

The Všeradice section seems to be either condensed or interrupted by a discrete unconformity in this interval, since *Ne. parultimus*, the index of the basal Pridoli, makes its first appearance less than 1 m above the last *Sl. balticus*. As in other Bohemian sections (Kříž *et al.* 1986), *Ne. parultimus* is accompanied by *Formosograptus formosus* in the Všeradice section. In the East European Platform (Paškevičius, 1979; Urbanek & Teller, 1997), Arctic Canada (Lenz & Kozłowska-Dawidziuk, 2004) and Tien Shan (Koren' & Sujarkova, 1997) *Formosograptus formosus* appears much lower and even gives its name to a combined biozone in the latest Ludfordian. Similarly, *P. fragmentalis* appears in Poland earlier; it co-occurs with *Ps. latilobus*, but disappeared already before the LA of *Ps. latilobus*.

4. Conclusions

Although late Ludfordian graptolites have rarely left a fossil record sufficient for detailed biostratigraphy and high-resolution correlation, a better understanding is of crucial importance as correlation of the Silurian System relies primarily on graptolite biozones. Benthic faunas and sequence boundaries can be used in correlations within individual basins, especially in stratigraphical intervals where conodont biozones lack the precision of those based on graptolites. Here, four graptolite biozones are distinguished in the latest Ludlow between the *B. tenuis* Biozone and the base of Pridoli Series. The Všeradice section provides the most complete graptolite record in the peri-Gondwanan realm. The late Ludlow graptolite biozonation previously applied in Bohemia and other parts of peri-Gondwanan Europe resulted rather from uncertain correlations between isolated partial sections.

The Kozlowskii extinction Event and subsequent recovery is recorded for the first time from both Bohemia and peri-Gondwana; this also represents the first record of the event in higher latitudes outside the tropical zone. The Všeradice section is unique also in its sedimentary record. Although situated in an offshore, open sea setting, it enables correlation with benthic and particularly conodont faunas, because it was situated close to a small shallow water area with carbonate sedimentation, which was colonized by benthic assemblages closely related to those inhabiting the carbonate platform situated to the north.

The Kozlowskii Event caused extinction of many graptolite lineages as previously suggested. Bohemograptids, neocucullograptids and *Polonograptus* all vanished from the fossil record. It is noteworthy that the pelagic orthocerids and nektonic *Ceratiocaris* passed through the extinction interval (Fig. 9). The pelagic ostracod *Entomis*, however, became extinct. Although a single taxon, its extinction is of note because it is a widespread, long-ranging generalist. Similarly, the conodont faunas in these deeper water settings were affected only slightly (see also Slavík, Kříž & Carls, 2010). Data from the Všeradice section further support the earlier thoughts of Lehnert *et al.* (2007*a*) and Eriksson & Calner (2008) that the Kozlowskii extinction Event coincides with a drop in sea-level and period of icehouse climate.

The interval between the graptolite extinction and subsequent recovery and radiation was relatively long (based on sedimentary rock thickness). Eroded shale and the intraformational conglomerate in the Všeradice section indicate a prominent gap in sedimentation during this time. The benthic faunas from the conglomerate (matrix and pebbles of different age), nevertheless, make correlation possible with coeval shallow water carbonate strata (Figs 8–10).

In terms of eustatic sea-level oscillations, the graptolite recovery recorded in the Prague Synform coincides with a period of rising sea-level after major eustatic drawdown. It was delayed far behind the recovery of benthic fauna. The graptolite recovery started after the end of the positive carbon isotope excursion and before the FAD of '*Oz.*' *snajdri*. The post-Kozlowskii Event graptolite recovery gave origin to a novel graptolite fauna of Pridoli type. Some graptolite taxa that emerged or reappeared above the Kozlowskii Event crisis are likely ancestors to substantial elements of Pridoli graptolite assemblages (e.g. *Sl. balticus* gave rise to *Sl. beatus* (Koren', 1983; Jaeger *in* Kříž *et al.* 1986) and *Ps. kosoviensis* may have evolved into *Ps. transgrediens*). In turn, *Ne. parultimus,* although remarkably similar to *Ps. latilobus*, has been derived from another, less specialized ancestor, after Urbanek (1997).

The latest Ludlow *F. formosus* and/or *Uncinatograptus acer*, *U. protospineus* and *U. spineus* biozones, distinguished in Baltica and elsewhere in lower palaeolatitudes, are missing in Bohemia and indeed in the whole of peri-Gondwana. *F. formosus*, which makes its lowest occurrence in middle Ludfordian strata in Poland, Lithuania, Kyrgyzstan, Kazakhstan and Arctic Canada, is unknown from below the *Ne. ultimus–Ne. parultimus* Biozone of the basal Pridoli Series in Bohemia and there are some discrepancies in stratigraphical ranges of some other taxa (e.g. *P. fragmentalis*). Differences may result from temporary palaeobiogeographical separation rather than an incomplete fossil record in peri-Gondwana owing to a condensed or missing sedimentary rock record.

Precise correlation of late Ludlow conodont and graptolite biozones is not yet possible from

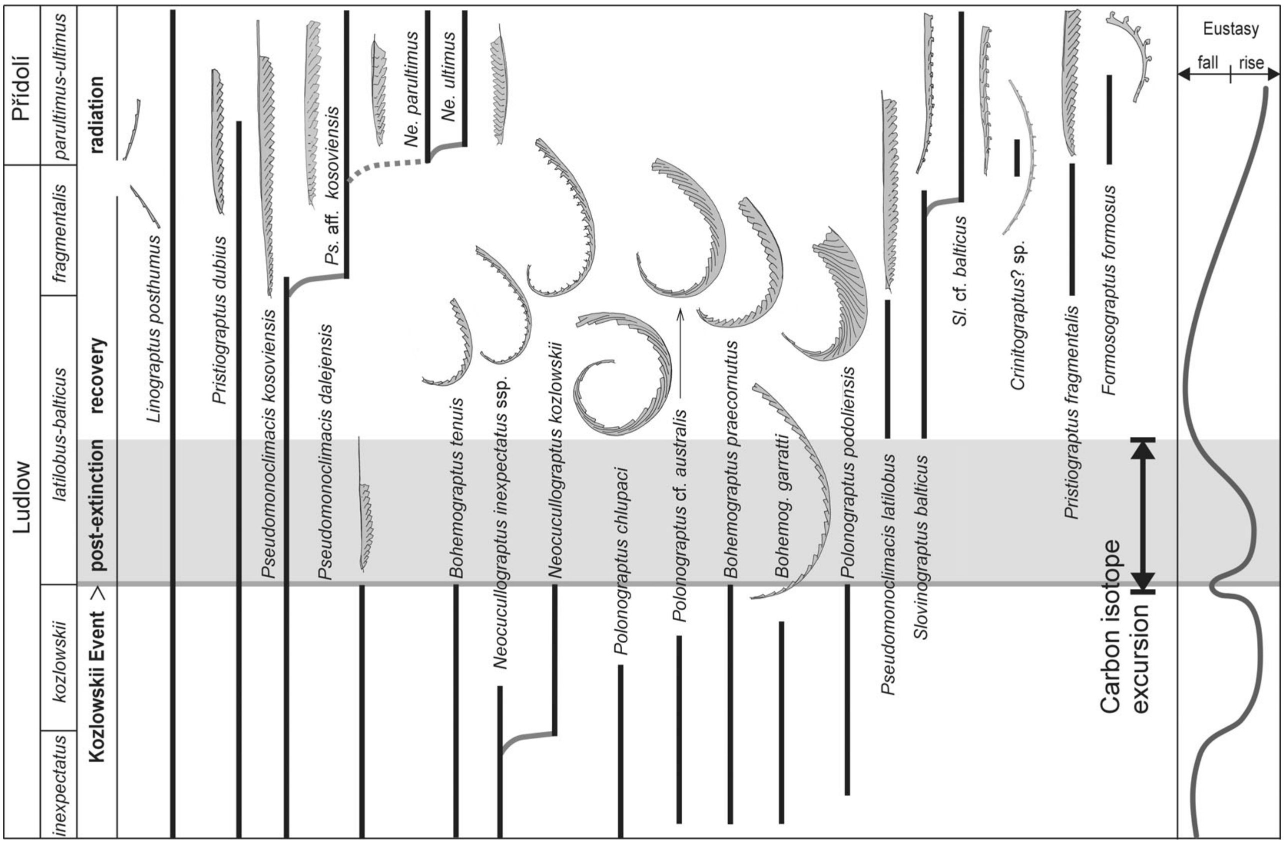

Figure 9. Kozlowskii Event: graptolite crisis recorded by Bohemian sections. Note that all ventrally curved graptolites disappeared from the fossil record. Most species recorded for the first time from the *Pr. fragmentalis* Biozone suggest striking evolutionary links between Ludfordian and Pridoli graptolite faunas.

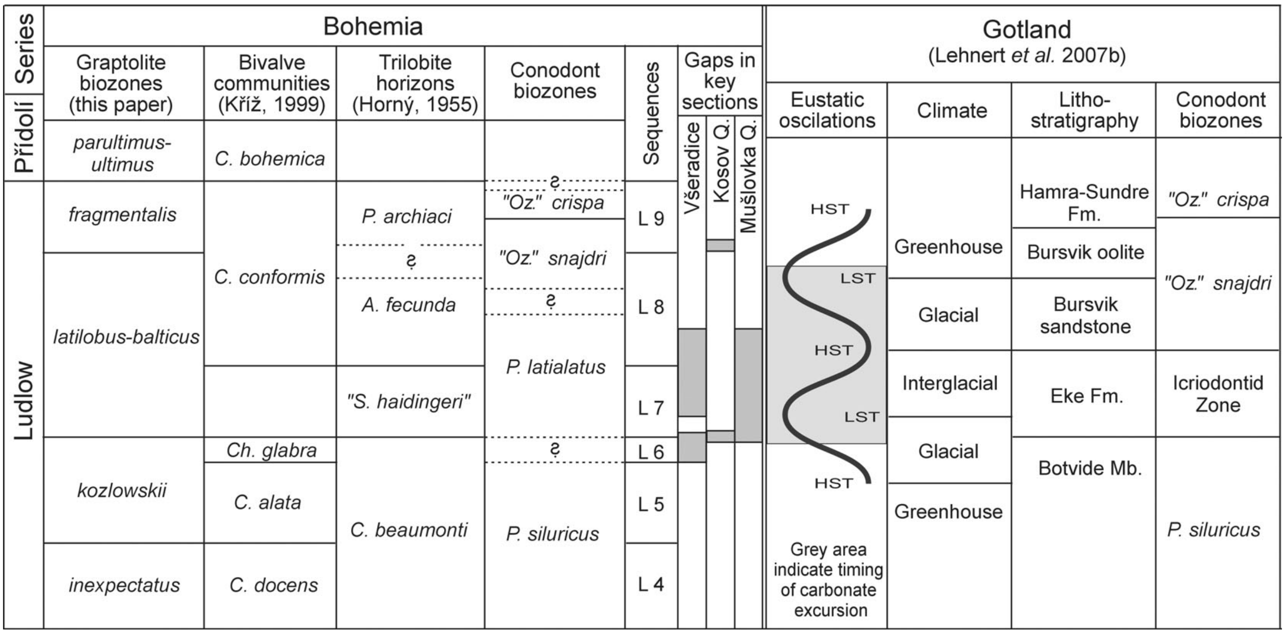

Figure 10. Correlation of late Ludlow graptolite and conodont biozones, bivalve communities and trilobite horizons in Bohemia with conodont biozones and formations in Gotland (including eustatic oscillation and climatic state as suggested by Lehnert *et al.* 2007*b*). Gaps in discussed Bohemian sections are indicated.

published data. Consequently, the correlation of the graptolite Kozlowskii and conodont Lau events is still unknown in detail, although that the two events are approximately coincident is suggested from their position at the beginning of the positive carbon isotope excursion.

5. Systematic palaeontology (by Petr Štorch)

All graptolite taxa previously unknown under the correct name from Bohemia, new species and new combinations are described. Illustrated and described specimens are housed in the official collection of the Czech Geological Survey, Prague (prefix PŠ); type specimens prefixed L are housed in the National Museum, Prague.

Pseudomonoclimacis kosoviensis (Bouček, 1931)

Figures 5i, 6g–j, 7s

1931 *Monograptus kosoviensis* n. sp. Bouček, pp. 2, 15, text-fig. 1c, d.
1936 *Monograptus kosoviensis* Bouček; Bouček, pp. 10–11, pl. 2, fig. 10; text-fig. 1g–k.
1943 *Pristiograptus kosoviensis* (Bouček); Přibyl, pp. 24–5, pl. 3, figs 14, 15.
1997 *Pristiograptus dubius* cf. *frequens* Jaekel; Rickards & Wright, pp. 219, 221–2, text-fig. 9i, j.

Material. Twenty-six flattened rhabdosomes from bed nos 1a, 1b, 3, 10 and 16 of the Všeradice section (see Fig. 2), several rhabdosomes from the middle part of trench VB below the present log and the type material figured by Bouček (1931) and Přibyl (1943).

Lectotype. Designated by Bouček (1936): specimen no L 19940 figured by Bouček (1931, text-fig. 1d); from the level corresponding with the *tenuis* Biozone of the present biozonal scheme; Koledník Quarry near Beroun, Bohemia.

Description. The sicula is straight or gently ventrally curved, 1.2–1.7 mm long, its apex attaining a level at or below the aperture of th 2. The sicular aperture is concave, 0.22–0.28 mm wide, furnished with a short and slender virgella. The nema is robust, 0.4 mm wide in mature specimens, and extending as much as 30 mm beyond the distalmost thecae. The rhabdosome gradually widens from 0.45–0.6 mm at the apertural margin of th 1, through 0.7–0.8 mm at th 3, 0.85–1.1 mm at th 5, 1.2–1.7 mm at th 10 and 1.55–1.95 mm at th 20 to a maximum of 2.5–2.7 mm attained 40–50 mm from the sicula. Isolated distal fragments are 2.8 mm wide. Proximal thecae are slightly geniculate and overlap for one-third their length. More or less prominent hook-like secondary apertural additions are developed in proximal thecae of mature rhabdosomes with a more than 30–40 mm long thecate part (Fig. 6i). Details are not seen owing to inadequate preservation. The two-thecae repeat distance (2TRD) increases from 1–1.35 mm at th 2 and 1.1–1.45 mm at th 5 to 1.3–1.7 mm at th 10 and then gradually until 2.1–2.3 mm is attained most distally. Proximal thecae number 12–13 in 10 mm of rhabdosome length; long, simply tubular distal thecae number 9.5–8.5 in 10 mm and overlap for almost three-quarters of their length. Distal thecal apertures are perpendicular to the thecal axis or are slightly everted.

Remarks. Our specimens agree in all dimensions with Bouček's (1931) type material, especially in their distal dorso-ventral width and thecal spacing. The sicular part of the rhabdosome is described for the first time and shows that this species is similar to *Pseudomonoclimacis contumax* (Bouček, 1936) and '*Monograptus*' sp. of Rickards & Palmer (1977). The apertural overgrowths observed in our mature rhabdosomes of *Ps. kosoviensis* (Bouček, 1931) are equally developed in '*Monograptus*' sp. (of Rickards & Palmer, 1977), which may be distinguished solely by its larger, up to 2.5 mm long sicula attaining a level above the aperture of th 2. *Pseudomonoclimacis contumax* differs from stratigraphically younger *Ps. kosoviensis* in having a less robust rhabdosome with a straight to slightly dorsally curved proximal part and more closely spaced thecae. Small apertural outgrowths have been found in one mature specimen of *Ps. contumax*.

Jaeger (1978) demonstrated that the hook-like apertural structures in '*Monograptus*' sp. of Rickards & Palmer (1977) are secondary structures formed during the late astogenetic or gerontic stage of colony development. He also reported similar secondary outgrowths in *Colonograptus colonus*, *Saetograptus chimaera* and *Monoclimacis haupti*. The tendency to thecal isolation and development of lateral apertural lobes, however, may represent, at least in part, natural variability rather than gerontic growth because of its occurrence in immature rhabdosomes.

Although the resemblance of the proximal and mesial thecae of *Ps. kosoviensis* to *Monoclimacis* thecae is commonly enhanced by flattening, the distinct thecal geniculation, hook-like apertural growth additions in the proximal thecae of mature rhabdosomes, very rigid nema and proximal part of the rhabdosome lacking ventral curvature clearly differentiate these graptolites from the *Pristiograptus dubius* group, including *Pristiograptus frequens* Jaekel figured by Jaeger (1991, pl. 25, figs 9, 11, 15). *M. kosoviensis* Bouček and related taxa are best assignable to the genus *Pseudomonoclimacis* (Mikhaylova, 1976) *sensu* Koren' (1986), Urbanek (1997) and Lenz & Kozłowska-Dawidziuk (2004).

Pseudomonoclimacis aff. *kosoviensis* (Bouček, 1931)

Figures 6l, 7r

Remarks. Nine rhabdosomes found in the *fragmentalis* Biozone can be distinguished from typical *Ps. kosoviensis* by their relatively robust proximal part and lesser distal maximum width (2.1 mm). Thecae are equally overlapping and exhibit the same tendency to develop hook-like apertural outgrowths proximally. Thecae are wider and slightly more widely spaced (2TRD th 10 = 2.1 mm). This stratigraphically distinctive form is left in open nomenclature referring to its close similarity to *Ps. kosoviensis* until more material is available.

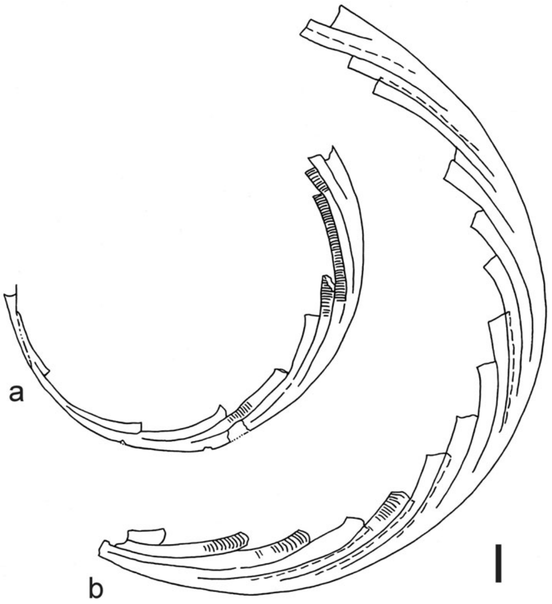

Figure 11. Type material of *Polonograptus chlupaci* sp. nov. (a) holotype PŠ 631; (b) paratype PŠ 667/1; *Nc. kozlowskii* Biozone, Kosov Quarry, × 5. Scale bar represents 1 mm.

Pseudomonoclimacis latilobus (Tsegelnjuk, 1976)
Figures 5d, e, j, r, s, 7q

1976 *Colonograptus latilobus* n. sp. Tsegelnjuk, p. 109, pl. 29, figs 9–11.
1983 *Saetograptus* (*Colonograptus*) *insignitus* n. sp. Přibyl, p. 160, pl. 1, figs 3–8; pl. 4, figs 11–13.
1988 *Ludensograptus latilobus* (Tsegelnjuk); Tsegelnjuk, p. 82, text-fig. 3.
1988 *Monograptus latilobus* (Tsegelnjuk); Koren', Lytochkin & Rinenberg, p. 17, text-figs 9–10.
1997 *Pseudomonoclimacis latilobus* (Tsegelnjuk); Urbanek, pp. 161–5, pls 17–19; text-figs 45–47.
1997 *Monograptus latilobus* (Tsegelnjuk); Koren' & Sujarkova, pp. 75–7, pl. 4, figs 3–4; text-fig. 11g–n.

Material. Twenty-two flattened rhabdosomes from bed nos 14, 16 and 20 of the Všeradice section (see Fig. 2) and several rhabdosomes from Velký Vrch near Koněprusy, including topotypical specimens of '*S. insignitus*' collected by Alois Přibyl.

Holotype. Specimen no N 1788/11 figured by Tsegelnjuk (1976) on plate 29 as figure 11; from the '?*leintwardinensis* Biozone' of the Gushcha borehole, Volynia, Ukraine.

Description. The dorsal wall of the medium-sized, 20–30 mm long rhabdosome is straight or slightly ventrally curved in the proximal part. The sicula is also ventrally curved. It is *c.* 2.0 mm long, including a rarely recognizable slender prosicular part. The readily visible metasicular portion is 1.4–1.5 mm long. Sicular aperture is 0.4 mm wide in profile, deeply concave, furnished with a *c.* 0.1 mm long dorsal lobe. The first theca initiates 0.2–0.3 mm above the sicular aperture. Th 1 is roughly triangular in outline, with a slightly everted aperture provided with more or less developed, ventrally directed, and paired lateral lobes. Distinct ventro-lateral apertural lobes are present on each theca throughout the rhabdosome. Thecae appear slightly geniculated owing to a gentle excavation on the ventral thecal wall. Flattened thecae exhibit somewhat isolated and introverted apertures with the lateral lobe separated by a notch from the ventral wall of the next theca. The ventral part of the apertural margin is either acuminate, when preserved in profile, or lobate, when obliquely flattened. Distal thecae are 2.1–2.4 mm long, straight and inclined at an angle of 40–50° to the rhabdosome. The rhabdosome is 0.85–0.95 mm wide at the th 1 aperture, 1.15–1.3 mm wide at th 3, 1.3–1.5 mm wide at th 5 and 1.6–1.8 mm wide at th 10. Maximum distal width of the rhabdosome, 2–2.1 mm, is attained by approximately the 14th theca. The 2TRD increases from 1.3–1.45 mm at th 2, to 1.5–1.7 mm at th 10 and then to the distal maximum of 1.75–1.95 mm, i.e. the distal thecae number 10.5–11.5 in 10 mm of rhabdosome length.

Remarks: The present material matches the typical specimens illustrated by Tsegelnjuk (1976, 1978) and Urbanek (1997). A morphologically less-advanced and stratigraphically younger morphotype, described and illustrated by Urbanek (1997, pl. 19) is similar to *Pseudomonoclimacis fecundus* (Přibyl, 1943), which can be distinguished by its poorly developed apertural lobes and less robust proximal-most part of the rhabdosome.

Polonograptus chlupaci sp. nov.
Figures 5o, 7o, 11a, b

1995a *Polonograptus egregius* (Urbanek); Štorch, p. 74–5, pl. 4, figs 1–5; text-figs 4d, 6f, i, j, l.

Name. After the late Prof. Ivo Chlupáč, distinguished Czech stratigrapher and palaeontologist.

Material. Eight complete and four incomplete flattened rhabdosomes and several fragments from Kosov Quarry and two incomplete rhabdosomes from the Všeradice section.

Holotype. Specimen no PŠ 631, figured by Štorch (1995*a*, pl. 4, fig. 3; text-fig. 6i) and refigured herein in Figure 11a, from the middle Ludfordian *Nc. kozlowskii* Biozone at Kosov Quarry near Beroun, Bohemia.

Diagnosis. Rhabdosome regularly ventrally coiled, almost circular. Sicula 1.3–1.7 mm long; the apex reaches about two-thirds up the 1.2–1.7 mm long th 1. Relatively short th 1 followed by considerably longer (2.4–3.6 mm) th 2. Thecae slender tubes terminated by simple apertures with gentle lateral apertural elevations; 4.4–4.9 mm long distal thecae overlap for about two-thirds their length.

Discussion. This unusual taxon was described by Štorch (1995*a*) from the *kozlowskii* Biozone of the Kosov Quarry as *Polonograptus egregius* (Urbanek, 1970). Two almost circular rhabdosomes encountered from the same level in the Všeradice section exhibit the same parameters medially and distally whereas their proximal parts are broken. The specimen shown in Figures 5o and 7o seems to have an incomplete th 1 and the sicula and initial bud are missing.

Urbanek (1970) erected '*Monograptus*' *egregius* based upon fragmentary material from the *kozlowskii* Biozone of the Mielnik Borehole in eastern Poland. The holotype is a distal fragment comprising four thecae and the paratype is a sicula with a very incomplete first theca. Urbanek (1970, pl. 42, fig. f) published a hypothetical complete development of the first theca based on isolated fragments, but subsequently this 'reconstruction' was used as the most essential part in the generic diagnosis of *Egregiograptus* Rickards & Wright, 1997. Koren' & Sujarkova (2004) encountered a rich and moderately well-preserved egregiograptid fauna in Tien Shan (Kyrgyzstan) and considered the extremely long th 1 a principal diagnostic feature of *Egregiograptus*. Accordingly, Koren' & Sujarkova referred Bohemian specimens with overall egregiograptid morphology combined with a short th 1 to a new, so far undescribed species of *Polonograptus*. This form, which is named *Polonograptus chlupaci* sp. nov. in this paper, can be barely distinguished from egregiograptids when its proximal part with its short th 1 and long th 2 is broken, since the mesial and distal parts of its rhabdosome match *Egregiograptus rinellae* Koren & Sujarkova, 2004, or *Egregiograptus egregius* Urbanek as illustrated by Tomcyzk, Urbanek & Teller (1990). The most similar polonograptid, *Polonograptus aloisi* Koren' & Sujarkova, 1997, differs from *P. chlupaci* in having an arcuately curved and more rapidly widening rhabdosome with strongly inclined, shorter and less-overlapping thecae.

Slovinograptus balticus (Teller, 1966)

Figures 5b, f, g, k–n, 7l, p

1966 *Monograptus balticus* n. sp. Teller, pp. 556–8, pl. 1, figs 6–11; text-fig. 4a, b.
1974 '*Monograptus*' *balticus* Teller; Paškevičius, p. 126, pl. 15, figs 1–5; pl. 19, figs 4–11; pl. 20, figs 1–2.
1976 *Wolynograptus balticus* (Teller); Tsegelnjuk, pp. 111–12, pl. 33, fig. 5.
1979 *Monograptus balticus* Teller; Paškevičius, pp. 168–9, pl. 12, figs 4–8; pl. 28, figs 1–12.
1983 '*Monograptus*' *balticus* Teller; Tsegelnjuk, pl. 145, fig. 34.
1983 *Monograptus* (*Wolynograptus*) *abhorrens* sp. nov.; Přibyl, pp. 159–60, pl. 2, figs 5–9; pl. 4, figs 5–9.
1988 *Monograptus balticus* Teller; Koren', Lytochkin & Rinenberg, p. 17, fig. 1.
1997 *Monograptus balticus* Teller; Koren' & Sujarkova, p. 71, pl. 1, figs 9–10; text-fig. 9e–h, (?a).

Material. Twenty rhabdosomes; mostly flattened. Several specimens are pyritized, either with periderm or preserved as internal moulds. An additional four flattened specimens originate from Velký Vrch (type locality of '*Monograptus* (*Wolynograptus*) *abhorrens* Přibyl).

Holotype. The specimen figured by Teller (1966, pl. 1, fig. 6) and refigured by Koren' & Sujarkova (1997, text-fig. 9g) from the upper Ludfordian of the Łeba 3 borehole in northern Poland.

Description. The otherwise straight rhabdosome is slightly dorsally curved in its slender proximal part. The sicula is 1.35–1.45 mm long, and gently ventrally recurved. Its apex reaches approximately two-thirds up th 1. The sicular aperture is concave in outline, 0.18–0.22 mm wide, furnished with a weakly developed dorsal lobe and short virgella. Slender, 1.25–1.45 mm long th 1 diverges at about 5° from the rhabdosome axis with its origin 0.25–0.4 mm above the sicular aperture. Thecal aperture is covered by tightly appressed, transversely extended hood. The succeeding thecae are slender, very gently inclined, straight or gently S-shaped tubes with prominent apertural hoods that may be responsible for the common subscalariform mode of rhabdosome preservation. A thecal length of 2.25 mm was measured in th 10, which overlaps for one-half of the succeeding theca (see also specimen in Fig. 5n). The rhabdosome widens gradually from 0.45 mm at the level of the first thecal aperture, to 0.6–0.7 mm at th 3, and 0.7–0.85 mm at th 5. A width of 0.85–1.2 mm is attained by about th 10 and is maintained in the distalmost parts of the present, still not fully mature rhabdosomes. The 2TRD is 1.7–2.0 mm at th 2, and 1.7–2.4 mm more distally.

Discussion. Tsegelnjuk (1976) assigned *Monograptus balticus* Teller, 1966 and another three species to his new genus *Wolynograptus*. He chose *Wolynograptus valleculosus* Tsegelnjuk, 1976 as the type species. This choice turned out to be unfortunate since *W. valleculosus* differs from other species included in this genus in having hooked metathecae without characteristic tightly appressed, globular and transversely extended apertural hoods. Its rhabdosome and described thecal morphology resemble *Uncinatograptus acer* (Tsegelnjuk, 1976) instead. Urbanek (1997) included slender wedge-shaped Ludfordian monograptids with thecal apertures covered by tightly appressed hoods in a new subgenus *Slovinograptus*. Morphological distinctiveness of its sigmoidally curved thecae and close affinities to *M. beatus* Koren' and *M. microdon* R. Richter (see Jaeger *in* Kříž *et al.* 1986) lead us to promote *Slovinograptus* to genus level. A successive series leading from Ludfordian *Sl. balticus* (Teller) through *Sl. beatus* (Koren') of Pridoli to Lochkovian *Sl. microdon* (R. Richter) has been suggested by Koren' (1983).

Flattened specimens of *Slovinograptus balticus* figured by Teller (1966) and Paškevičius (1974, 1979) differ from the present material in their more abrupt widening within the first 5–7 thecae, when measured without the apertural hoods. This apparent difference may be explained by the largely box-like mode of flattening of Polish and Lithuanian specimens, as suggested by pressed-through interthecal septa. The Bohemian specimens, by contrast, have been partly pyritized in calcareous shale and argillitic limestone. Specimen PŠ 2015 (Fig. 5n) is a pyritized internal mould preserved in relief. It is obvious that the dorsal rhabdosome curvature, missing in the specimens of '*Monograptus abhorrens* Přibyl, 1983' and specimens of *Sl. balticus* studied by Urbanek (1997, pl. 3, figs 2, 4, 5) is partly due to natural intraspecific variation and, in part, due to the subscalariform orientation of the rhabdosomes. No Bohemian specimen exhibits such pronounced and ventrally extended apertural hoods as does the rhabdosome figured by Koren' & Sujarkova (1997, text-fig. 9A). *Sl. balticus* either varies in its rhabdosomal curvature and apertural hood development or still comprises several palaeogeographically isolated populations of so far unrecognized taxonomic status. The type material of '*Monograptus abhorrens*' has been missing for at least 20 years. Owing to the considerable morphological variability caused by different preservation, observed already within our material from the Všeradice section, we have retained all material in a single species.

Slovinograptus cf. *balticus* (Teller, 1966)
Figures 6e, 7f

Remarks. This form is slender, gently S-shaped or almost straight except for a slightly dorsally curved proximal part comprising 2–3 initial thecae. The dorso-ventral width increases from 0.45 mm at th1, through 0.6 mm at th 3 and 0.75 mm at th 5, to 0.85 mm at th 10. The 2TRD of 1.9–2.1 mm is constant throughout the rhabdosome.

Sl. beatus (Koren', 1983) can be differentiated by its wider, more robust proximal part. *Sl. balticus* is distinguishable by its ventrally curved to almost straight, more rapidly widening proximal part and by its interthecal septa, which are inclined to the rhabdosome axis. Eleven rhabdosomes of *Slovinograptus* cf. *balticus* from the upper *fragmentalis* and *parultimus–ultimus* biozones in the Všeradice section help to fill a stratigraphical gap between the late Ludfordian slovinograptids (*Sl. hamulosus* and *Sl. balticus*) and forms ranging from the late Pridoli (*Sl. beatus* (Koren'), *Sl. aksajensis* (Koren')) through to the earliest Devonian *M. uniformis* Biozone (*Sl. microdon* (R. Richter)).

The narrow wedge-shaped rhabdosomes, ventral thecal walls parallel to the rhabdosome axis or sloping slightly inwards, and dorsal thecal walls terminated by an apertural hood transversely extended into a tabular or semicircular roof make this group of graptolites fairly distinctive.

Crinitograptus? sp.
Figures 6f, 7h

Remarks. About 20 dorsally arcuate, slender rhabdosomes of nearly uniform width were collected from a restricted interval of the uppermost *fragmentalis* and lowermost *parultimus–ultimus* biozones. Material is poorly preserved but obviously represents a distinctive form previously unknown from Bohemian sections. It is readily recognizable by its prominent apertural hoods combined with long and slender prothecae with ventral wall parallel to the rhabdosome. Short metathecae terminate with ventrally to proximo-ventrally directed apertural hoods which, in some specimens, appear to be transversely extended. Dorso-ventral width is 0.4–0.5 mm across the parallel-sided part of the theca and *c.* 0.85 mm across the apertural hood. The 2TRD is 2.3–2.55 mm in the majority of our specimens that are, however, either incomplete or just fragments. The proximal end is barely recognizable and the sicula is not preserved.

A similar taxon, designated as *Crinitograptus* cf. *operculatus* (Münch), has been encountered by Lenz & Kozłowska-Dawidziuk (2004) from the lowermost Pridoli of the Arctic Islands of Canada. The Canadian specimens are broader (0.6–0.7 mm without hoods and 1.0–1.2 mm across the hoods) and their thecae are more widely spaced (3 thecae in 5 mm). Until better specimens are available, the Všeradice material has also been tentatively assigned to *Crinitograptus* owing to the nearly uniform rhabdosome width, slender thecae with ventral walls parallel to the rhabdosome axis and apertural hoods. The hooded apertural structure and prothecae parallel to the rhabdosome, however, suggest that this taxon may have evolved from *Slovinograptus* instead.

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