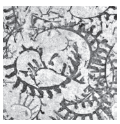
Graptolite biostratigraphy and biodiversity dynamics in the Silurian System of the Prague Synform (Barrandian area, Czech Republic)

Petr Štorch



Forty six graptolite biozones and seven subzones are recognized in the first compilation of high-resolution Silurian graptolite biostratigraphy in central Bohemia. The durations of these graptolite biozones, deduced from correlation with the Geological Time Scale 2020 age model and the global standard graptolite biozonation, range between *ca* 0.1 and 1.74 Myr. Each biozone is defined as an interval biozone named after the biozone index species, characterized by a typical biozone assemblage and delineated by bounding horizons with the stratigraphically lowest and/or highest occurrences of the respective index taxa. The *Petalolithus folium* Biozone is introduced as a replacement of the nearly equivalent *Pribylograptus leptotheca* Biozone, because the latter is a less common and less easily identified index taxon. Detailed range charts of 385 species of planktic graptolites based on *in situ* records from 88 localities and section logs in the offshore Silurian succession of the Prague Synform provide a solid data source for the proposed biozonal scheme and subsequent study of regional graptolite faunal dynamics, traced by means of species richness per biozone, mean standing diversity, time-normalized Van Valen's metrics, and FADs/LADs score per biozone. The moderate graptolite diversity of the lower Rhuddanian biozones rose to the mid-Aeronian maximum succeeded by stepwise decline forced by five globally recognized extinction events (mid-Aeronian *sedgwickii* Event, early Sheinwoodian *murchisoni* Event, mid-Homerian *lundgreni* Event, early Ludfordian *leintwardinensis* Event, and mid-Ludfordian *kozlowskii* Event). Sixth, early Telychian *utilis* Event is not observed in the Prague Synform as a results of a graptolite barren interval that separates *linnaei* and *turriculatus* biozones. Each mass extinction, although succeeded by recovery and adaptive radiation, resulted in a progressive step-wise reduction of graptolite diversity. • Key words: biozones, Prague Basin, range chart, diversity curve, mass extinction.

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The planktic graptolites are the fossils of primary choice in biostratigraphical subdivision and correlation of offshore Silurian strata worldwide. The rapid evolution, morphological diversity and complexity of graptolite rhabdosomes, combined with high numerical abundance and wide geographical distribution, have made graptolites the optimal biozone fossils in largely siliciclastic outer-shelf and deeper marine facies. It has been a long journey from the pioneer stratigraphical studies using graptolites (Lapworth 1878, Törnquist 1879, Marr 1880, Tullberg 1883) to the globally applicable graptolite biozonal schemes and correlation charts of Koren' *et al*. (1996) and Loydell (2012). Particularly high resolution graptolite biozonal schemes have been attained in the oxygen-depleted offshore facies of graptolitic black shales. Integrated graptolite, conodont, chitinozoan, spore, and microvertebrate biostratigraphy, combined with radiometric data and carbon isotope stratigraphy, have achieved remarkably high temporal resolution for the Silurian timescale (Cramer *et al*. 2011; Melchin *et al*. 2012, 2020)

The Prague Synform in the Barrandian area of Central Bohemia (Fig. 1) is among those regions in which the most detailed biostratigraphical studies have been undertaken. The Silurian succession is almost complete in this region and for the most part can be studied in graptolite-rich, offshore marine facies. The first comprehensive biostratigraphical subdivision of the Silurian succession of the Prague Synform, proposed in this study, is based upon data from 88 graptolite-bearing localities and sections, commonly studied bed by bed. New data are complemented by earlier graptolite records published by B. Bouček, A. Přibyl, H. Jaeger and J. Kříž from other localities, in particular temporary building excavations and dump-filled abandoned quarries and brick-pits.

Most of the Silurian graptolite biozones recognized herein (Fig. 2) have the potential for broad application in

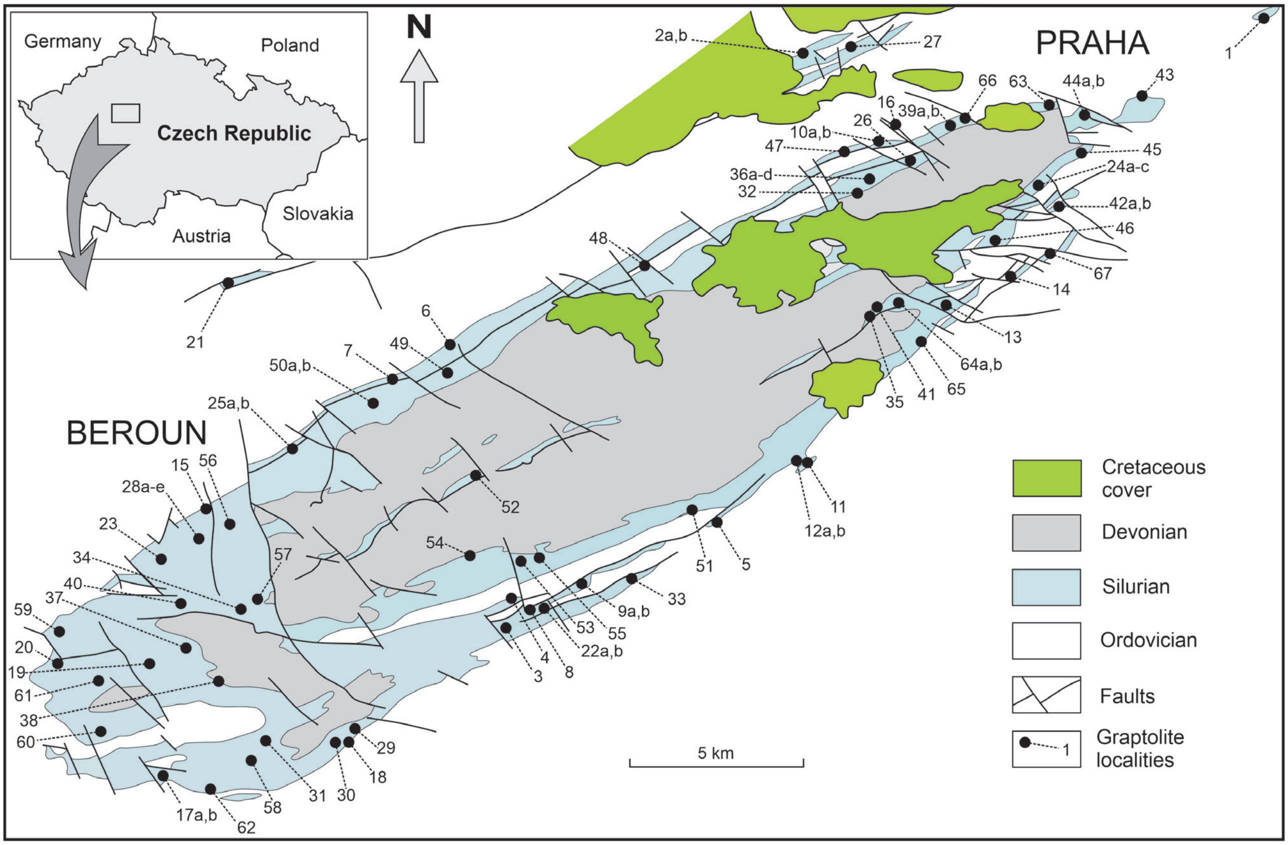


Figure 1. Location of the Prague Synform within the Czech Republic (small inset) and location of principal reference sections of Silurian graptolite biozones within the Silurian outcrop area of the Prague Synform. Base map provided by Š. Manda. See Appendix for locality names and further details.

the global correlation of Silurian strata, whereas several of the recognized subzones are intended mainly for regional correlations with possible usage across peri-Gondwanan Europe. Further refinement and improvement in the accuracy of the proposed biozonal scheme is limited by the available exposures, preservation of graptolites, a few taxonomic problems, and the sampling resolution that can be achieved in this relatively condensed sedimentary succession. Some parts of the Silurian succession, namely the Rhuddanian, Aeronian, Homerian and Gorstian strata, are better exposed and have more diverse graptolites whereas the middle Telychian is poorly exposed and the upper Ludfordian and upper Přídolí yield less well-preserved and markedly uniform, low diversity graptolite faunas.

Individual biozones tend to range from less than one metre to a few metres thick in the shale-dominated facies of the Prague Basin. Detailed range charts reveal that first appearances and last appearances of species are rarely concentrated in narrow intervals, except for the few mass-extinction events recognized both here and elsewhere around the world. Abrupt change in graptolite assemblages, especially if associated with an abrupt change of lithology, may well indicate a stratigraphical disconformity. This is also how graptolites have enabled recognition and dating of discrete stratigraphical unconformities associated with local gaps in sedimentation (*e.g.* Štorch 1986, 2006).

Geological setting and lithostratigraphy

The Lower Palaeozoic of Central Bohemia comprises the sedimentary cover of the Teplá–Barrandian Cadomian terrane, referred to as an independent microplate named Perunica by Havlíček *et al*. (1994), detached from the north-western Gondwana mainland and separate and distant from the eastern Cadomian-type terranes of Linnemann *et al.* (2004). Cocks & Torsvik (2002, 2006) and Torsvik & Cocks (2013, 2017) assumed that Perunica had remained close to Gondwana until the late Silurian but Stampfli *et al.* (2002), Robardet (2003) and von Raumer & Stampfli (2008) considered that the Teplá-Barrandian terrane, as a part of the Armorican terrain assemblage or HUN superterrain, was still an integral part of Gondwana at that time. The palaeogeographical position of Perunica (*e.g.* of the Teplá-Barrandian Unit) within the Rheic Ocean (Fig. 3) is still uncertain due to the wide range of palaeolatitudes indicated by palaeomagnetic data (Tait *et al.* 1994, 1995; Krs & Pruner 1995, 1999; Krs *et al.* 2001; Patočka *et al.* 2003; Aïfa *et al.* 2007; Tasáryová *et al.* 2014) and faunal affinity to different palaeocontinents among different fossil groups (Ebbestad *et al.* 2013, Eriksson *et al.* 2013, Goldman *et al.* 2013, Kröger 2013, Meidla *et al.* 2013, Molyneux *et al.* 2013).

The Silurian rocks of central Bohemia are formally divided into four successive formations (Fig. 2) and are preserved in the inner part of the Prague Synform (Fig. 1), a structure formed during the Variscan Orogeny. The Silurian succession represents an erosional remnant of the offshore part of a failed continental rift zone, named the Prague Basin by Havlíček (1981). This incomplete failed-rift basin was infilled by an Ordovician to Middle Devonian marine sedimentary succession associated with synsedimentary basaltic volcanics (see Chlupáč *et al*. 1998 for summary). The subsequent Variscan Orogeny affected the basin infill only slightly (Kříž 1998a), as demonstrated by a few major thrust faults (Melichar 2004), transverse faulting, local folding and low to moderate thermal maturity (Suchý *et al*. 2002).

Želkovice Formation

The Rhuddanian and Aeronian stages of the Prague Synform are represented by the Želkovice Formation (Fig. 2), defined by Perner & Kodym (1919) as the Želkovice Beds and redefined and upgraded to formation status by Kříž (1975). The formation is represented by a condensed offshore marine, anoxic sedimentary succession 0–16 m thick. Black silty shales, siliceous shales and thin-bedded silicites predominate; clayey shales are confined to the lowermost and uppermost parts of the Želkovice Formation (Štorch 2006). The beds are rich in planktic graptolites associated with organic walled microfossils (Dufka *et al*. 1995). Shelly faunas are confined to an isolated block of shallow-water volcanic-carbonate facies preserved along the Prague Fault northwest of the main Silurian synform (Havlíček & Kříž 1973, Štorch 2001). The Želkovice Formation overlies pale-coloured uppermost Hirnantian mudstones of the Kosov Formation. The onset of its anoxic black shale sedimentation was in the lowermost Silurian *Akidograptus ascensus* Biozone (Horný 1956; Štorch 1986, 2006). Sedimentation temporarily ceased in the early Rhuddanian, revived in the upper *Cystograptus vesiculosus* Biozone in the majority of studied sections, and continued without further interruption across the Rhuddanian–Aeronian boundary interval, through the entire Aeronian, capped by deposition of one or more non-fossiliferous beds of pale-coloured mudstone and claystone intercalated with black shale containing graptolites of the lower Telychian *Rastrites linnaei* Biozone.

Litohlavy Formation

Pale-coloured mudstone, dated by its black-shale intercalations to the lowermost Telychian *linnaei* Biozone within a substantial part of the Silurian synform, marks the base of the Litohlavy Formation (Fig. 2), defined by Kříž (1975) and further described by Dufka *et al*. (1995) and Štorch (2006). The most complete black-shale succession, with little or no gap in sedimentation, is developed in the south-western and northeasternmost parts of the Prague Synform. By contrast, a long-lasting gap in sedimentation, comprising the whole of the Rhuddanian, Aeronian and also lower Telychian, is known from the north-central part of the Prague Synform (Štorch 1986, 2006). In the Velká Ohrada and Praha-Pankrác sections the basal mudstone of the Litohlavy Fm. is directly overlain by a black shale with a graptolite fauna indicating the *Monoclimacis griestoniensis* Biozone. In many sections the lower Silurian black-shale succession is sandwiched by alkaline doleritic basalt sills (Kříž 1998a). The middle Telychian, comprising the *griestoniensis*, *tullbergi* and *spiralis* biozones, is the least studied part of the Silurian succession. The beds are graptolite-rich black argillitic shales rhythmically alternating with non-fossiliferous pale mudstone interbeds. Greenish-grey mudstone intercalations disappear at about the base of the *Oktavites spiralis* Biozone. The Litohlavy Formation, 11–40 m thick, is commonly weathered and decomposed near the surface, leaving few outcrops except those shales hardened by the thermal influence of a neighbouring basalt sill. Stratigraphically significant surface sections are absent.

Motol Formation

The overlying Motol Formation (Fig. 2), defined by Perner & Kodym (1919), was promoted to formation status by Kříž (1975). The base of the Motol Fm., marked by the disappearance of pale-coloured mudstone intercalations, approximately correlates with the lower limit of the *spiralis* Biozone. The graptolitic shales of lower Motol Fm. become marly close to the Llandovery–Wenlock boundary. The first limestone intercalations with abundant shelly fauna appear in the lower Sheinwoodian *Cyrtograptus bohemicus*–*Cyrtograptus murchisoni* Biozone in Beroun-Lištice (Kříž 1992), Malá Chuchle-Vyskočilka (Havlíček & Štorch 1990) and between Řeporyje and Velká Ohrada (Bouček 1937). The stratigraphically higher part of the Motol Fm. witnessed progressive environmental differentiation within the Prague Basin in response to synsedimentary basalt volcanism giving rise to a complex facies suite, up to 250 m thick. The minimum thickness, about 80 m, has been recorded in the offshore facies of

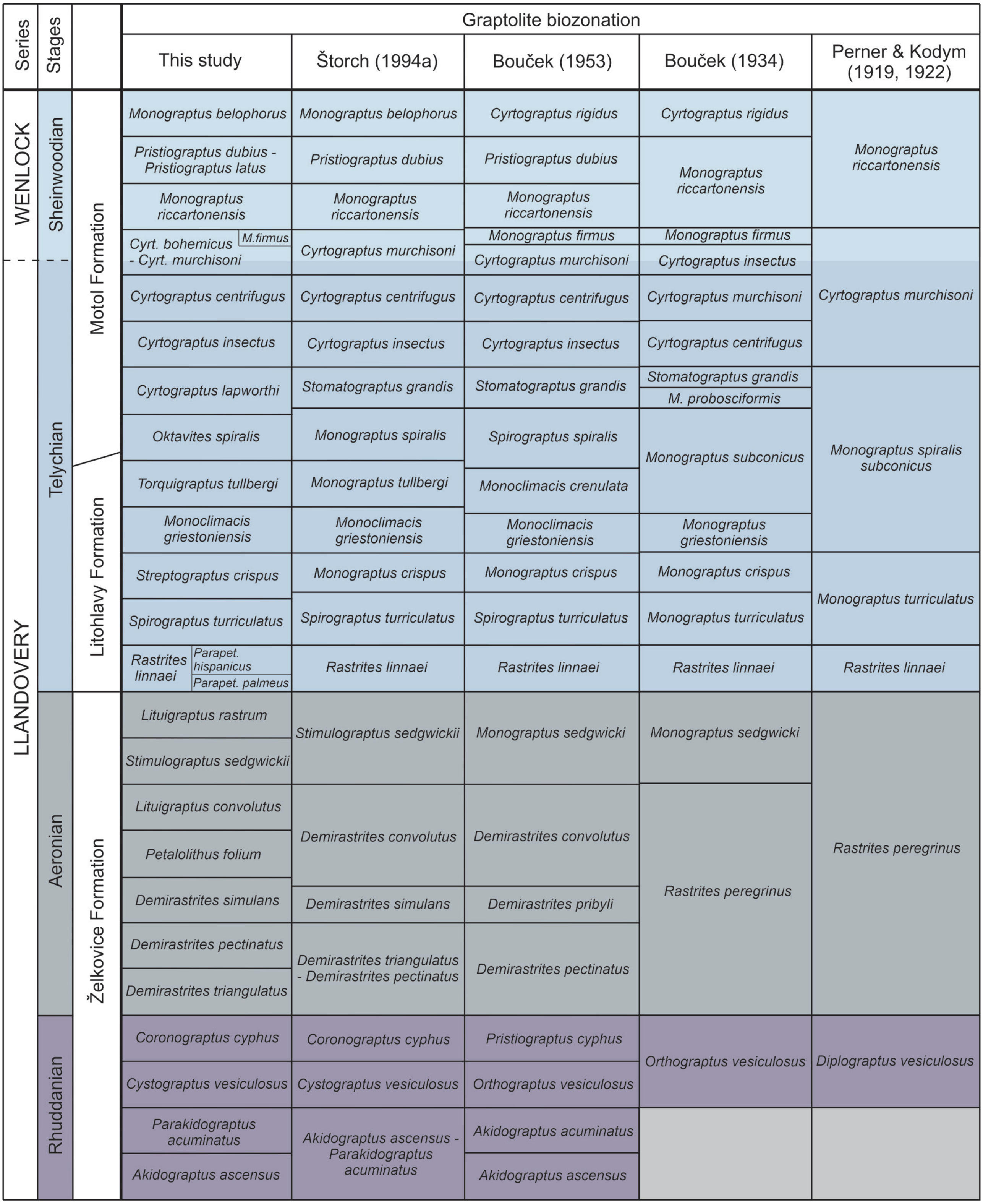


Figure 2. Graptolite biozones and subzones recognized in the Silurian System of the Prague Synform correlated with the biozonal schemes developed by Přibyl (1948, 1983), Štorch (1994a), Bouček (1934, 1953), and Perner & Kodym (1919, 1922). The biozones are grouped by colours that pertain to the respective Silurian stages. The same colours are used in Figs 5, 7, 9, 11, 13, 14, 16, 19, 22, 24 and 26. Abbreviations: W – Wenlock biozonation; LU-P – Ludlow and Přídolí biozonation.

Series	Stages	Formation	Graptolite biozonation: This study	Přibyl (1983) LU-P Štorch (1994a) W	Přibyl (1948)	Bouček (1934)	Perner & Kodym (1919, 1922)
PŘÍDOLÍ		Požáry Formation	*Skalograptus transgrediens*	*Colonograptus transgrediens*	*Pristiograptus transgrediens*	*Monograptus* n. sp.	*Monograptus ultimus*
			Wolynograptus perneri	*Monograptus perneri*	*Monograptus perneri*		
			Slov. beatus *Wolynograptus bouceki*	*Monograptus bouceki*	*Monograptus bouceki*	*Monograptus tumescens*	*Monograptus transgrediens*
			Sk. lochkovensis *U. pridoliensis*	*Col. lochkovensis* *Monograptus pridoliensis*	*Colonograptus lochkovensis*		
			Skalograptus parultimus - Skalograptus ultimus	*Pseudomcl. ultima*	*Monograptus ultimus*	*Monograptus ultimus*	
LUDLOW	Ludfordian	Kopanina Formation	*Pristiograptus fragmentalis*	*Pristiograptus fragmentalis*	*Pristiograptus tumescens* *Pristiograptus fragmentalis*		
			Pseudomcl. latilobus - Slovinograptus balticus	*Pristiograptus fecundus* *Colonograptus insignitus*			
			Neocucullograptus kozlowskii	*Neocucullograptus inexpectatus*			
			Neocucullograptus inexpectatus				
			Bohemograptus tenuis	*Bohemograptus bohemicus* *Pristiograptus longus*	*Pristiograptus longus*		
			Saetograptus leintwardinensis	*Saetograptus linearis* *Pristiograptus tumescens*	*Saetograptus leintwardinensis primus*		
	Gorstian		*Saetograptus chimaera - Lobograptus scanicus*	*Lobograptus scanicus*	*Monograptus scanicus*	*Monograptus scanicus*	
			Saet. fritschi *Lobograptus progenitor*	*Lobograptus progenitor*	*Pristiograptus nilssoni*	*Pristiograptus nilssoni*	*Monograptus colonus*
			Neodiversograptus nilssoni	*Neodiversograptus nilssoni*			
WENLOCK	Homerian	Motol Formation	*Colonograptus ludensis - Colonograptus gerhardi*	*Pristiograptus ludensis*			
			Col. praedeubeli - Col. deubeli	*Prist. praedeubeli - Pristiograptus deubeli*			
			Gothograptus nassa - Pristiograptus frequens	*Gothograptus nassa - Prist. dubius frequens*			
			Pristiograptus parvus	*Pristiograptus parvus*			
			Monograptus flemingii	*Cyrtograptus lundgreni*	*Monograptus testis*	*Monograptus testis*	*Monograptus testis*
			T. testis *Cyrtograptus lundgreni*		*Cyrtograptus lundgreni* *Cyrtograptus radians*	*Cyrtograptus radians*	
	Sheinwoodian		*Cyrtograptus ramosus - Cyrtograptus perneri*	*Cyrtograptus ramosus - Cyrtograptus perneri*	*Cyrtograptus perneri* *Cyrtograptus ramosus*	*Cyrtograptus perneri* *Cyrtograptus ramosus*	
			Cyrtograptus rigidus	*Cyrtograptus rigidus*	*Monograptus flexilis*	*Monograptus flexilis*	
			Monograptus belophorus	*Monograptus belophorus*	*Cyrtograptus rigidus*	*Cyrtograptus rigidus*	*Monograptus riccartonensis*

Figure 2. Continued.

the Silurian strata preserved in the SE limb of the Prague Synform. The proximal volcano-sedimentary facies that developed in the proximity of volcanic fissures consists of effusive alkaline basalts, agglomerates, hyaloclastites, coarse-grained pyroclastics and shallow-water bioclastic limestones restricted to calm periods without volcanic activity. The hard substrates provided by rising volcanic accumulations rich in nutrients prompted the rapid growth

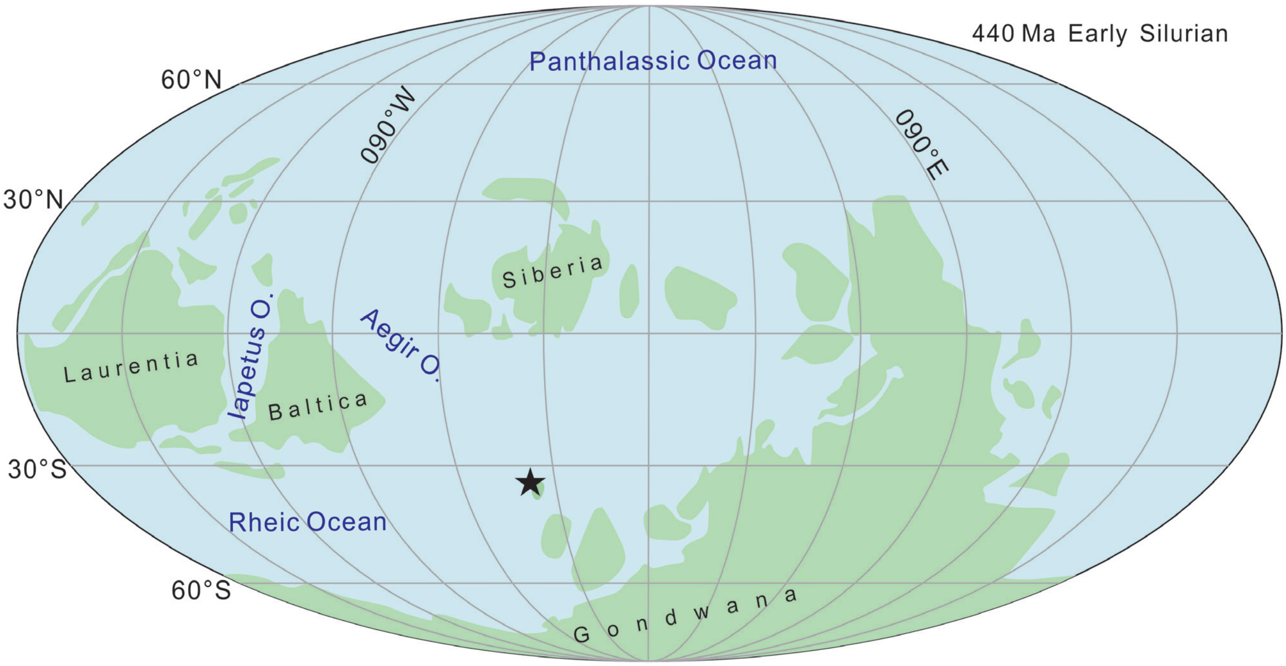


Figure 3. Presumed palaeogeographical location of the Perunica microplate (highlighted by the black asterisk) within the Silurian world. Base map modified from the palaeomap of Torsvik & Cocks (2017).

of benthic faunal communities and consequent formation of biodetrital limestones. The distal volcano-sedimentary facies deposited around the volcanic highs consists of alternating tuffites, hyaloclastites, subordinate effusive basalts and platy biodetrital limestones. The Kozel Limestone Member, comprising a thick succession of biodetrital and tuffitic limestones of Homerian age, has been distinguished by Frýda & Frýdová (2014) in the Svatý Jan Volcanic Centre. The truly offshore facies of the Motol Fm., which was deposited distal to the volcanic centres beyond the direct influence of local volcanic events, is confined for the most part to south-western closures and the southern limb of the present-day Prague Synform. Black laminated calcareous shales with a tuffitic admixture, limestone nodules, thin beds of tuffites and local, largely tuffitic slump beds are the most important source of high-resolution graptolite biostratigraphical data in the middle and upper parts of the formation. First evidence of the volcanic activity occcurs below the *Monograptus belophorus* Biozone in the Svatý Jan area; the subsequent major volcanic period was late in the Sheinwoodian but minor events continued through the early Homerian and formed small, probably short-lived volcanic islands as documented by land-plant fossils recorded in this area (Libertín *et al*. 2018). The most widespread tuff and/or tuffite bed occurs in sections across the whole Prague Synform where the mid-Homerian *Pristiograptus parvus* Biozone is exposed.

Kopanina Formation

The same sedimentary and volcanic regimen continued during deposition of the lower part of the Kopanina Formation, a unit first distinguished by Prantl & Přibyl (1948) who defined its lower limit biostratigraphically at the base of *Neodiversograptus nilssoni* Biozone (Fig. 2). Lithostratigraphical definition of the base of Kopanina Fm. is problematical due to the very diverse facies development and limited biostratigraphical control in and around the volcanic centres, as noted by Horný *et al*. (1958), Kříž *et al*. (1993) and Kříž (1998a). All earlier attempts at lithostratigraphical definition of the lower boundary of the Kopanina Fm. failed. Several volcanic centres redeveloped in the third and most extensive volcanic period that marks the Wenlock–Ludlow boundary interval across the whole Prague Synform (Kříž 1991, 1998a). The lower limit of the Kopanina Fm., based on lithology, and correlative with its original biostratigraphical definition by Prantl & Přibyl (1948), can be recognized in the offshore shale-dominated facies less affected by the eruptions of the relatively distant volcanic centres. In the shale-dominated facies, the uppermost Homerian *Colonograptus ludensis*–*Col. gerhardi* Biozone is separated from the lowermost Gorstian *nilssoni* Biozone by a prominent, basin-wide, single or multiple layer of basalt pyroclastics, which may be potentially used as a lithological marker of the lower limit of the

Kopanina Fm. An extensive lava sheet of the Svatý Jan Volcanic Centre formed a significant volcanic island that probably persisted until the early–middle Přídolí in the north-western limb of the Silurian synform (Havlíček & Štorch 1990). The total thickness of the Kopanina Fm. ranges from 50 m in the shale-dominated south-western closures of the Prague Synform (Western Segment of Kříž 1998a, b) to a maximum of 150 m south of the major volcanic centres. The upper Gorstian succession of the Kopanina Fm. (*Saetograptus chimaera–Lobograptus scanicus* Biozone) is characterized by a rapid decrease of volcanic activity and further spread of biodetrital limestones. The Svatý Jan volcanic island was surrounded by extensive shallow marine areas covered by crinoid thickets and coral-stromatoporoid dominated biostromes. Redeposited tuffs and tuffaceous limestones prevail in the SE limb of the Prague Synform. Cephalopod limestones and biodetrital limestones rich in varied benthic faunas mark the lower Ludfordian part of the formation (Kříž 1998a, b). A widespread "*linguata*" bank of brachiopod limestone was deposited in shallow-water, subtidal settings. Subsequent mid-Ludfordian deepening of the basin is marked by the sudden replacement of massive skeletal limestones by platy limestones and calcareous shales with deeper water benthic faunas and graptolites of the *Neocucullograptus inexpectatus* and *Nc. kozlowskii* biozones. Subsequent environmental changes and sea-level fluctuations (Lau Event and/or Kozlowskii Event) manifest themselves in faunal change and extinction, local disconformities, channel like structures filled by debris flows and slumps (Horný 1955, Štorch *et al*. 2014). The upper Ludfordian part of the Kopanina Fm. consists of a limestone-dominated succession. The topmost part is widely represented by a prominent bank of biodetrital and cephalopod limestones (Kříž *et al*. 1986; Kříž 1998a, b). Shale-dominated off-shore facies with subordinate limestones continue in south-western closures, the southern limb, and Pankrác segment of the Silurian synform.

Požáry Formation

The Požáry Formation, of Přídolí Age, was defined by Kříž (1989) as a formal replacement of the Přídolí Formation distinguished by Prantl & Přibyl (1948). The new formation name was introduced to avoid confusion with the Přídolí Series – then a newly accepted international chronostratigraphical unit (Kříž *et al*. 1986). The lower boundary of the 20–80 m thick Požáry Fm. is defined by the onset of platy limestones interbedded with shales (Kříž 1998a). This change in lithology coincides with the Ludlow–Přídolí boundary and base of the *Skalograptus parultimus–Sk. ultimus* Biozone (Fig. 2) in many sections, but, elsewhere the thick-bedded biodetrital limestones of the upper Kopanina Fm. continue into the lower Přídolí or, on the contrary, terminated in the uppermost Ludlow below the base of the Přídolí (Kříž *et al*. 1986, Manda *et al*. 2023). The Požáry Fm. is represented by two principal facies. A biodetrital (skeletal) limestone facies without any graptolites is limited to former volcanic elevations and adjacent areas (Horný 1955, 1962; Kříž 1998b). The early Ludlow basalt sheet of the Svatý Jan Volcanic Centre is overlain by shallow subtidal grainstones of mid-Přídolí age with a prominent erosional unconformity. Biodetrital limestones pass basin-ward into muddy skeletal, largely cephalopod limestones. Despite local temporary incursions of the more offshore facies, a general trend of basin-ward progradation of the biodetrital limestone facies can be observed in the middle and upper part of the formation (Kříž 1998a). The upper part of the formation is further marked by abundant crinoid columnals, coarse sands and lobolite bearing beds pertaining to a time-specific faunule of pelagic crinoids of the *Scyphocrinites* group (Havlíček & Štorch 1990). The graptolitic offshore facies consists of platy limestones, usually laminated lime mudstones, intercalated with black shales (Horný 1955, Kříž 1998a). Interbedded platy limestones and shales are most widespread in the lower part of the formation but, in the SE limb of the Silurian synform, persisted up to the upper limit of the formation (Horný 1955), which has been dated biostratigraphically (Chlupáč 1998) and coincides with the Silurian–Devonian boundary.

Research history

The earliest biostratigraphical subdivision of Barrande's Étage E (Barrande 1846, 1852) based on graptolites was introduced in the central Bohemian Prague Synform by Marr (1880, Fig. 5) who recognized three biozones, and listed (pp. 604, 605) characteristic species from them, in ascending order: the *Diplograptus*-zone, the *Priodon*-zone and the *Colonus*-zone in the upper part of the Silurian succession. More advanced subdivision was introduced by Perner & Kodym (1919, 1922) who recognized nine graptolite biozones (Fig. 2) within an interval embracing the middle Rhuddanian – lower Gorstian in the current sense. Key biostratigraphical and taxonomic work carried out by B. Bouček before World War II increased the number of graptolite biozones recognized in the Silurian succession of the Prague Synform to 25. Major refinement of the biozonal scheme was achieved in the upper Llandovery and Wenlock interval (Bouček 1931a, 1932a, 1934), but new assemblage biozones were established also in the Ludlow (Bouček 1936). Detailed revision of Barrande's so-called colonies (Barrande 1861, 1862, 1865, 1870, 1881) resulted in a further upgrade of the

Llandovery biozonation by Přibyl (1940a). Systematic and biostratigraphical research based on extensive field studies led to the first subdivision of the Přídolí succession, then known as the upper Budňanium (Přibyl 1940b). New biozones were introduced and existing ones altered by Přibyl (1948) in the frame of expanded catalogue of Czech Silurian graptolites (Fig. 2).

Temporary building excavations and new geological mapping carried out since the 1950s revealed several globally recognized lowermost Silurian graptolite biozones, not known from the Prague Basin until then (Marek 1951, Bouček 1953, Horný 1956). Bouček (1953) published a still more refined biozonal scheme for the Llandovery and Wenlock succession (Fig. 2) along with faunal lists and brief description of the graptolite biozones. Horný *et al*. (1958) shed more light on the graptolite biostratigraphy across Wenlock–Ludlow boundary interval.

Přibyl (1983) developed a graptolite biozonation for the long overlooked upper Silurian. He established and redefined 11 graptolite biozones in the Ludlow and 6 biozones in the Přídolí (Fig. 2), and provided correlation with biozonal schemes then used in Poland, Thuringia, Eastern Serbia, Great Britain and North Africa. A similar account was published by Štorch (1994a) who summarized published and new data and provided range charts for taxonomically valid graptolite species then known from the Llandovery and Wenlock of the Prague Basin. All of the 27 biozones recognized (Fig. 2) were defined as various types of taxon range biozones. Kříž *et al*. (1986) revised the graptolite biozonation of the Přídolí as part of their formal proposal of the Přídolí for the fourth series of the Silurian System (Kříž 1989). Jaeger *in* Kříž *et al*. (1993) recognized in the Prague Synform new biozones formerly established in the upper Homerian of Thuringia. Štorch (2006) paid particular attention to the stratigraphical and regional extent of gaps in Llandovery sedimentation recognized by means of high-resolution graptolite stratigraphy and correlation. He defined 19 biozones and 5 subzones in the Llandovery succession as interval biozones.

Further taxonomic work and detailed stratigraphical examination of both traditional and temporary sections (Manda *et al*. 2012, 2019; Štorch & Frýda 2012; Štorch *et al*. 2014, 2016, 2018), along with the increasing need for fine resolution of stratigraphical subdivision and global correlation, resulted in the present biozonal system (Fig. 2) comprising 46 graptolite biozones spanning the 24.07 Myr of the Silurian Period (duration from Melchin *et al*. 2020).

Methods

Biostratigraphical data

The graptolite fossil record of the Prague Synform summarized in this study is based extensively on the author's own sampling of 46 localities and sections, for the most part studied bed by bed. This data-set has been complemented by published graptolite records from another 42 localities, largely building excavations no longer accessible for study (see the Appendix for locality names, current status and GPS coordinates). Graptolites from Czech sections are usually preserved as flattened impressions, either carbonized or partly pyritized, without apparent effects of tectonic strain (Fig. 4A–J). Cling-film preservation (Jones *et al*. 2002), indicating sea bottom sealed by bacterial mats, is particularly well developed in the Lower Telychian (Fig. 4J) but probably existed in muddy offshore facies of the Prague Basin through much of the Silurian Period. Fine apertural details, ancorae, and membranous tissues as well as some internal structures such as interthecal and rhabdosome septa and nemata are seen pressed through in shales bleached by fossil weathering (Fig. 4B, C, F, G, I). Some limestones bear full-relief rhabdosomes entombed in the rock

Figure 4. Modes of graptolite preservation in the Silurian succession of the Prague Synform. • A – full-relief pyritized rhabdosomes of *Streptograptus plumosus* (Baily), *Torquigraptus involutus* (Lapworth), *Torquigraptus planus* (Barrande) and juvenile *Spirograptus guerichi* Loydell *et al*., preserved in argillaceous black shale of the *linnaei* Biozone, PŠ 4601, lowermost Litohlavy Formation, Radotín-tunnel. • B – flattened *Akidograptus ascensus* Davies in partly bleached argillaceous shale of the lowermost Želkovice Formation, PŠ 141/2, *ascensus* Biozone, Běleč. • C – delicate rhabdosome of *Gothograptus domeyki* Kozłowska preserved in partly bleached calcareous shale of Motol Formation, PŠ 3869, upper *lundgreni* Biozone, Kosov quarry, 4th level. • D – *Monograptus belophorus* (Meneghini) in tuffitic muddy limestone of the Motol Formation, D 553, *belophorus* Biozone, Loděnice-Černidla. • E – full-relief *Colonograptus colonus* (Barrande) entombed in limestone nodule in the lowermost Kopanina Formation, BB 6997, *nilssoni* Biozone, Praha-Butovice, Na Břekvici. • F – mass occurrence of flattened *Wolynograptus bouceki* (Přibyl) in bleached calcareous shale of Požáry Formation, PŠ 4463, *bouceki* Biozone, Radotín-Hvížďalka. • G – limonite coated imprint of *Petalolithus folium* (Hisinger) showing internal structure pressed-through, bleached siliceous shale of middle Želkovice Formation, PŠ 730, *folium* Biozone, Tmaň-Sv. Jiří. • H – *Lituigraptus rastrum* (Törnquist) preserved in low relief in argillaceous black shale of the uppermost Želkovice Formation, PŠ 1008, *rastrum* Biozone, Želkovice-behind farm. • I – bleached siliceous shale of the middle Želkovice Formation covered by flattened limonitized rhabdosomes of *Lituigraptus richteri* (Perner), *Rastrites approximatus* Perner and *Monograptus mirificus* Štorch, PŠ 795, *folium* Biozone, Tmaň-Sv. Jiří. • J – clingfilm-preserved *Spirograptus turriculatus* (Barrande) in black shale of the lower Litohlavy Formation, PŠ 4600, uppermost *turriculatus* Biozone, Litohlavy-railway cut. Scale bars represent either 5 mm in figs A, D–F, H–J or 1 mm in figs B, C, G.


A
B
C
D
E
F
G
H
I
J

Table 1. List of sources for graptoloid species recorded in nine graptolite range charts (beginning with Fig. 5).

Source number	Reference	Source number	Reference
1	Bouček (1930)	43	Přibyl (1942a)
2	Bouček (1931a)	44	Přibyl (1942b)
3	Bouček (1931b)	45	Přibyl (1943a)
4	Bouček (1932a)	46	Přibyl (1943b)
5	Bouček (1932b)	47	Přibyl (1943c)
6	Bouček (1933)	48	Přibyl (1945)
7	Bouček (1936)	49	Přibyl (1946)
8	Bouček (1937)	50	Přibyl (1981)
9	Bouček (1944)	51	Přibyl (1983)
10	Bouček (1953)	52	Přibyl & Münch (1942)
11	Bouček & Münch (1944)	53	Přibyl & Štorch (1983)
12	Bouček & Münch (1952)	54	Přibyl & Štorch (1985)
13	Bouček & Přibyl (1942a)	55	Štorch (1980)
14	Bouček & Přibyl (1942b)	56	Štorch (1982)
15	Bouček & Přibyl (1943)	57	Štorch (1983a)
16	Bouček & Přibyl (1952a)	58	Štorch (1983b)
17	Bouček & Přibyl (1952b)	59	Štorch (1985)
18	Bouček & Přibyl (1953)	60	Štorch (1986)
19	Dufka *et al*. (1995)	61	Štorch (1988)
20	Horný (1956)	62	Štorch (1991)
21	Kozłowska (2021)	63	Štorch (1992)
22	Kozłowska-Dawidziuk *et al*. (2001)	64	Štorch (1994a)
23	Kříž (1992)	65	Štorch (1994b)
24	Kříž *et al*. (1986)	66	Štorch (1995a)
25	Kříž *et al*. (1993)	67	Štorch (1998)
26	Libertín *et al*. (2018)	68	Štorch (2001)
27	Loydell *et al*. (1993)	69	Štorch (2006)
28	Loydell *et al*. (1997)	70	Štorch (2015)
29	Manda *et al*. (2012)	71	Štorch & Frýda (2012)
30	Manda *et al*. (2019)	72	Štorch & Manda (2019)
31	Manda *et al*. (2023)	73	Štorch & Melchin (2018)
32	Piras (2006a)	74	Štorch & Loydell (1992)
33	Piras (2006b)	75	Štorch *et al*. (2009)
34	Prantl & Přibyl (1940)	76	Štorch *et al*. (2014)
35	Prantl & Přibyl (1944)	77	Štorch *et al*. (2016)
36	Přibyl (1940a)	78	Štorch *et al*. (2018)
37	Přibyl (1940b)	79	Štorch *et al*. (unpublished data)
38	Přibyl (1940c)	80	Sun *et al*. (2022)
39	Přibyl (1940d)	81	Turek (1990)
40	Přibyl (1941a)	82	Zalasiewicz *et al*. (1995)
41	Přibyl (1941b)	•	Author's personal observation
42	Přibyl (1941c)		

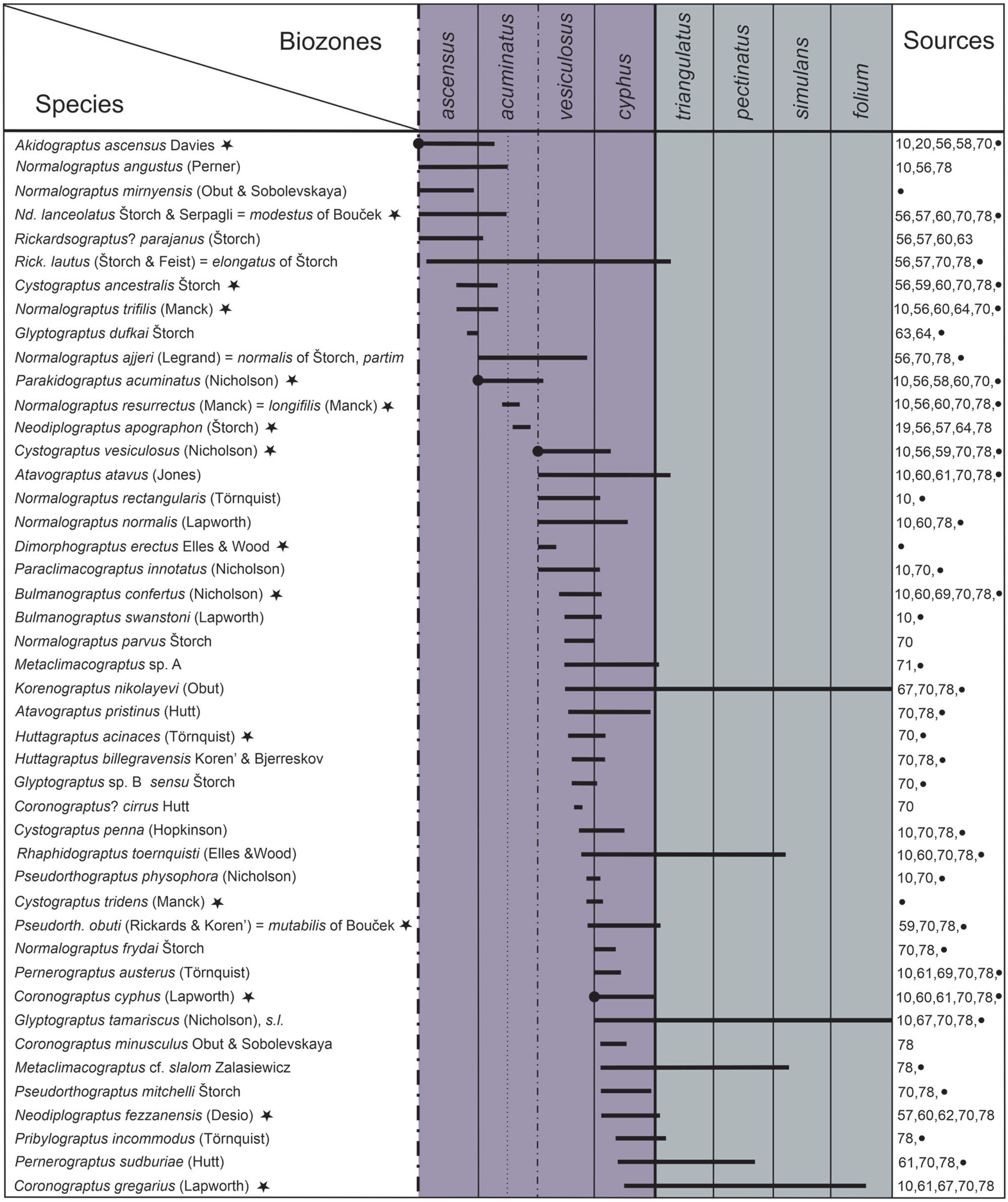


Figure 5. Stratigraphical ranges of Rhuddanian graptolites in the Prague Synform. Solid black circles terminating the taxon-range line mark the lowest and/or highest occurrence of index species defining the bounding biohorizon. Numbers refer to published sources of graptolite ranges that may have been supplemented or corrected by new, unpublished data (black dot). Vertical dash-and-dot lines indicate that the graptolite record is missing between neighbouring biozones due to a gap in sedimentation or a graptolitically barren interval. Figured species are marked by an inverted black star. See Table 1 for list of graptolite data sources.

through early lithification (Fig. 4E). Organic structures of such rhabdosomes, however, are commonly densely fragmented by post-diagenetic processes.

Most of the 385 graptoloid species recorded in nine graptolite range charts (beginning with Fig. 5) have been already documented and figured in published papers listed in Table 1. This source of data has been supplemented by recent, as yet unpublished personal observations by the author. Some of the species recorded from the Prague Synform for the first time are figured along with biozone-index species and other age-diagnostic taxa of the respective Silurian stages in Fig. 6 and subsequent graptolite figures. Some of the species defined by earlier authors have had to be revised, reassigned to a different taxon or listed under their senior name. A misidentification or junior name naturalized in the earlier papers on Czech graptolite fauna is presented after the valid name. Some other species reported from the Prague Synform without sufficient material evidence from examined stratigraphic sections have not been included in the range charts. Generic classification has been updated to follow the new edition of the Graptolite Treatise (Maletz 2017, 2019a, b; Maletz & Loydell 2021; Lenz *et al*. 2018).

Biozonal concept

Early graptolite biozonal charts for the Silurian succession of the Prague Synform (or Barrandian area) utilized some kind of "Oppel zones" or assemblage biozones without precise definition (Marr 1880; Kettner & Kodym 1919; Perner & Kodym 1919, 1922; Kettner & Bouček 1936; Přibyl 1948), better specified assemblage biozones (Bouček 1953), or taxon-range biozones (Štorch 1994a). More recently Štorch (2006) re-defined the graptolite biozones of the Llandovery Series of the Prague Synform as interval biozones in the sense of second edition of the International Stratigraphic Guide (Salvador 1994) and third edition of the Czech Stratigraphic Guide (Chlupáč & Štorch 1997). This approach, not very different from the assemblage biozones advocated by Rickards (1995), is followed in the present paper.

Each interval biozone or subzone included in the present biozonal scheme is named after the most significant, preferably traditional index species and delineated by its bounding biohorizons defined, as a rule, by the lowest occurrence of a distinct taxon, usually but not necessarilły the name-giving one (Fig. 3 and subsequent range chart figures). Bounding biohorizons defined by the highest occurrence of a distinct taxon can be also applied if needed. An interval biozone is further characterized by a distinct graptolite assemblage. The name giving biozone fossil may be missing in some samples between the boundary horizons, which is a common case in biostratigraphical sampling. The biozonal assemblage may vary in composition but, combined with bounding horizons, allows for long-range, high-resolution correlation less affected by stratigraphical overlaps or gaps among the name-giving biozone species, as it is not dependent on just a single species. Each biozonal assemblage as a whole provides an improved basis for global correlation, including the recognition of different graptolite faunal provinces and biofacies. It is also useful in correlation with less well known or less fossiliferous sections. A few biozones following some mass graptolite extinction events equate with the interregna of Jaeger (1959) and Zalasiewicz *et al*. (2009). These intervals are of significant value in both correlation and in understanding graptolite faunal dynamics and are named after long-ranging species which may proliferate in the low graptolite diversity interval with boundaries delineated by the highest and lowest occurrences of index taxa of adjacent biozones. Some biozones, informally designated as combined biozones, are named after two, largely or entirely overlapping index taxa. The first named species is that delineating the lower limit of the combined biozone.

The graptolite biozones recognized in this study are mostly based upon published reference sections to allow for subsequent revisions and improvements of stratigraphy and correlation. Many reference sections are no longer accessible but all have been documented by a more-or-less detailed section logs and located by GPS coordinates recorded in the Appendix.

Estimation of diversity trends

The global diversity and faunal dynamics of Silurian graptoloids were analyzed by Melchin *et al*. (1998) and later revealed in more detail through global composite analyses by Sadler *et al*. (2011) and Cooper *et al*. (2014) using advanced time-scale calibrated numerical correlation by constrained optimization (CONOP). The present study has focussed on regional faunal dynamics decoded from the high-resolution stratigraphical record of the 385 graptolite species identified in the Silurian succession of the Prague Synform, without integration of other biological, geochemical, isotopic and sequence-stratigraphical proxies. Meaningful application of CONOP, or the Horizon annealing (HA) method of Melchin *et al*. (2017b) in the Prague Synform would be devalued by the low number of equally well-documented correlative sections, while the faunal composition and stratigraphical range of the respective taxa is markedly isochronous across this relatively small area.

The simplest approach to the estimation of trends in graptolite diversity is to consider diversity as the total number of species recorded in a biozone (species richness,

Fig. 7). Graptolite biozones are shown as markedly unequal in their time duration by time-calibrated standard biozonation of the Geological Time Scale 2020 (Melchin *et al*. 2020). Duration of the respective biozones of the Prague Synform is estimated through biostratigraphical correlation with the standard graptolite biozones of Melchin *et al*. (2020) using both index taxa and the associated graptolite assemblages. Correlation has revealed that some biozones recognized in the Prague Synform may have lasted only 0.1–0.2 Myr, whereas others represent up to 1.3–1.7 Myr. The mean time interval represented by a graptolite biozone in the Silurian sedimentary succession of the Prague Synform is 0.52 Myr. Since the GTS 2020 is based on limited number of radiometric dates, significant changes in time-callibration may be expected in the years to come.

A relationship can be expected between interval length and species richness. The longer the interval that the particular biozone represents, the more species are contained. In addition, diversity appears artificially high when turnover (originations and extinctions) is high within a biozone. In practice, and as is always the case in the fossil record, lowest occurrences and highest occurrences (referred as FADs and LADs in Fig. 7) are dealt with rather than real originations and extinctions. Unequal presence of the short ranging and long ranging species in different biozones is normalized by means of standing diversity (MSD, Fig. 7) – the average number of taxa at any point in time through the biozone (Hammer & Harper 2006). The mean standing diversity is calculated in this study as a sum of proportional species ranges in the respective biozone. Species that range through the biozone count as one unit each. Species that appear or disappear in this biozone count as 0.1–0.9 depending on the proportion of the interval thickness occupied by the species that does not range through the whole biozone. This is to record and count even short-lived taxa confined to a short stratigraphical interval embracing, for instance, only ten per cent (0.1) of the biozone.

Estimation of major fluctuations in graptolite extinction and origination rates through the Silurian Period is made by means of time-normalized Van Valen's metrics (Van Valen 1984) which is number of extinctions (E) /originations (O) within the biozone divided by the mean standing diversity (MSD). This number is further divided by the time interval (t) (= duration) of the corresponding unit (the biozone or part of the biozone) to get the origination/extinction rate per unit of time represented by the biozone or part of the biozone (time-normalized extinctions rate – TNER; time-normalized origination rate – TNOR).

$$\mathrm{TNER} = \frac{E}{MSD\,.\,t} \qquad \mathrm{TNOR} = \frac{\mathrm{O}}{MSD\,.\,t}$$

Origination and, in particular, extinction rates vary considerably within many biozones and calculating extinction and origination rates over relatively long biozones averages together episodes of low and high rates, that makes either episode hard to identify. Foote (1994, 2000) has shown that time-normalized Van Valen's metrics are still biased by unequal length of intervals counted; however, according to Hammer & Harper (2006), the metrics still behave well in exploration of major diversity trends in time, without particular focus on sudden drops in diversity ascribed to mass extinction events. Origination episodes are generally more protracted than extinction episodes. The number of extinctions and originations in a biozone depends on its length and number of species present. Diversity-dependence of the origination and extinctions rates was tested by Foote *et al*. (2018) using equal time intervals of 0.25 Myr instead of biozones of unequal duration. The latter approach has not been applied in this study, not having direct time related stratigraphical distribution of graptolite species without unavoidable correlation bias.

At least partial compensation is needed for differing biozonal duration. The numerical impact of different short-lived taxa that appear in different parts of long biozones can be reduced by subdivision of particularly long biozones into two or three subintervals that are counted separately for their species richness and mean standing diversity. Nine of the longest biozones (0.72–1.46 Myr) are subdivided into two subintervals of equal duration that were counted separately to achieve partial compensation for excessive differences in biozonal duration. Very long interval of the *transgrediens* Biozone (*ca* 1.77 Myr) is subdivided into three equally long parts, each 0.59 Myr. The overall impression of the diversity trend within the biozone is complemented by the ratio (Fig. 7) between the number of originations (FADs) and the number of extinctions (LADs), which is independent of the biozone length, species richness, species turnover, and mean standing diversity.

Taxonomic and institutional abbreviations

Graptolite genera have been abbreviated, when appropriate, in the following manner: *A*. – *Akidograptus*, *At*. – *Atavograptus*, *Barr*. – *Barrandeograptus*, *Boh*. – *Bohemograptus*, *C*. – *Coronograptus*, *Ceph*. – *Cephalograptus*, *Coch*. – *Cochlograptus*, *Col*. – *Colonograptus*, *Com*. – *Comograptus*, *Cr*. – *Crinitograptus*, *Cyrt*. – *Cyrtograptus*, *Cyst*. – *Cystograptus*, *Dem*. – *Demirastrites*, *F*. – *Formosograptus*, *Gig*. – *Giganteograptus*, *Gl*. – *Glyptograptus*, *Goth*. – *Gothograptus*, *H*. – *Heisograptus*, *Hutt*. – *Huttagraptus*, *K*. – *Korenograptus*, *L*. – *Lobograptus*, *Lapw*. – *Lapworthograptus*, *Lin*. – *Linograptus*, *Lit.* – *Lituigraptus*, *M.* – *Monograptus*, *Mcl.* – *Monoclimacis*, *Med.* – *Mediograptus*, *Metacl.* – *Metaclimacograptus*, *N.* – *Normalograptus*, *Nd.* – *Neodiplograptus*, *Ng.* – *Neogothograptus*, *Nl.* – *Neolagarograptus*, *Neodiv.* – *Neodiversograptus*, *O.* – *Oktavites*, *Par.* – *Parakidograptus*, *Parapet.* – *Parapetalolithus*, *Paraplect.* – *Paraplectograptus*, *Pc.* – *Paraclimacograptus*, *Pern.* – *Pernerograptus*, *Pet.* – *Petalolithus*, *Plect.* – *Plectograptus*, *Pol.* – *Polonograptus*, *Prib.* – *Pribylograptus*, *Prist.* – *Pristiograptus*, *Pseudomcl.* – *Pseudomonoclimacis*, *Pseudoplegm.* – *Pseudoplegmatograptus*, *Pseudorth.* – *Pseudorthograptus*, *R.* – *Rastrites*, *Ret.* – *Retiolites*, *Rh.* – *Rhaphidograptus*, *Rick.* – *Rickardsograptus*, *S.* – *Spirograptus*, *Saet.* – *Saetograptus*, *Sk.* – *Skalograptus*, *Slov.* – *Slovinograptus*, *Sok.* – *Sokolovograptus*, *Sp.* – *Spinograptus*, *St.* – *Stomatograptus*, *Stim.* – *Stimulograptus*, *Str.* – *Streptograptus*, *T.* – *Torquigraptus, Test.* – *Testograptus*, *U.* – *Uncinatograptus, W.* – *Wolynograptus*. Graptolite material referred in this study is housed in the Czech Geological Survey, Prague (figured specimens bearing institutional abbreviations BB, HJ, MŠ and PŠ) and in the National Museum, Prague (abbreviations L and D).

Graptolite biozones

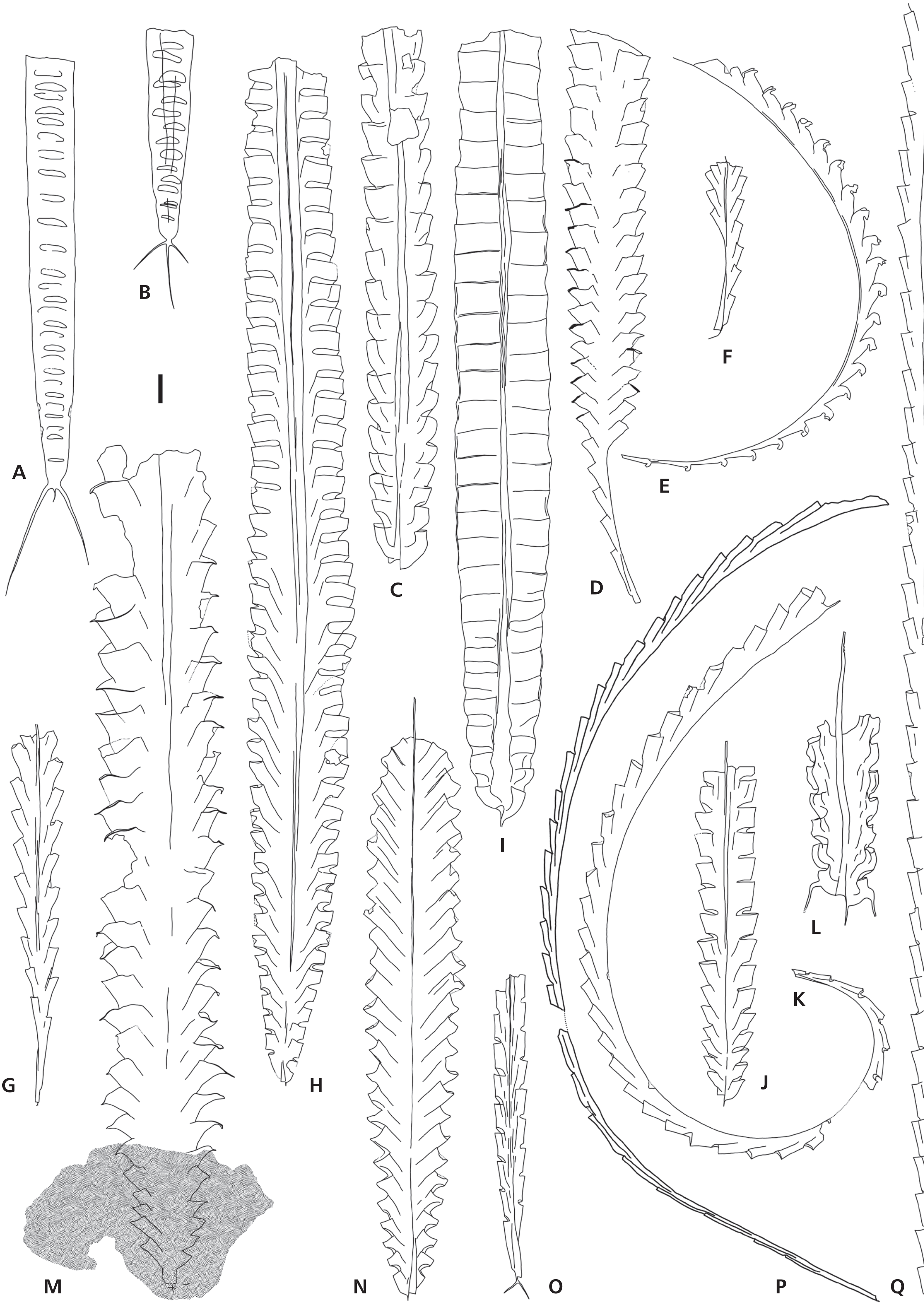
Akidograptus ascensus Biozone

The graptolite assemblage characteristic of this biozone (Fig. 5) was first recognized in the Prague Synform by Bouček (1953) at Praha-Běchovice and subsequently identified by Horný (1956) in the southwestern part of the Silurian outcrop area, between Želkovice and Všeradice. Its occurrence has been further documented in both north-western and south-eastern limbs of the Synform (Štorch 1986, 2006).

The *ascensus* Biozone is defined as an interval between the lowest occurrence of *Akidograptus ascensus* and the lowest *Parakidograptus acuminatus* – the biozonal index of the overlying biozone. It is a thin, but easily recognizable biostratigraphical unit delineating the very base of the Silurian succession (Melchin *et al*. 2020). Rather condensed clayey black shales of the *ascensus* Biozone overlie light-grey mudstones of the upper Hirnantian Kosov Formation with a distinct paraconformity (Štorch 2006) interpreted as a firmground (Fig. 8). The uppermost Kosov Formation hosts a Hirnantia brachiopod fauna (Marek & Havlíček 1967, Havlíček & Marek 1973, Štorch 1986) and locally also *Metabolograptus persculptus* (see Štorch & Loydell 1996) – the biozonal index species of the topmost Ordovician graptolite biozone.

Biostratigraphical correlation of the Czech succession with complete and less condensed sections abroad suggests that the lower part of the *ascensus* Biozone is actually missing at this paraconformity (Štorch *et al*. 2019). *Korenograptus bifurcus* (Mu *et al*.), *Korenograptus bicaudatus* (Chen & Lin), *Normalograptus rhizinus* (Li & Yang), *Normalograptus crassus* Štorch & Feist, *Parakidograptus praematurus* (Davies) and some faunal elements inherited from the Hirnantian upper *persculptus* Biozone are missing in the Prague Synform. The lowermost black-shale strata are marked by abundant *Neodiplograptus lanceolatus*, which has its lowest occurrences well above the base of the *ascensus–acuminatus* Biozone in Spain (Štorch *et al*. 2019). In the Prague Synform the maximum thickness of the *ascensus* Biozone was recorded at Beroun-Jarov (*ca* 0.9 m), with a thick succession (for this biozone) recorded also in the Praha-Nové Butovice housing estate (0.75 m), Praha-Řepy housing estate (Štorch 1982, 0.5 m), and Běleč (0.5 m), but the usual thickness of this biozone ranges between 0.1 m and 0.3 m in other studied sections (Štorch 1986, 2006). The lower part of the *ascensus* Biozone is characterized by the common occurrence of *A. ascensus* (Fig. 6O) associated with abundant *Nd. lanceolatus* (Fig. 6N) and *Normalograptus mirnyensis*. *Rickardsograptus*? *parajanus* and *Rickardsograptus lautus* are rare elements of the assemblage. An upper part of the *ascensus* Biozone can be recognized in the Prague Synform in a few sections with the most complete sedimentary record. It is marked by the lowest occurrences of *Normalograptus trifilis* (Fig. 6B) and *Cystograptus ancestralis* (Fig. 6C) accompanied by rare *Glyptograptus dufkai.*

Figure 6. Age-diagnostic Rhuddanian graptolites. • A – scalariform view of *Normalograptus resurrectus* (Manck), PŠ 4388, lower *acuminatus* Biozone. • B – immature specimen of *Normalograptus trifilis* (Manck) in scalariform view, PŠ 4389, upper *ascensus* Biozone. • C – *Cystograptus ancestralis* Štorch, PŠ 4387a, upper *ascensus* Biozone. • D – *Bulmanograptus confertus* (Nicholson), PŠ 3482, uppermost *vesiculosus* Biozone. • E – *Pernerograptus difformis* (Törnquist), PŠ 4380, upper *cyphus* Biozone. • F – *Dimorphograptus erectus* Elles & Wood, PŠ 4367, *vesiculosus* Biozone. • G – *Parakidograptus acuminatus* (Nicholson), PŠ 4395, lower *acuminatus* Biozone. • H – *Neodiplograptus fezzanensis* (Desio), PŠ 4386, *cyphus* Biozone. • I – *Cystograptus vesiculosus* (Nicholson) in common biscalariform mode of flattening, PŠ 4384, *vesiculosus* Biozone. • J – *Neodiplograptus apographon* (Štorch), PŠ 72/2, upper *acuminatus* Biozone. • K – *Coronograptus cyphus* (Lapworth), PŠ 4383/1, *cyphus* Biozone. • L – *Cystograptus tridens* (Manck), PŠ 4379a, *vesiculosus–cyphus* biozone boundary interval. • M – *Pseudorthograptus obuti* (Rickards & Koren'), PŠ 3501, lower *cyphus* Biozone. • N – *Neodiplograptus lanceolatus* Štorch & Serpagli, PŠ 4381, *ascensus* Biozone. • O – *Akidograptus ascensus* Davies, PŠ 4385, *ascensus* Biozone. • P – *Huttagraptus acinaces* (Törnquist), PŠ 3601, upper *vesiculosus* Biozone. • Q – *Atavograptus atavus* (Jones), PŠ 4366, *vesiculosus* Biozone. A, D, E, G, I, K–N, P – Všeradice-field; B, C, H, O – Běleč; F, Q – Praha-Běchovice; J – Praha-Řepy housing estate. All figures × 5, scale bar represents 1 mm.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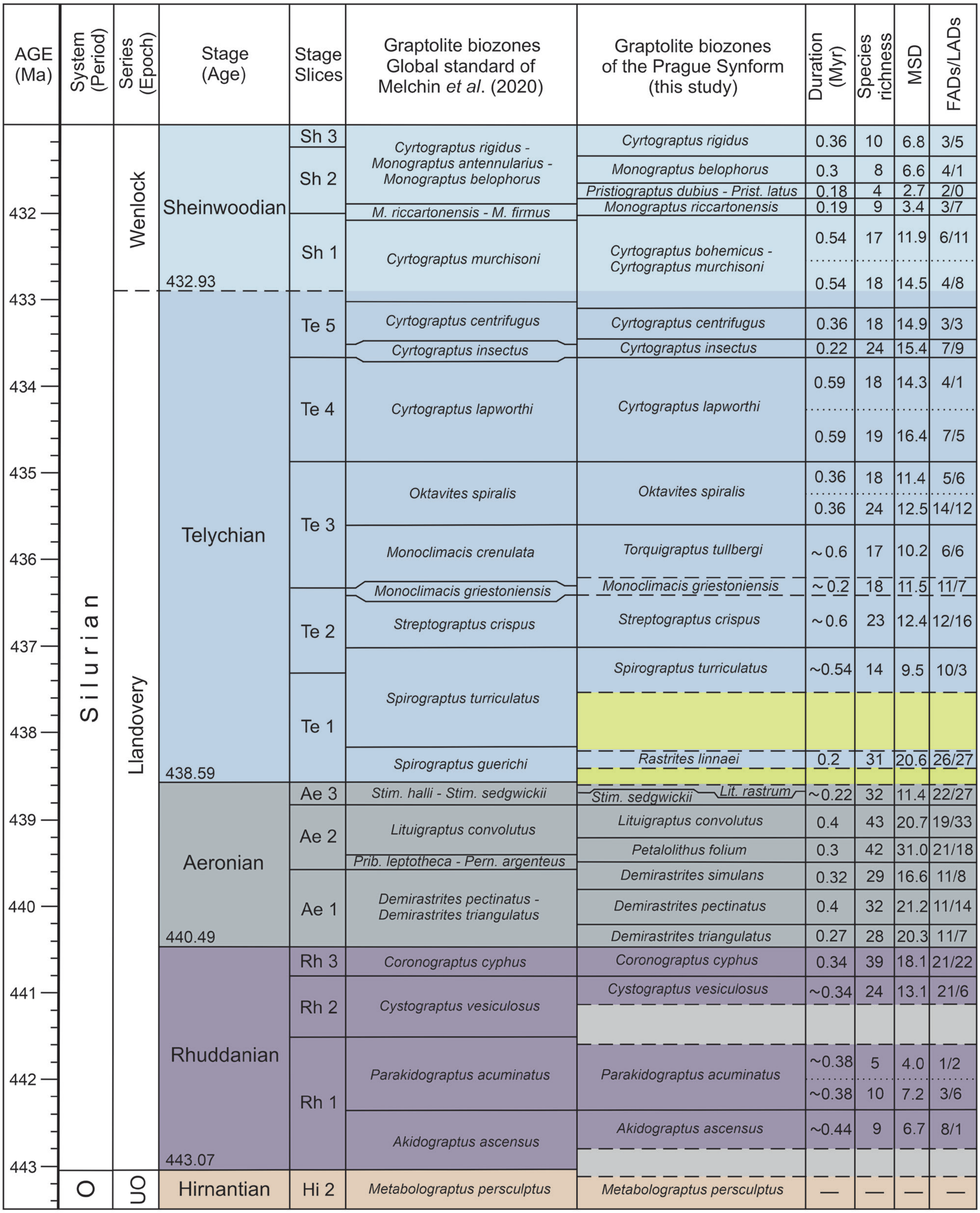


Figure 7. Silurian time scale, geochronology, chronostratigraphy and graptolite biostratigraphy. Time duration of graptolite biozones recognized in the Prague Synform is derived from correlation with the standard graptolite biozonal scheme calibrated with the Silurian time scale (Melchin *et al*. 2020) and stage slices of Cramer *et al*. (2011). Dashed horizontal lines mark tentative delineation of zonal boundaries. Dotted horizontal lines indicate subdivision or particularly long biozones into two or three subintervals of equal duration. Diversity trends are documented by species richness per biozone, mean standing diversity (MSD), and originations/extinctions ratio (FADs/LADs). Basin-wide gaps in the Rhuddanian stratigraphical record

AGE (Ma)	System (Period)	Series (Epoch)	Stage (Age)	Stage slices	Graptolite biozones Global standard of Melchin *et al.* (2020)	Graptolite biozones of the Prague Synform (this study)	Duration (Myr)	Species richness	MSD	FADs/LADs
	D	LD	Lochkovian 419.0	—	*Uncinatograptus uniformis*	*Uncinatograptus uniformis*	—	—	—	—
419	Silurian	Přídolí		Pr 2	*Istrograptus transgrediens* - "*Monograptus*" *perneri*	*Skalograptus transgrediens*	0.59	2	2.0	0/1
420							0.59	3	2.8	0/1
							0.59	4	3.2	0/1
						Wolynograptus perneri	0.19	6	5.2	1/2
421					"*Monograptus*" *bouceki*	*Wolynograptus bouceki*	0.54	9	5.1	3/4
				Pr 1	*Neocolonograptus lochkovensis* - *Neocolonograptus branikensis*	*Skalograptus lochkovensis*	0.39	7	5.2	2/1
422							0.39	8	5.4	3/3
			422.73		*Neocolonograptus ultimus* - *Neocolonograptus parultimus*	*Skalograptus parultimus* - *Skalograptus ultimus*	0.47	8	4.9	4/3
		Ludlow	Ludfordian	Lu 3	*Formosograptus formosus*	*Pristiograptus fragmentalis*	0.22	7	4.9	4/3
423						*Pseudomcl. latilobus* - *Slov. balticus*	0.24	5	4.6	2/2
				Lu 2	*Neocucullograptus kozlowskii* - *Polonograptus podoliensis*	*Neocucullograptus kozlowskii*	0.28	12	9.6	1/9
						Neocucullograptus inexpectatus	~0.29	12	8.2	6/1
424				Lu 1	*Bohemograptus*	*Bohemograptus tenuis*	~0.63	10	6.4	7/5
					Saetograptus leintwardinensis	*Saetograptus leintwardinensis*	0.38	8	5.7	2/5
			425.01				0.38	12	7.1	3/5
425			Gorstian	Go 2	*Lobograptus scanicus*	*Saetograptus chimaera* - *Lobograptus scanicus*	0.65	13	8.9	4/4
426							0.65	18	11.7	3/9
						Lobograptus progenitor	0.23	26	11.5	15/11
			426.74	Go 1	*Neodiversograptus nilssoni*	*Neodiversograptus nilssoni*	0.22	18	11.0	10/7
427		Wenlock	Homerian	Ho 3	*Colonograptus ludensis*	*Colonograptus ludensis* - *Colonograptus gerhardi*	0.55	9	7.6	3/1
							0.55	10	7.2	4/4
428				Ho 2	*Colonograptus praedeubeli* - *Colonograptus deubeli*	*Colonograptus praedeubeli* - *Colonograptus deubeli*	0.47	11	6.0	5/5
					Gothograptus nassa - *Pristiograptus parvus*	*Gothograptus nassa* - *Pristiograptus frequens*	0.48	6	4.1	4/0
						Pristiograptus parvus	0.22	2	1.5	2/1
429				Ho 1	*Cyrtograptus lundgreni*	*Monograptus flemingii*	~0.1	2	2	0/2
						Cyrtograptus lundgreni	0.73	16	9.7	7/13
430			430.62				0.73	14	7.8	6/5
			Sheinwoodian	Sh 3	*Cyrtograptus rigidus* - *Monograptus antennularius* - *Monograptus belophorus*	*Cyrt. ramosus* - *Cyrt. perneri*	0.4	12	7.7	7/4
431						*Cyrtograptus rigidus*	0.33	10	6.8	3/5
				Sh 2		*Monograptus belophorus*	0.28	8	6.6	4/1

are marked by a light grey colour. Major layers of pale-coloured, non-fossiliferous lower Telychian mudstones deposited during a significant time interval are marked by yellow-green colour. Other colours pertain to individual stages of the Silurian System.

The *ascensus* Biozone is easily accessible and rich in well-preserved graptolites in the Běleč section (Štorch 1986) although a more complete section was described by Štorch (1982) from temporary building excavations in the Praha-Řepy housing estate. Rich material has been collected from loose rocks and subcrops in the field at the northern periphery of Všeradice (Štorch 2015).

Parakidograptus acuminatus Biozone

The *acuminatus* Biozone, distinguished by Lapworth (1878) in southern Scotland, originally embraced also the present *ascensus* Biozone as well as the upper Hirnantian *Metabolograptus persculptus* Biozone. Marek (1951) first identified the *acuminatus* Biozone at Praha-Běchovice – a section briefly described by Bouček (1953). Štorch (1994, 1996) combined the *acuminatus* Biozone with that of *A. ascensus*, but subsequent studies (Štorch 2006 and present paper) confirm the distinctiveness of the two graptolite assemblages and usefulness of a separate *acuminatus* Biozone for high resolution correlation, in particular within the Prague Synform.

This lower Rhuddanian biozone is defined as an interval between the lowest occurrence of *Par. acuminatus* and the first *Cystograptus vesiculosus* (Fig. 5). *Akidograptus ascensus* – the biozonal index of the *ascensus* Biozone – ranges well into the lower part of the *acuminatus* Biozone. Upper and even middle parts of the *acuminatus* Biozone are either missing due to non-deposition (Štorch 2006) or represented by condensed silty-micaceous laminites with prolific, aligned, poorly preserved rhabdosomes of biserial graptolites. The maximum thickness and relative completeness of the *acuminatus* Biozone were recorded at the Praha-Řepy housing estate (Štorch 1982, *ca* 2.5 m) and Praha-Běchovice (Bouček 1953, 2.0 m). However, other localities (Hlásná Třebaň-section, Zadní Třebaň-railway cut, Karlík, Loděnice-water tank above the limeworks, Všeradice-field) exhibit only the lower, 0.1–0.6 m thick, part of the biozone with *N. trifilis*, *Cyst. ancestralis*, common *Par. acuminatus* (Fig. 6G) and the last occurrences of *A. ascensus*, *Nd. lanceolatus* and *Rick.*? *parajanus*. *Normalograptus resurrectus* (formerly *N. longifilis*), with its two long basal spines and a short virgella (Fig. 6A), is confined to the middle part of the biozone, being replaced by significant proliferation of *Normalograptus ajjeri* with a single long virgella, just a few centimetres higher in the succession in association with *Neodiplograptus apographon* (Fig. 6J). Stratigraphically higher silty-micaceous laminites, encountered in Praha-Řepy housing estate and Praha-Běchovice (personal observation), yield very long and broad, commonly sabre-shaped rhabdosomes of *Par. acuminatus* along with prolific but undeterminable normalograptids. Also, the lowest occurrence of *Cyst. vesiculosus*, indicating the base of the overlying *Cystograptus vesiculosus* Biozone at the Praha-Řepy housing estate (Štorch 1982), is from this laminite interval. The exact placement of graptolite assemblages preserved in the Prague Synform within the graptolite succession of the *acuminatus* Biozone was made possible through high-resolution correlation with the less condensed, complete succession exposed in the Estana section in the Spanish Pyrenees (Štorch *et al*. 2019, new personal observation).

A section log of the former temporary outcrop in Praha-Běchovice has been neither described in detail nor figured. Another section spanning a relatively thick and nearly complete *acuminatus* Biozone with a rich and well preserved graptolite fauna was described by Štorch (1982) from building excavations in Praha-Řepy housing estate. A less well-developed lower part of the biozone occurs in Karlík and Velká Chuchle-Barrande's Colony Haidinger (Štorch 1986) and in the Hlásná Třebaň section (Štorch *et al*. 2018). Nicely preserved graptolites of the lower *acuminatus* Biozone have been collected from loose rocks and subcrops in Všeradice-field (Štorch 2015).

Cystograptus vesiculosus Biozone

The *Cystograptus vesiculosus* Biozone, first distinguished by Lapworth (1878) in southern Scotland, was first recognized in the Silurian succession of Bohemia by Perner & Kodym (1919, 1922) in Běleč and near Libomyšl, solely by the occurrence of *Cystograptus vesiculosus*, which occurred with undeterminable normalograptids. The presence of the *vesiculosus* Biozone was subsequently questioned (Bouček 1936, Přibyl 1937), but undoubted evidence from the Praha-Běchovice, Hlásná Třebaň and Zadní Třebaň-railway cut sections, including a short list of graptolites, was published by Bouček (1953) and later extended by Štorch (1986).

The *vesiculosus* Biozone is defined herein as an interval delineated by lowest occurrences of *Cyst. vesiculosus* at the base and lowest *Coronograptus cyphus* at the top. A major part of this mid-Rhuddanian interval is entirely missing in the Prague Synform (Fig. 2) or developed in the form of a condensed, usually 0.3–0.75 m thick succession dominated by silty micaceous laminites with prolific but indeterminable, largely biserial graptolites (Štorch 2006). The most complete graptolite record of the *vesiculosus* Biozone came from building excavations in Praha-Běchovice (Bouček 1953). A graptolite assemblage with abundant *Atavograptus atavus* (Fig. 6Q), *Normalograptus normalis* and *Normalograptus rectangularis*, associated with *Rickardsograptus lautus*, *Cyst. vesiculosus* and *Dimorphograptus erectus* (Fig. 6F), was identified in the material from Praha-Běchovice

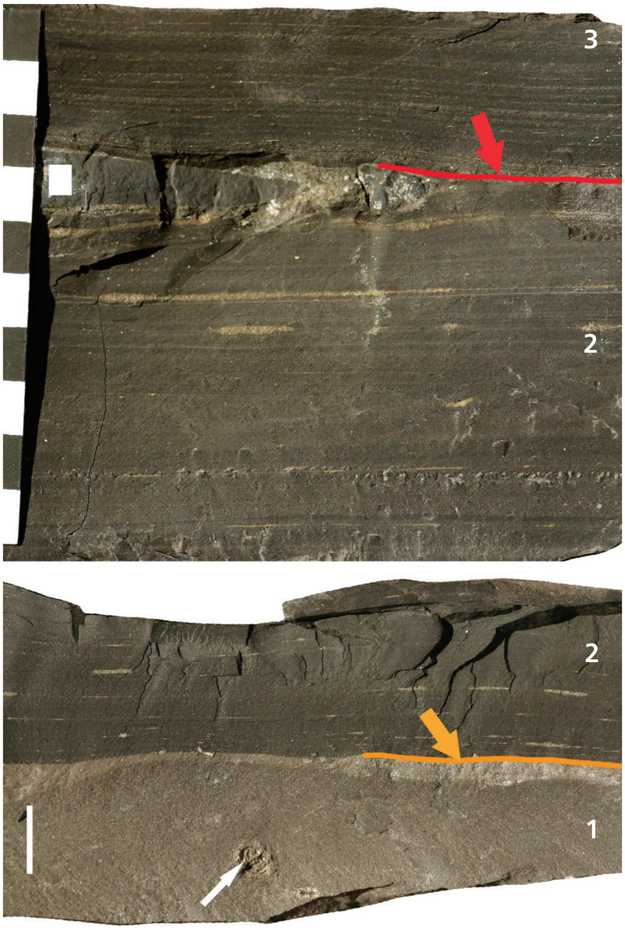


Figure 8. Close-up view of the Ordovician-Silurian boundary and lowermost Silurian strata of the Radotín-tunnel section. Graptolite data indicate that the lower *ascensus* Biozone and presumably also the upper *persculptus* Biozone of the uppermost Hirnantian are missing at the sharp but conformable interface between the light-grey calcareous mudstone of the uppermost Kosov Formation (1) and black argillitic shale of the Želkovice Formation (2). The uppermost Hirnantian firmground (orange arrow) exhibits tubular burrows (white arrow) referable to the *Glossifungites* ichnofacies. The second and major unconformity (red arrow) is marked by a thin layer of phosphatic nodules (white square) overlain by sandy micaceous laminites of the lower Aeronian *triangulatus* Biozone (3). The stratigraphical gap comprises the upper *ascensus*, *acuminatus*, *vesiculosus*, and *cyphus* biozones, representing almost 2 Myr, when correlated with the Geological Time Scale 2020 (Melchin *et al*. 2020). Scale bar represents 10 mm.

donated to the present author by the late Alois Přibyl. This assemblage, correlatable with the graptolite fauna of the upper *atavus* Biozone reported from the UK by Hutt (1974) and Zalasiewicz *et al*. (2009), has not been traced elsewhere in the Prague Synform. Most Czech sections (Hlásná Třebaň section, Zadní Třebaň-railway cut, Karlík, Vočkov near Karlštejn, Běleč, Všeradice-field) exhibit a graptolite assemblage above the *acuminatus* Biozone fauna corresponding with that of the upper part of the *vesiculosus* Biozone of Toghill (1968a, b) or upper *Huttagraptus acinaces* Biozone of Bjerreskov (1975) and Hutt (1974). This fauna, particularly well-represented in the Všeradice-field (Štorch 2015) and Běleč, is marked by abundant *Bulmanograptus confertus* (Fig. 6D), *Cyst. vesiculosus* (Fig. 6I), *Rhaphidograptus toernquisti*, *Huttagraptus acinaces* (Fig. 6P), *Huttagraptus billegravensis* and *Atavograptus pristinus* accompanied by *Paraclimacograptus innotatus*, *Metaclimacograptus* sp. A, *Normalograptus parvus*, *Cystograptus penna*, *Rickardsograptus lautus*, *Korenograptus nikolayevi*, *At. atavus* and some other species. Semiquantitative data suggest that the assemblage, as a whole, is dominated by biserial and uni-biserial graptolites. *Pseudorthograptus obuti* has its lowest occurrence in a thin boundary interval with the overlying *Coronograptus cyphus* Biozone. *Cystograptus tridens* (Fig. 6L) and *Pseudorthograptus*? *physophora*, recorded in the Všeradice-field and Běleč-trench, appear to be limited to this stratigraphical level.

Well-preserved graptolites from the upper *vesiculosus* Biozone have been collected from loose rocks and subcrops in Všeradice-field (Štorch 2015); a similar fauna representing a still more stratigraphically restricted interval of the upper *vesiculosus* Biozone has been collected from the Běleč-trench section (Štorch 1986 and this study). A more complete succession, albeit with less favourably preserved graptolites, crops out in Karlík (Štorch 1986) and in the Hlásná Třebaň-section (Štorch *et al*. 2018).

Coronograptus cyphus Biozone

The *Coronograptus cyphus* Biozone, originally recognized by H. Lapworth (1900) in Wales, was first identified in the Prague Synform by Přibyl (1940a) in his thorough revision of the classical "colonies" of J. Barrande. The graptolite assemblage and then known localities of the *cyphus* Biozone were discussed by Bouček (1953).

The base of the upper Rhuddanian *cyphus* Biozone is defined by the lowest occurrence (Fig. 5) of *Coronograptus cyphus* and the top by the incoming of *Demirastrites triangulatus* – the index fossil of the lowermost Aeronian *triangulatus* Biozone and proposed marker species delineating the base of the Aeronian Stage. The graptolite faunal succession recorded in the southwestern part of the Prague Synform (Všeradice-field, Běleč, Vočkov near Karlštejn, Hlásná Třebaň-section, Zadní Třebaň-railway cut, Karlík, Černošice-Barrande's Colony Solopisky) indicates continuous sedimentation, despite the irregular alternation of argillitic shale and micaceous laminite. The maximum thickness of definite *cyphus* Biozone, 1.2 m, has been recorded in Karlík (Štorch 1986), but the common thickness varies between 0.5 m and 0.7 m (Praha-Nové Butovice housing estate, Černošice-Colony Solopisky, Vočkov near Karlštejn, Běleč, Zadní Třebaň-railway cut, Hlásná Třebaň-section).

The biozonal index *C. cyphus* (Fig. 6K) is common throughout its biozone having some overlap with *Cyst. vesiculosus* in the lower part. Other taxa of the lower *cyphus* Biozone include the incoming *Normalograptus frydai*, *Pseudorthograptus mitchelli* and *Pernerograptus austerus*. Other elements, inherited from the *vesiculosus* Biozone, are *Pc. innotatus*, *N. normalis*, *Cyst. penna*, *Rick. lautus*, *Pseudorth. obuti* (Fig. 6M), *At. pristinus*, *At. atavus*, *Huttagraptus acinaces* and *Huttagraptus billegravensis. Rhaphidograptus toernquisti* outnumbers *Normalograptus* from the lower *cyphus* Biozone onwards.

The middle part of the *cyphus* Biozone is marked by the robust rhabdosomes of abundant *Neodiplograptus fezzanensis* (Fig. 6H) and *Pseudorth. obuti* in association with the incoming *Coronograptus gregarius*, rare *Hercograptus* cf. *introversus* and many other species, including *Cyst. penna* and *N. frydai*, continuing from the lower part of the biozone.

The upper part of the *cyphus* Biozone displays a highly diverse and distinctive graptolite assemblage marked by significant proliferation of biform monograptids represented by *Pernerograptus pribyli*, *Pernerograptus sudburiae*, *Pernerograptus revolutus* and *Pernerograptus difformis* (Fig. 6E) – possible ancestor of the triangulate monograptids with isolated metathecae (Rickards *et al*. 1977). *Neodiplograptus fezzanensis* and prolific *Rh. toernquisti* co-occur with the rare and short-ranging *Coronograptus minusculus*. Several species appear in the uppermost part of the biozone, including *Glyptograptus perneri*, *Pseudorthograptus radiculatus* (formerly *Pseudorth*. *finneyi*), *Pseudorthograptus inopinatus*, *Pristiograptus concinnus* and *Pernerograptu*s sp. nov. formerly referred to *Pernerograptus difformis* by some authors (*e.g.* Elles & Wood 1911, *partim*). The last species has been recorded in the uppermost part of the *cyphus* Biozone in the Hlásná Třebaň section (Štorch *et al.* 2018, Fig. 5k). The Rhuddanian–Aeronian boundary interval in Spain (El Pintado and Estana sections) has this short ranging species of *Pernerograptus* in the same stratigraphical level (author's unpublished observation).

The lower part of the *cyphus* Biozone, with persisting *Hutt. acinaces* and cystograptids, is clearly correlatable with the upper *acinaces* Biozone of British and Scandinavian biozonal schemes. The upper part, marked by common biform monograptids, likely equates with the *revolutus* Biozone, as suggested by rare *Pern. revolutus* recorded in the upper part of the Czech *cyphus* Biozone. *Coronograptus cyphus* is a preferred choice for the index species in Bohemia being distinctive and common throughout the whole interval bounded by the rapid demise of dimorphograptids and *Cyst. vesiculosus*, and the appearance of triangulate monograptids.

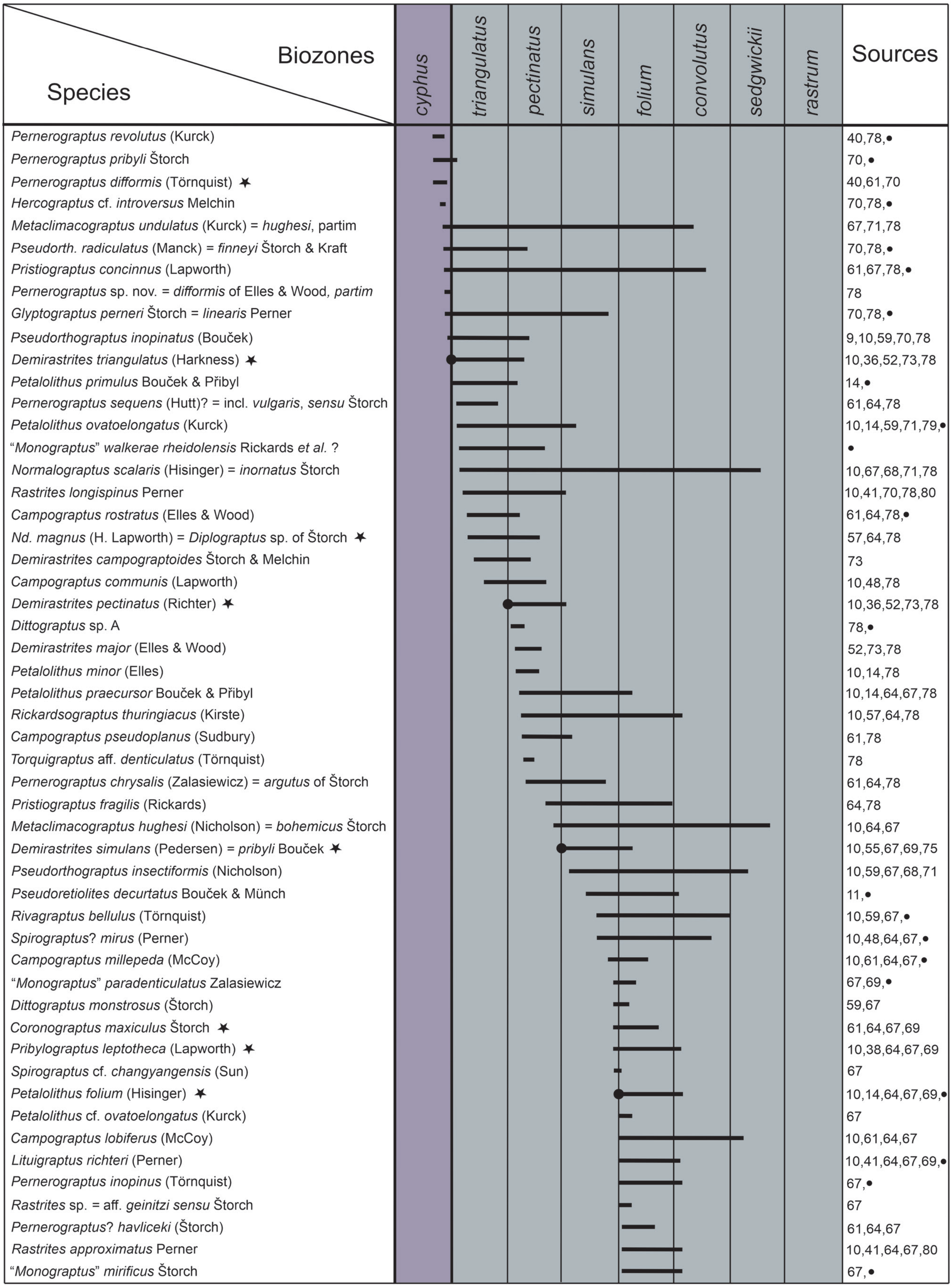
Several sections through the *cyphus* Biozone can be used for reference, all exposed in the southeastern limb of the Prague Synform, namely the Hlásná Třebaň section (Štorch *et al*. 2018), Karlík (Štorch 1986), and Běleč. Rich and well-preserved faunas came from loose rocks and field subcrops in Všeradice (Štorch 2015).

Demirastrites triangulatus Biozone

The *triangulatus* Biozone corresponds with the lower part of a considerably broader interval distinguished by Lapworth (1878) as the *Monograptus gregarius* Biozone. Přibyl (1937) distinguished a "*Monograptus*" *triangulatus* Biozone above a *Monograptus fimbriatus* (= junior synonym of *Demirastrites pectinatus*) Biozone in the Hlásná Třebaň section and the same inverted biozonal succession appeared in Přibyl (1940a). Bouček (1953) rectified the lower Aeronian biozonal scheme and delineated a *Demirastrites triangulatus* Band in the lower part of his *Demirastrites pectinatus* Biozone. Štorch (1994a) introduced a merged *Demirastrites triangulatus–Demirastrites pectinatus* Biozone because of the similar graptolite assemblages and much overlap of the stratigraphical ranges of the index species. However, subsequent work in the lower Aeronian succession led to recognition and definition of two separate units (Štorch *et al*. 2018, Štorch & Melchin 2018), instead of combined *triangulatus–pectinatus* Biozone.

The base of an up to 1.2 m thick *triangulatus* Biozone (Beroun-Jarov) is defined by the lowest occurrence of the biozonal index *Demirastrites triangulatus* and equates with the proposed definition of the base of the Aeronian Stage (Fig. 9, Štorch *et al*. 2018). The top of the *triangulatus* Biozone is delineated by the incoming of *Demirastrites pectinatus*. The graptolite fauna, moderately well-preserved in a 0.35–0.6 m thick succession of fine, somewhat siliceous shale, is rich and diversified, for the first time with a moderate prevalence of uniserial rhabdosomes. The narrow boundary interval of the upper Rhuddanian *cyphus* Biozone and lower Aeronian *triangulatus* Biozone is marked by proliferation of *Pseudorth. radiculatus* and *Pern. sudburiae*, along with successive first appearances of *Gl. perneri, Pseudorth. inopinatus*, *Dem. triangulatus* (Fig. 10M), *Pernerograptus sequens*?, *Petalolithus ovatoelongatus*, *Normalograptus scalaris*, *Rastrites longispinus*, *Campograptus rostratus* and, surprisingly, also *Neodiplograptus magnus* (Fig. 10E)

Figure 9. Stratigraphical ranges of upper Rhuddanian and Aeronian graptolites in the Prague Synform. See Fig. 5 for further explanation.


Biozones
Species
cyphus
triangulatus
pectinatus
simulans
folium
convolutus
sedgwickii
rastrum
Sources
Pernerograptus revolutus (Kurck) 40,78,•
Pernerograptus pribyli Štorch 70,•
Pernerograptus difformis (Törnquist) ✶ 40,61,70
Hercograptus cf. introversus Melchin 70,78,•
Metaclimacograptus undulatus (Kurck) = hughesi, partim 67,71,78
Pseudorth. radiculatus (Manck) = finneyi Štorch & Kraft 70,78,•
Pristiograptus concinnus (Lapworth) 61,67,78,•
Pernerograptus sp. nov. = difformis of Elles & Wood, partim 78
Glyptograptus perneri Štorch = linearis Perner 70,78,•
Pseudorthograptus inopinatus (Bouček) 9,10,59,70,78
Demirastrites triangulatus (Harkness) ✶ 10,36,52,73,78
Petalolithus primulus Bouček & Přibyl 14,•
Pernerograptus sequens (Hutt)? = incl. vulgaris, sensu Štorch 61,64,78
Petalolithus ovatoelongatus (Kurck) 10,14,59,71,79,•
“Monograptus” walkerae rheidolensis Rickards et al. ? •
Normalograptus scalaris (Hisinger) = inornatus Štorch 10,67,68,71,78
Rastrites longispinus Perner 10,41,70,78,80
Campograptus rostratus (Elles & Wood) 61,64,78,•
Nd. magnus (H. Lapworth) = Diplograptus sp. of Štorch ✶ 57,64,78
Demirastrites campograptoides Štorch & Melchin 73
Campograptus communis (Lapworth) 10,48,78
Demirastrites pectinatus (Richter) ✶ 10,36,52,73,78
Dittograptus sp. A 78,•
Demirastrites major (Elles & Wood) 52,73,78
Petalolithus minor (Elles) 10,14,78
Petalolithus praecursor Bouček & Přibyl 10,14,64,67,78
Rickardsograptus thuringiacus (Kirste) 10,57,64,78
Campograptus pseudoplanus (Sudbury) 61,78
Torquigraptus aff. denticulatus (Törnquist) 78
Pernerograptus chrysalis (Zalasiewicz) = argutus of Štorch 61,64,78
Pristiograptus fragilis (Rickards) 64,78
Metaclimacograptus hughesi (Nicholson) = bohemicus Štorch 10,64,67
Demirastrites simulans (Pedersen) = pribyli Bouček ✶ 10,55,67,69,75
Pseudorthograptus insectiformis (Nicholson) 10,59,67,68,71
Pseudoretiolites decurtatus Bouček & Münch 11,•
Rivagraptus bellulus (Törnquist) 10,59,67,•
Spirograptus? mirus (Perner) 10,48,64,67,•
Campograptus millepeda (McCoy) 10,61,64,67,•
“Monograptus” paradenticulatus Zalasiewicz 67,69,•
Dittograptus monstrosus (Štorch) 59,67
Coronograptus maxiculus Štorch ✶ 61,64,67,69
Pribylograptus leptotheca (Lapworth) ✶ 10,38,64,67,69
Spirograptus cf. changyangensis (Sun) 67
Petalolithus folium (Hisinger) ✶ 10,14,64,67,69,•
Petalolithus cf. ovatoelongatus (Kurck) 67
Campograptus lobiferus (McCoy) 10,61,64,67
Lituigraptus richteri (Perner) 10,41,64,67,69,•
Pernerograptus inopinus (Törnquist) 67,•
Rastrites sp. = aff. geinitzi sensu Štorch 67
Pernerograptus? havliceki (Štorch) 61,64,67
Rastrites approximatus Perner 10,41,64,67,80
“Monograptus” mirificus Štorch 67,•

which is regarded by the present author as the successor of the late Rhuddanian *Nd. fezzanensis*. Considerable faunal change is further highlighted in the *cyphus-triangulatus* boundary interval by the last occurrences of *Pseudorth. obuti*, *C. cyphus*, *At. pristinus*, *Pribylograptus incommodus*, *Pern. revolutus* and *Pern. difformis*. Stratigraphically higher parts of the *triangulatus* Biozone are marked by the first appearances of *Demirastrites campograptoides* and *Campograptus communis*. *Rhaphidograptus toernquisti* is the most abundant of a few long-ranging taxa.

A reference section of the *triangulatus* Biozone is readily accessible at Hlásná Třebaň (Štorch *et al*. 2018), with a similar section exposed near Karlík (Štorch 1986). Well-preserved graptolites have been described also from the field locality in Všeradice (Štorch 2015).

Demirastrites pectinatus Biozone

Originally recognized as the *Monograptus fimbriatus* Biozone by Kettner & Bouček (1936) and Přibyl (1940a), the biozone was named after the senior synonym *Demirastrites pectinatus* by Přibyl (1948) and Bouček (1953). The graptolite assemblage of the lower *pectinatus* Biozone (Štorch *et al*. 2018) equates with that of the British middle and upper *triangulatus* Biozone recognized by Zalasiewicz *et al*. (2009) and Melchin *et al*. (2018). The upper part of the Czech *pectinatus* Biozone should correspond with the British *Neodiplograptus magnus* Biozone but the latter index species has its first occurrence much lower in the Czech succession, as early as in the middle *triangulatus* Biozone of the Czech biozonal scheme.

The base of the *pectinatus* Biozone is defined by the lowest occurrence of the biozonal index *Dem. pectinatus* (Fig, 10L) and the top is delineated by the incoming of *Demirastrites simulans*. The largely monotonous black-shale succession of the nearly 1.5 m thick *pectinatus* Biozone is gradually replaced by alternation with siliceous beds in the majority of studied sections (Hlásná Třebaň, Karlík, Černošice-Colony Solopisky, Beroun-Jarov). The minimum thickness has been recorded in the Loděnice-water tank above the limeworks and Loděnice-Sedlec section (0.2 m), and in the Nové Butovice-housing estate (0.9 m) in condensed facies of micaceous laminites. In other sections silty laminae crowded with graptolite rhabdosomes are rare.

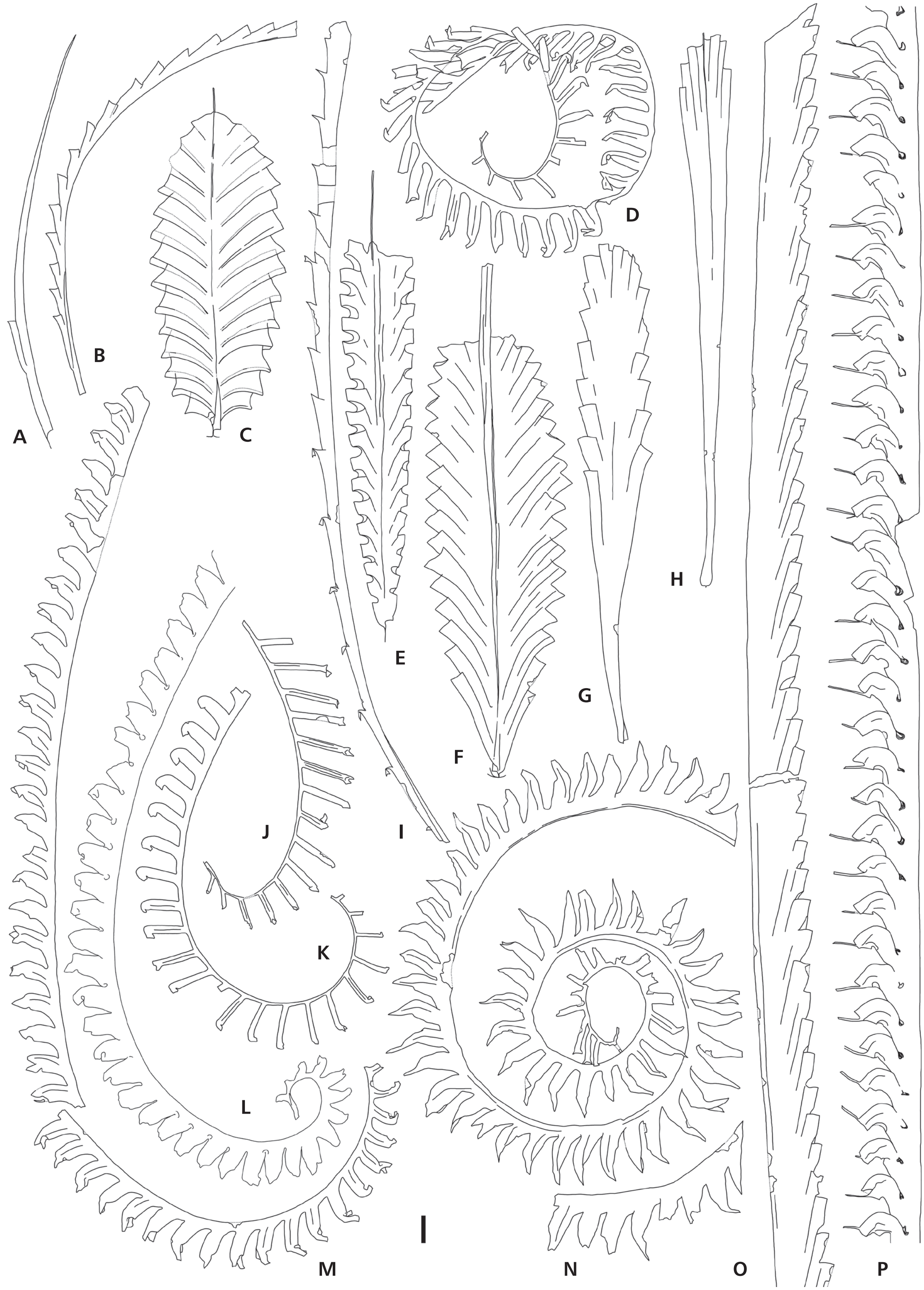
The graptolite assemblage of the *pectinatus* Biozone (Fig. 9) evolved gradually from that of the *triangulatus* Biozone which lead Štorch (1994a, 2006) to adopt a combined *triangulatus–pectinatus* Biozone. Subsequent work at the Hlásná Třebaň, Karlík and Černošice-Colony Solopisky sections (Štorch *et al*. 2018) and reassessment of morphologies and ranges of the triangulate monograptids (Štorch & Melchin 2018) enabled differentiation of the two biozonal assemblages and delineation of the bounding horizon by the first *Dem. pectinatus*. Other incoming taxa include *Demirastrites major*, *Petalolithus minor*, *Rickardsograptus thuringiacus*, *Pristiograptus fragilis*, *Pernerograptus chrysalis* and *Campograptus pseudoplanus*. *Pseudorthograptus radiculatus*, *Pseudorth. inopinatus*, *Dem. triangulatus* (form C of Štorch & Melchin 2018) are common in association with rare *Dem. campograptoides*. The last species, which continues from the *triangulatus* Biozone, vanished in the lower part of the *pectinatus* Biozone, being followed by the last appearances of *Neodiplograptus magnus* and the short-ranging *Dem. major.* The lower part of the *pectinatus* Biozone also witnessed significant proliferation of *C. gregarius* (Fig. 10B), *R. longispinus* and *Pseudorth. inopinatus*, whereas *Dittograptus* sp. is a rare element of the graptolite assemblage. The last named genus is common in the lower Aeronian of Siberia (Obut *et al*. 1968) and South China (personal observation).

The reference section of the *pectinatus* Biozone, with abundant and well-preserved graptolites, is at Hlásná Třebaň (Štorch *et al*. 2018). Other typical sections are accessible in Karlík and Černošice-Colony Solopisky.

Demirastrites simulans Biozone

The *simulans* Biozone of the present biozonal scheme was originally defined by Štorch (1994a) as a partial-range

Figure 10. Age-diagnostic Aeronian graptolites. • A – *Coronograptus maxiculus* Štorch, PŠ 754, lower *folium* Biozone. • B – *Coronograptus gregarius* (Lapworth), PŠ 3922, upper *triangulatus* Biozone. • C – *Petalolithus clandestinus* Štorch, MŠ 11633, *sedgwickii* Biozone. • D – *Lituigraptus rastrum* (Törnquist), PŠ 1008, *rastrum* Biozone. • E – *Neodiplograptus magnus* (H. Lapworth), PŠ 3916, *triangulatus* Biozone. • F – *Petalolithus folium* (Hisinger), PŠ 4372a, *folium* Biozone. • G – *Cephalograptus cometa* Nicholson, PŠ 4377, lower *convolutus* Biozone. • H – *Cephalograptus extrema* Bouček Přibyl, PŠ 798, *convolutus* Biozone. • I – *Neolagarograptus tenuis* (Portlock), MŠ 11621, *sedgwickii* Biozone. • J – *Rastrites peregrinus* Barrande, PŠ 4376, *convolutus* Biozone. • K – *Demirastrites simulans* (Pedersen), PŠ 740a, upper *simulans* Biozone. • L – *Demirastrites pectinatus* (Richter), PŠ 4057, *pectinatus* Biozone. • M – *Demirastrites triangulatus* (Harkness), PŠ 4382/1, *triangulatus* Biozone. • N – *Lituigraptus convolutus* (Hisinger), PŠ 748b, *convolutus* Biozone. • O – *Pribylograptus leptotheca* (Lapworth), distal part of mature rhabdosome, PŠ 4362, *folium* Biozone. • P – *Stimulograptus sedgwickii* (Portlock), distal part of mature rhabdosome, PŠ 4363, *sedgwickii* Biozone. A, F–H, J, K, N, O – Tmaň-Sv. Jiří; B, E, L – Hlásná Třebaň section; C, I – Hýskov-V Jakubince; D – Želkovice-behind farm; G, P – Radotín-tunnel; M – Všeradice-field. All figures × 5, scale bar represents 1 mm.


A
B
C
D
E
F
G
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K
L
M
N
O
P

biozone. It is a replacement of the *Demirastrites pribyli* Biozone established by Bouček (1953) with the biozone index species subsequently recognized by Štorch (1994a, 1998) as a junior synonym of *Demirastrites simulans* (Pedersen, 1922). The upper part of the biozone, with early *Pribylograptus leptotheca*, "*Monograptus*" *paradenticulatus*, and *Campograptus millepeda*, equates to the lower part of the *Pribylograptus leptotheca* Biozone of the British biozonal scheme described by Zalasiewicz *et al*. (2009). The lower part of the *simulans* Biozone, however, is lacking any formal equivalent in the British biozonation where it may well be represented by graptolite-barren strata. It is a tentative equivalent of an unnamed interval between the *pectinatus* and *convolutus* biozones on Bornholm (Bjerreskov 1975) and correlates, at least in part, with *Rastrites norilskensis* (= *orbitus*) Biozone of northern Canada and Alaska (Melchin 1989, Melchin *et al*. 2017a, Sun *et al*. 2022).

This interval biozone is delineated by the lowest occurrence of *Demirastrites simulans* at the base and lowest occurrence of *Petalolithus folium* at the top (Fig. 9). The biozone index species is uncommon in the upper part of its biozone, but marginally overlaps with first *Pet. folium*. Distal fragments of *Dem. simulans* may be misidentified as those of "*M.*" *paradenticulatus*, which is common in the upper part of the biozone, but proximal parts of their rhabdosomes can be readily distinguished (see Štorch 1998). More work is needed on the upper part of the *simulans* Biozone to make sure whether a separate *paradenticulatus* Biozone, considered by Štorch (2006), can be recognized. The *simulans* Biozone, in the present stratigraphical concept in which it has been extended upward, is formed by a 0.6–1.6 m thick succession of alternating shale and siliceous shale with subordinate beds of silty silicites recorded in the Hlásná Třebaň-section, Karlík, Černošice-Colony Solopisky, Radotín-tunnel and Loděnice-water tank above the limeworks. Micaceous laminites prevail in the somewhat condensed succession (0.6 m) at Praha-Nové Butovice housing estate.

The first *Dem. simulans* (Fig. 10K), represented by largely immature, rastritiform rhabdosomes, is closely succeeded by the first *Pseudorthograptus insectiformis*. *Rh. toernquisti* and *R. longispinus* have their highest occurrences in the lower part of the biozone. *Spirograptus*? *mirus* appears mid-biozone along with a proliferation of *Dem. simulans*, *Rickardsograptus thuringiacus*, and *Petalolithus praecursor*.

A complete succession of the *simulans* Biozone is well exposed near Černošice-Barrande's Colony Solopisky (Bouček 1953, Štorch 1980); other sections are accessible in Hlásná Třebaň (Štorch *et al*. 2018) and Karlík. A rich graptolite fauna came from the about 1 m thick *simulans* Biozone of the Radotín-tunnel (Štorch *et al*. 2009).

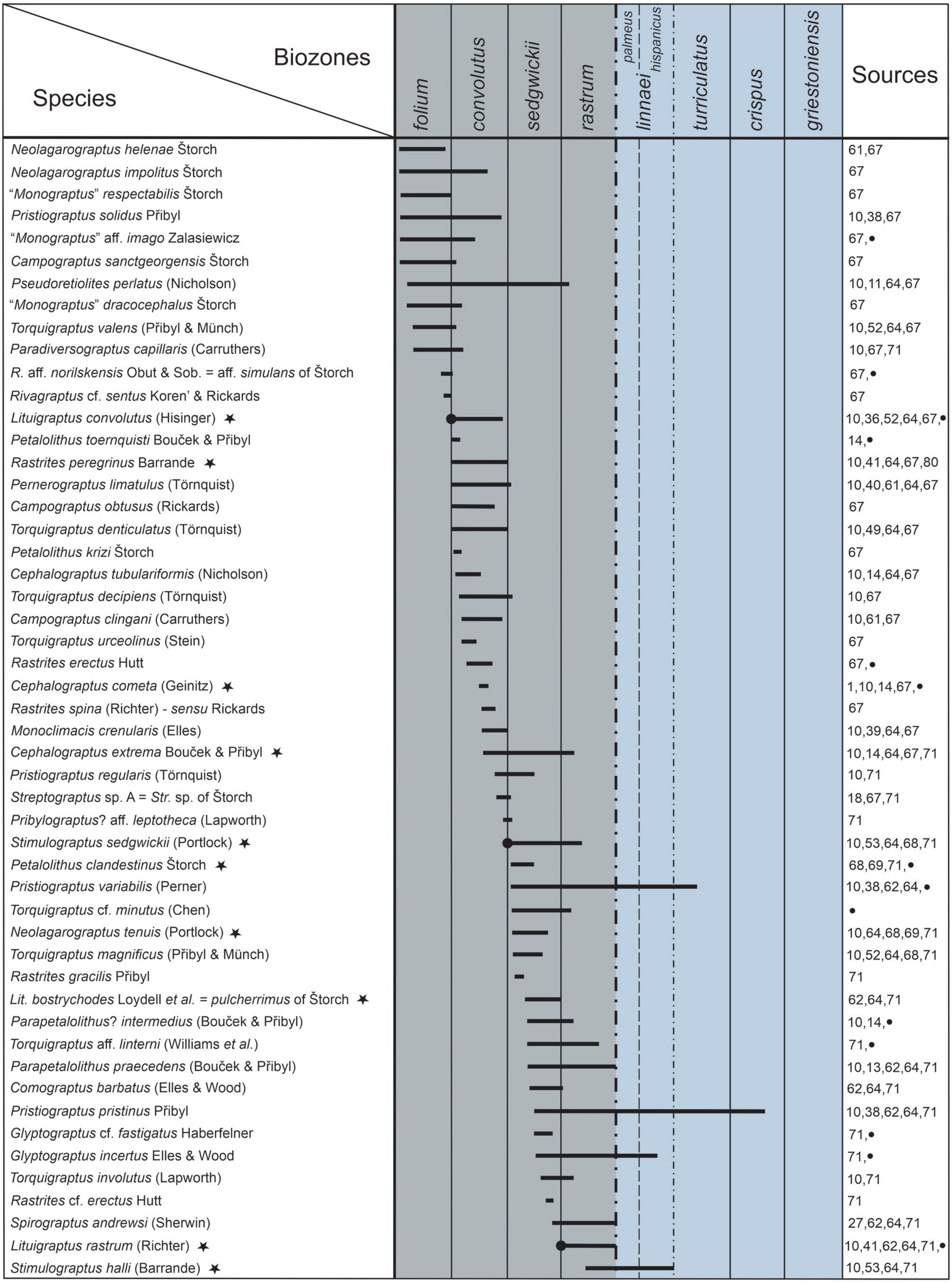
Petalolithus folium Biozone

The *Petalolithus folium* Biozone, recognized by some earlier authors in Scandinavia (*e.g.* Törnquist 1897, 1899; Waern 1948), is re-introduced here as a more easily distinguishable and correlatable replacement of the *Pribylograptus leptotheca* Biozone, first identified by Jones & Pugh (1916) in Wales and then recognized in Bohemia by Bouček (1953) as a subzone in the middle part of the *Lituigraptus convolutus* Biozone. Bouček (1953) introduced the *Petalolithus folium* Subzone as the highest of the three subzones he identified in the *convolutus* Biozone in Barrande's Colony Solopisky near Černošice. Further field work on more complete and less tectonized sections (Velká Chuchle-Colony Haidinger, Radotín-tunnel and Tmaň-Sv. Jiří), and supplemented by revision the Černošice-Colony Solopisky section, revealed that Bouček's *folium* Subzone largely represents an interval below the first occurrence of *Lituigraptus convolutus* and associated *Rastrites peregrinus*, *Cephalograptus* div. sp., and *Torquigraptus denticulatus.*

The lower limit of the *folium* Biozone is delineated by the lowest occurrence of *Petalolithus folium* and the top is defined by the incoming index species of the overlying *convolutus* Biozone (Fig. 11). According to this definition, the *folium* Biozone is an approximate equivalent of the *leptotheca* Biozone with a lower boundary that occurs somewhat higher in the graptolite faunal succession than that of the latter biozone (Fig. 7).

The proximal part of *Prib. leptotheca* is rare, or rarely identified in flattened material, and, remarkably for a species that has been widely recorded, the sicula remains unknown. Distal fragments with very low thecal inclination and considerable but rarely recognized thecal overlap can be easily confused with other equally robust species having pristiograptid thecae (*e.g.* distal parts of *Pristiograptus solidus*), which does not make its biostratigraphical application easy. The lowest *Prib. leptotheca*, accompanied by *Pet. praecursor*, "*M.*" *paradenticulatus*, *Camp. millepeda*, *Dem. simulans* and lowest *Coronograptus maxiculus*, appears markedly below the lowest *Pet. folium*. Both *Pet. folium* (Fig. 10F) and *Prib.*

Figure 11. Stratigraphical ranges of middle Aeronian to lower Telychian graptolites in the Prague Synform. Dashed vertical line mark subzonal boundary, dash-and-dot vertical lines mark tentatively delineated boundaries. See Fig. 5 for further explanation.


Biozones
Species
folium
convolutus
sedgwickii
rastrum
linnaei
palmeus
hispanicus
turriculatus
crispus
griestoniensis
Sources
Neolagarograptus helenae Štorch
61,67
Neolagarograptus impolitus Štorch
67
"Monograptus" respectabilis Štorch
67
Pristiograptus solidus Přibyl
10,38,67
"Monograptus" aff. imago Zalasiewicz
67,•
Campograptus sanctgeorgensis Štorch
67
Pseudoretiolites perlatus (Nicholson)
10,11,64,67
"Monograptus" dracocephalus Štorch
67
Torquigraptus valens (Přibyl & Münch)
10,52,64,67
Paradiversograptus capillaris (Carruthers)
10,67,71
R. aff. norilskensis Obut & Sob. = aff. simulans of Štorch
67,•
Rivagraptus cf. sentus Koren' & Rickards
67
Lituigraptus convolutus (Hisinger) ✶
10,36,52,64,67,•
Petalolithus toernquisti Bouček & Přibyl
14,•
Rastrites peregrinus Barrande ✶
10,41,64,67,80
Pernerograptus limatulus (Törnquist)
10,40,61,64,67
Campograptus obtusus (Rickards)
67
Torquigraptus denticulatus (Törnquist)
10,49,64,67
Petalolithus krizi Štorch
67
Cephalograptus tubulariformis (Nicholson)
10,14,64,67
Torquigraptus decipiens (Törnquist)
10,67
Campograptus clingani (Carruthers)
10,61,67
Torquigraptus urceolinus (Stein)
67
Rastrites erectus Hutt
67,•
Cephalograptus cometa (Geinitz) ✶
1,10,14,67,•
Rastrites spina (Richter) - sensu Rickards
67
Monoclimacis crenularis (Elles)
10,39,64,67
Cephalograptus extrema Bouček & Přibyl ✶
10,14,64,67,71
Pristiograptus regularis (Törnquist)
10,71
Streptograptus sp. A = Str. sp. of Štorch
18,67,71
Pribylograptus? aff. leptotheca (Lapworth)
71
Stimulograptus sedgwickii (Portlock) ✶
10,53,64,68,71
Petalolithus clandestinus Štorch ✶
68,69,71,•
Pristiograptus variabilis (Perner)
10,38,62,64,•
Torquigraptus cf. minutus (Chen)
•
Neolagarograptus tenuis (Portlock) ✶
10,64,68,69,71
Torquigraptus magnificus (Přibyl & Münch)
10,52,64,68,71
Rastrites gracilis Přibyl
71
Lit. bostrychodes Loydell et al. = pulcherrimus of Štorch ✶
62,64,71
Parapetalolithus? intermedius (Bouček & Přibyl)
10,14,•
Torquigraptus aff. linterni (Williams et al.)
71,•
Parapetalolithus praecedens (Bouček & Přibyl)
10,13,62,64,71
Comograptus barbatus (Elles & Wood)
62,64,71
Pristiograptus pristinus Přibyl
10,38,62,64,71
Glyptograptus cf. fastigatus Haberfelner
71,•
Glyptograptus incertus Elles & Wood
71,•
Torquigraptus involutus (Lapworth)
10,71
Rastrites cf. erectus Hutt
71
Spirograptus andrewsi (Sherwin)
27,62,64,71
Lituigraptus rastrum (Richter) ✶
10,41,62,64,71,•
Stimulograptus halli (Barrande) ✶
10,53,64,71

leptotheca (Fig. 10O) overlap slightly with the lowest occurrences of *Lit. convolutus*.

Petalolithus folium better fulfills the requirements of a good biozonal index fossil. 1) It has an almost cosmopolitan distribution, being recorded throughout Europe, Saudi Arabia (Williams *et al*. 2016), China (Mu *et al*. 2002) and Northern Canada (Lenz 1982, Melchin 1989); 2) its rhabdosome represents a distinct grade of petalolithid morphology well anchored within *Petalolithus* and *Cephalograptus* phylogeny (Bouček & Přibyl 1942b, Štorch 1998, Snelling & Zalasiewicz 2011); 3) it is associated with a typical assemblage, easily distinguishable from stratigraphically neighbouring assemblages below and above; 4) it is an easily recognizable taxon with relatively low intraspecific morphological variation; 5) complete specimens are common in many sections around the world, and 6) it can be sucessfully identified even unfavourably preserved in shales affected by moderate tectonic strain (Schauer 1971, Gutiérrez-Marco & Štorch 1998, Štorch & Kraft 2009). This is why *Pet. folium* is proposed as a biozonal index species of a new, potentially standard, globally applicable middle Aeronian *folium* Biozone, which could replace the middle Aeronian *leptotheca* and *argenteus* biozones or the upper part of the *gregarius* Biozone.

The overall assemblage of 0.5–1.8 m thick *folium* Biozone is quite diverse (see Štorch 1998 and Figs 9 and 11 for a full list of species), and comprises a number of incoming taxa (*Pet. folium*, *Prist. solidus*, *Neolagarograptus helenae*, *Neolagarograptus impolitus*, *Pernerograptus inopinus*, "*Monograptus*" *respectabilis*, "*Monograptus*" *dracocephalus*, "*Monograptus*" *capillaris*, "*Monograptus*" *mirificus*, *Campograptus lobiferus*, *Campograptus sanctgeorgensis*, *Torquigraptus valens*, *Rastrites approximatus*, *Rastrites* aff. *geinitzi* and *Lituigraptus richteri*), most of which are restricted to this biozone. Other species, such as *Metaclimacograptus hughesi*, *Metaclimacograptus undulatus*, *N. scalaris*, *K. nikolayevi*, *Glyptograptus tamariscus*, *Rivagraptus bellulus*, *Rick. thuringiacus*, *Pseudorth. insectiformis*, *Pet. praecursor*, *Pristiograptus concinnus*, *C. gregarius*, *C. maxiculus* (Fig. 10 B), *Prib. leptotheca*, *Camp. millepeda*, "*M.*" *paradenticulatus*, *S.*? *mirus*, and *Dem. simulans*, continue from the underlying *simulans* Biozone and half of these, including the long ranging *C. gregarius*, have their highest occurrences in the *folium* Biozone.

The best section through the *folium* Biozone is accessible between Černošice and Solopisky (Černošice-Barrande's Colony Solopisky section described by Bouček 1953 and Štorch 1986); closely similar lithologies and faunas were recorded in the Radotín-tunnel (Štorch *et al*. 2009). A less favourably developed succession was recorded in the Hlásná Třebaň section, with the best preserved graptolites and maximum species richness to be found in loose rocks and subcrops in the field at Tmaň-Sv. Jiří (Štorch 1998).

Lituigraptus convolutus Biozone

The *convolutus* Biozone was initially described in England by Marr & Nicholson (1888) and first adopted for use in the Prague Synform (then Barrandian area) by Přibyl (1940a) as a replacement of the *Rastrites peregrinus* Biozone recognized by Perner & Kodym (1919, 1922) and Bouček (1930, 1934) and the *Monograptus lobiferus* Biozone recognized by Kettner & Bouček (1936). A loosely used *convolutus* Biozone was subsequently studied by Bouček (1953) and subdivided into a *Campograptus millepeda* Band overlain by *Pribylograptus leptotheca* and *Petalolithus folium* subzones. More recent work at the Černošice-Col. Solopisky, Hlásná Třebaň and Radotín-tunnel sections, supplemented by detailed study of the faunal assemblages at Tmaň-Sv. Jiří (Štorch 1998), enabled thorough revision of the *Lituigraptus convolutus* Biozone, which is now restricted to the interval marked by the occurrence of true *Lituigraptus convolutus* (Fig. 10N) with its rather high and slender tubular, strictly rastritiform proximal thecae and long, high-triangular distal thecae with long dorsally facing apertural processes. This biozonal index species has not been always distinguished from its rather similar praecursor, *Lit. richteri*. The new definition, introduced by Štorch (2006), recognized the *convolutus* Biozone as an interval delineated by the lowest occurrence of *Lit. convolutus* at the base and the first *Stimulograptus sedgwickii* (index species of the overlying biozone) at the top (Fig. 11). The *convolutus* Biozone, as it is presently understood, is most likely restricted to the uppermost part of the *convolutus* Biozone imprecisely-defined by Bouček (1953) and similarly correlates with the upper *convolutus* Biozone in the sense of Zalasiewicz *et al*. (2009) as indicated also by stratigraphic record of the *Petalolithus–Cephalograptus* evolutionary lineage by Snelling & Zalasiewicz (2011).

The maximum thickness of the redefined *convolutus* Biozone probably does not exceed 3 m in the Prague Synform, its whole thickness being represented by alternating black siliceous shales and silty silicites. A complete section of the 2.1 m thick biozone was documented in the Radotín-tunnel (Štorch *et al*. 2009, Štorch & Frýda 2012).

The biozonal index *Lit. convolutus* is typically accompanied by advanced petalolithids [*Petalolithus krizi*, *Petalolithus toernquisti*, *Cephalograptus tubulariformis*, *Cephalograptus cometa* (Fig. 10G) and *Cephalograptus extrema* (Fig. 10H)], in association with *Monoclimacis crenularis*, *Pernerograptus limatulus*, *Campograptus clingani*, *Campograptus obtusus*, *Torquigraptus denticulatus*, *Torquigraptus decipiens*, *Torquigraptus urceolinus*, *R. peregrinus* (Fig. 10J), *Rastrites spina* and *Rastrites erectus*. Many longer-ranging taxa, including *N. scalaris*, *Metacl. hughesi*, *Gl. tamariscus*, *Pseudorth. insectiformis*, *Rivagraptus bellulus*, *Pseudoretiolites perlatus*, *Prist. solidus*, *Nl. impolitus*, *Prib. leptotheca*, "*Monograptus*" aff. *imago*, *S.*? *mirus*, *Paradiversograptus capillaris*, "*M.*" *mirificus* and *T. valens*, continue from the underlying *folium* and *simulans* biozones. Most of this diverse and distinctive graptolite fauna vanished from the fossil record in the course of the *convolutus–sedgwickii* boundary interval leaving few survivors in the *sedgwickii* Biozone, as shown by Štorch & Frýda (2012) in the Radotín-tunnel section.

The only complete succession through the *convolutus* Biozone has been studied for reference in the subsurface Radotín-tunnel section (Štorch *et al*. 2009). The lower part of the biozone is accessible in the Hlásná Třebaň section, Karlík and Černošice-Colony Solopisky. Bleached rocks and subcrops rich in well-preserved graptolites are known from Tmaň-Sv. Jiří (Bouček 1953, Štorch 1998).

Stimulograptus sedgwickii Biozone

Bouček (1930) formerly recognized a *Monograptus involutus* Biozone above the *peregrinus* Biozone in his revision of the stratigraphical succession of Barrande's Colony Lapworth near Zdice but later (Bouček 1934) adopted *Monograptus sedgwickii* as index-fossil of this internationally recognized biozone. Štorch & Frýda (2012) took account of a separate *Stimulograptus halli* Biozone in Britain (Loydell 1991), as occurs also in Spain (Loydell *et al*. 2015), but instead distinguished a *Lituigraptus rastrum* Biozone in the upper part of Bouček's (1953) *sedgwickii* Biozone.

The present concept of the *sedgwickii* interval Biozone, after Štorch & Frýda (2012), defines its base by the incoming of *Stim. sedgwickii* (Fig. 10P) and the top is delineated by the lowest *Lituigraptus rastrum*. The latter authors distinguished two successive graptolite assemblages in the *sedgwickii* Biozone but the limited number and incompleteness of sections prevent potential subdivision of the *sedgwickii* Biozone. The biozone's sedimentary succession, 1.1–1.7 m thick, is represented in the lower part by fine black shale with abundant pyrite nodules and lenses. The upper part is more silty and micaceous.

The lower graptolite assemblage was impoverished by a mass extinction event (*sedgwickii* Event) and comprises *Pseudorth. insectiformis*, *Prist. regularis*, *Pribylograptus* aff. *leptotheca*, *Pern. limatulus*, *Camp. lobiferus*, and *T. decipiens* surviving from the previous biozone. *Cephalograptus extrema* and *Metacl. undulatus* also survived and range up to the *rastrum* Biozone in Bohemia. The incoming of *Stim. sedgwickii* is followed by the appearance of *Petalolithus clandestinus* (Fig. 10C), *Neolagarograptus tenuis* (Fig. 10I), *Pristiograptus variabilis*, *Rastrites gracilis* and *Torquigraptus magnificus*. The upper *sedgwickii* Biozone sees proliferation of *Metacl. undulatus* and *Stim. sedgwickii* in association with taxa ranging from the lower assemblage and the incoming *Parapetalolithus praecedens*, *Comograptus barbatus*, *Glyptograptus* cf. *fastigatus*, *Glyptograptus incertus*, *Pristiograptus pristinus*, *Torquigraptus* aff. *linterni*, and *Torquigraptus involutus*. The uppermost part of the *sedgwickii* Biozone is marked by the lowest occurrences of *Spirograptus andrewsi*.

The only complete section through the *sedgwickii* Biozone was documented by Štorch & Frýda (2012) from the Radotín-tunnel. Other, partial sections, without the lower part of the biozone, are accessible in Zadní Třebaň-railway station, and Barrande's Colony Lapworth near Zdice. A peculiar, at least 6.5 m thick succession of tuffaceous shales and carbonates with a mixed graptolite and benthic fauna (Štorch 2001), was found by Havlíček & Kříž (1973) in a tectonic block along the Prague Fault near Hýskov (Hýskov-V Jakubince).

Lituigraptus rastrum Biozone

The upper part of *sedgwickii* Biozone of Bouček (1934, 1953) and Štorch (1994a, 2006) was defined by Štorch & Frýda (2012) as a separate interval biozone delineated by the lowest occurrence of the biozone-index *Lituigraptus rastrum* (Fig. 10D) at the base and the lowest occurrence of the index species of the overlying *Rastrites linnaei* Biozone at the top. The *rastrum* Biozone is, significantly, actually separated from the *linnaei* Biozone also by the first graptolite-barren calcareous mudstone bed indicating the base of the Litohlavy Formation in all stratigraphically relevant sections of the Prague Synform (Kříž 1975, Štorch 2006, Štorch & Frýda 2012). Graptolitic black shale referred to the *rastrum* Biozone is the equivalent of the middle part of the *Stimulograptus halli* Biozone recognized in Wales (Loydell 1991) and also in Spain, where a separate *rastrum* Subzone was recognized (Loydell *et al*. 2015). *Lituigraptus rastrum* is readily identified and common index species in the Czech sections. Base of an interval biozone defined by *Stimulograptus halli*, as used by Loydell (1991), Zalasiewicz *et al*. (2009) and Loydell *et al*. (2015) is hard to delineate in the Prague Synform due difficulties in distinguishing between incomplete rhabdosomes of *Stim. sedgwickii* and *Stim. halli* without their proximal part in conjunction with the stratigraphical overlap of the two biozone-index taxa.

The graptolite fauna of the 0.4–0.75 m thick fine black shale of the *rastrum* Biozone is dominated by *Lit. rastrum* in association with the incoming of *Spirograptus andrewsi* (first appearance in uppermost *sedgwickii* Biozone), *Stim. halli* (Fig. 12O), *Rastrites schaueri*, *Parapetalolithus* cf. *palmeus*, rare *Parapetalolithus intermedius*, and relatively long-ranging *Metacl. undulatus*, *Prist. variabilis*, and *Pristiograptus pristinus*. *Comograptus barbatus*, *Gl. incertus*, *Stim. sedgwickii*, *Torquigraptus* cf. *minutus*, *T. involutus*, and *T.* aff. *linterni* have their highest occurrences in Bohemia in the course of this interval. *Parapetalolithus praecedens* and the biozone-index *Lit. rastrum* reach the top of the black shale succession below the pale mudstone.

Graptolite-bearing black shales of the *rastrum* Biozone have been documented in detail from the subsurface Radotín-tunnel section (Štorch & Frýda 2012); partial sections are accessible at Zdice-Barrande's Colony Lapworth, Zadní Třebaň-railway station, and Karlík-valley. Bouček (1953) collected rich graptolite assemblage of this level at the classical Barrande's locality Želkovice-behind farm.

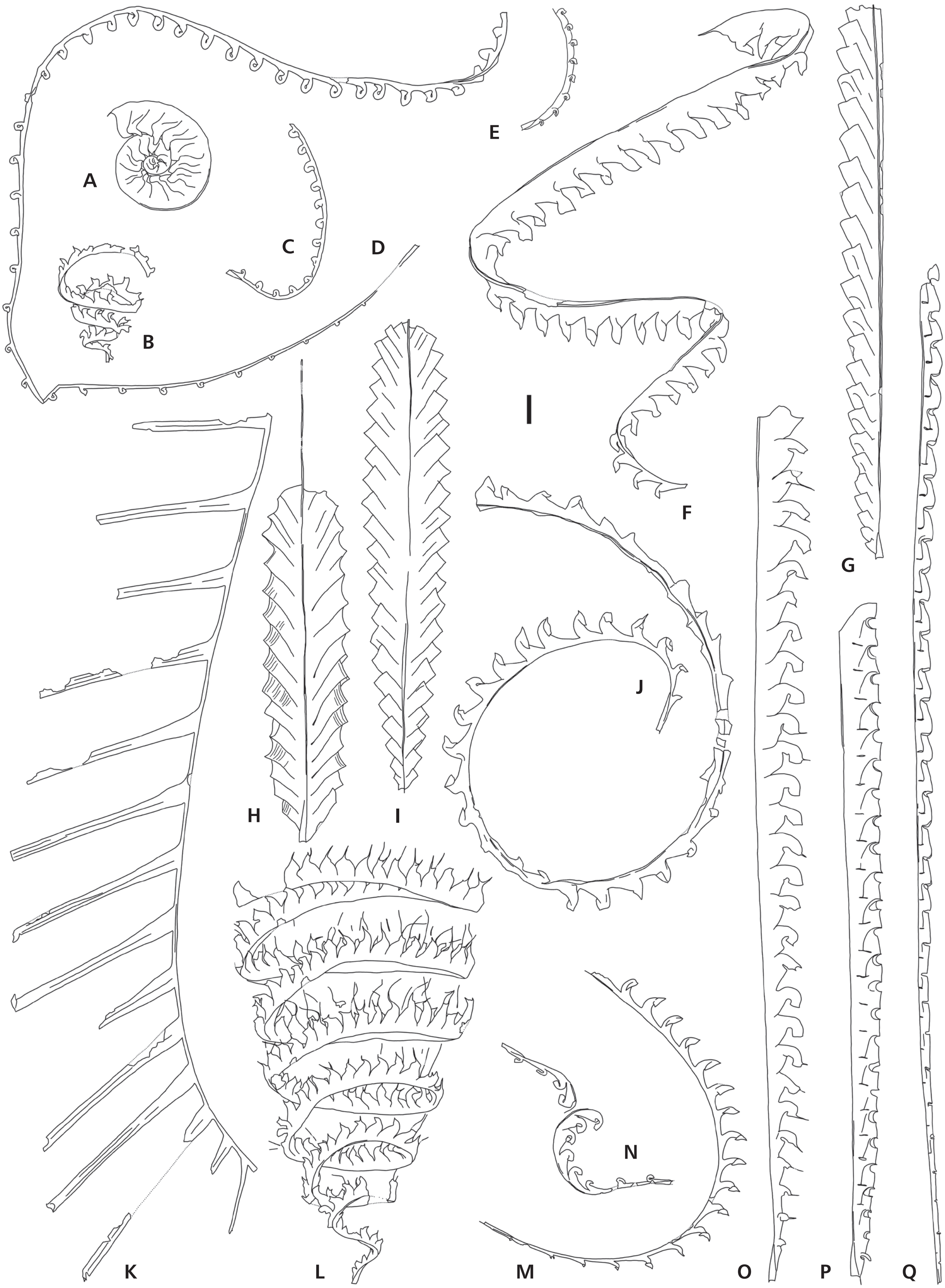
Rastrites linnaei Biozone

The *linnaei* Biozone was one of the earliest nine graptolite biozones recognized by Perner & Kodym (1919, 1922) in the Silurian succession of central Bohemia. Bouček (1953) described and subdivided the *linnaei* Biozone into two subzones distinguished upon parapetalolithid species – a lower *Parapetalolithus palmeus* Subzone and an upper *Parapetalolithus hispanicus* Subzone. This subdivision was adopted by Štorch (2006) in his definition of the *linnaei* Interval Biozone. *Rastrites linnaei* has historical preference as it was used before *Spirograptus guerichi*, now used as a biozone fossil in many global correlation schemes (Loydell 2012, Melchin *et al*. 2020). *Spirograptus guerichi* is hard to distinguish from *Spirograptus turriculatus*, its probable descendant (Loydell *et al.* 1993) and index species of the next biozone, namely in specimens preserved obliquely to bedding, tectonically distorted or immature without well-preserved sicula and first theca. Overall graptolite assemblages indicate correlation of the Czech *linnaei* Biozone with about the middle part of the *guerichi* Biozone (Fig. 7) of Welsh sections but its precise position and correlation with the subzones recognized by Loydell (1991) is unclear. It is important to note that in Wales (Loydell 1991) and in the El Pintado section, Spain (Loydell *et al*. 2015), *Rastrites linnaei* has its first appearance in the uppermost Aeronian, a level represented by graptolitically barren strata in Bohemia. Gutiérrez-Marco & Štorch (1998) recognized *runcinatus–gemmatus*, *palmeus* and *hispanicus* Subzones within the *linnaei* Biozone in the Spanish Western Iberian Cordillera. The latter two subzones equate with those recognized in Czech sections whereas the lowest one, the *runcinatus-gemmatus* Biozone, is largely missing in the Prague Basin due to the lack of graptolite-bearing lithologies.

The lower and upper limits of the *linnaei* Biozone cannot be precisely delineated as the graptolitic black shale bands lie within pale mudstone beds barren of graptolites (Fig. 7). The biozone index *R. linnaei* (Fig. 12K), characteristic of this high diversity graptolite assemblage, spans the whole interval biozone although being less common in the *hispanicus* Subzone. *Parapetalolithus palmeus* (Fig. 12H), *Parapetalolithus clavatus* and rare "*Monograptus*" *gemmatus* occur in the lower subzone. The relatively long-ranging *Gl. incertus*, *Prist. variabilis*, *Prist. pristinus*, and *R. schaueri* continued in both subzones from the underlying biozone. Many incoming species, *Parapetalolithus elongatus*, *Parapetalolithus linearis*, *Parapetalolithus ovatus*, *Torquigraptus planus*, *Oktavites contortus*, *Spirograptus guerichi* (Fig. 12B), *Streptograptus plumosus*, *Rastrites carnicus*?, and *Rastrites fugax*, occur in both the *palmeus* and *hispanicus* subzones. *Monograptus marri* continues high into the overlying *Spirograptus turriculatus* and *Streptogratus crispus* biozones. *Parapetalolithus hispanicus* (Fig. 12I), *Pseudoretiolites dentatus*, *Stimulograptus becki* and *Torquigraptus obtusus* are restricted, for the most part, to the *hispanicus* Subzone in Bohemia.

The lower Telychian of the Prague Synform is developed as alternating graptolitic black shale and pale calcareous mudstones that vary greatly among sections.

Figure 12. Age-diagnostic lower and middle Telychian graptolites. • A – *Cochlograptus veles* (Richter), PŠ 4397, upper *crispus* Biozone. • B – *Spirograptus guerichi* Loydell *et al*., PŠ 4393, *linnaei* Biozone. • C – *Streptograptus exiguus* (Lapworth), PŠ 464/2, uppermost *turriculatus* Biozone. • D – *Streptograptus crispus* (Lapworth), PŠ 453/1, lower *crispus* Biozone. • E – *Streptograptus* sp. B, PŠ 4398, lower *crispus* Biozone. • F – *Torquigraptus proteus* (Barrande), PŠ 4350, uppermost *turriculatus* Biozone. • G – *Pristiograptus bjerringus* (Bjerreskov), PŠ 4351/1, upper *turriculatus* Biozone. • H – *Parapetalolithus palmeus* (Barrande), PŠ 4392, *palmeus* Subzone of the *linnaei* Biozone. • I – *Parapetalolithus hispanicus* (Haberfelner), PŠ 4390, *hispanicus* Subzone of the *linnaei* Biozone. • J – *Torquigraptus spiraloides* (Přibyl), L62397, upper *tullbergi* Biozone. • K – *Rastrites linnaei* (Barrande), PŠ 4391, *linnaei* Biozone. • L – *Spirograptus turriculatus* (Barrande)*, PŠ 4356, upper turriculatus* Biozone. • M – *Torquigraptus tullbergi* (Bouček), PŠ 601b, *tullbergi* Biozone. • N – "*Monograptus*" *drepanoformis* Toghill & Strachan, PŠ 4354/2, upper *griestoniensis* Biozone. • O – *Stimulograptus halli* (Barrande), PŠ 4353, upper *linnaei* Biozone. • P – *Monoclimacis crenulata* (Elles & Wood), BB 6990, *tullbergi* Biozone. • Q – *Monoclimacis griestoniensis* (Nicol) s.l., BB 6988, *griestoniensis* Biozone. A, C–G, L – Litohlavy-railway cut; B, H, I, K, O – Želkovice, behind farm; J – Jinonice-Nová Ves; M – Beroun-Jarov, borehole B49; N – Praha-Pankrác, borehole Pp-2/J3; P, Q – Praha-Braník, sewerage gallery near brewery. All figures × 5, scale bar represents 1 mm.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No particular black-shale band is correlatable across the whole Prague Synform. A complete section through the *linnaei* Biozone in a temporary building excavation at Praha-Nové Butovice housing estate exhibits significant prevalence of pale calcareous mudstones devoid of graptolites. Black shales are limited to four intercalations with a total thickness of 0.4 m. Similar dominance of pale mudstones in the lowermost Telychian succession was recorded by Kříž (1975) in several boreholes.

A relatively greater proportion of graptolite-bearing black shales has been recorded in the classical Želkovice section – type locality of several important species described by Barrande (1850), Perner (1897) and Bouček & Přibyl (1942a). An incomplete section of the *linnaei* Biozone was exposed in Želkovice by a trench along the field tract (Appendix, locality 17b). The *palmeus* Subzone was identified in three black-shale bands, each *ca* 0.1 m thick, and a major 0.9 m thick interval, all underlain and overlain by pale mudstones. Graptolitic shale of the *hispanicus* Subzone, 1.4 m in total thickness, is divided in two parts by a thin basalt sill in the Želkovice section. Black graptolite-bearing bands of the *hispanicus* Subzone, interbedded with pale mudstones, have also been recorded in the Hlásná Třebaň-rock (Bouček 1953) and Radotín-tunnel (Štorch *et al*. 2009) sections. Bouček (1930) reported the *linnaei* Biozone from Zdice-Barrande's Colony Lapworth.

Spirograptus turriculatus Biozone

The *turriculatus* Biozone was first used in Bohemia by Perner & Kodym (1919, 1922), and placed immediately above the *linnaei* Biozone in their biozonal scheme. Since then, the biozonal subdivision and correlation of the lower Telychian has undergone significant changes both in the Prague Synform and worldwide. The two Czech biozones (*linnaei* and *turriculatus*) equated to the *turriculatus* Biozone of Rickards (1976) and earlier British authors. Loydell *et al*. (1993) separated the lower part of the former British *turriculatus* Biozone, with the newly distinguished *S. guerichi* selected as a biozone fossil of the new biozone. In the Prague Synform Bouček (1930), Prantl & Přibyl (1940) and Přibyl (1940a, 1948) distinguished a *Streptograptus runcinatus* Biozone between the *S. turriculatus* and *Streptograptus crispus* biozones based on a misidentification of *Paradiversograptus runcinatus*, with the Czech species subsequently described by Loydell (1991) as *Streptograptus storchi*. This graptolite is common in the upper *turriculatus* and lower *crispus* biozones in Britain (Loydell 1992, Zalasiewicz 1994), similarly as in the Prague Synform. True *Paradiversograptus runcinatus* is missing in the Prague Synform. Its stratigraphical range is confined to the *guerichi* Biozone and it is particularly common in Wales in the lower part of this biozone which is represented by barren mudstones in all Czech sections. Up to nine subzones recognized by Loydell (1992), Zalasiewicz (1994) and Zalasiewicz *et al*. (2009) in the British biozonal scheme within the *guerichi*, *turriculatus* and *crispus* biozones have proved very difficult to recognize in the Prague Synform, at least in part due to incomplete fossil record repeatedly interrupted by barren mudstone beds. The relatively thin succession of graptolite-rich black shales accessible to study above the yellow-greenish mudstone beds of the lowermost Litohlavy Formation (Kříž 1975) appears to include only the upper part of the global standard *turriculatus* Biozone that corresponds with the *Torquigraptus proteus* Subzone of the British biozonal scheme.

Loydell (1992) defined the *turriculatus* Biozone as an interval between the stratigraphically lowest occurrence of *Spirograptus turriculatus* (Fig. 12L) and first occurrence of *Stretograptus crispus*, biozonal index species of the overlying biozone. This definition has been adopted by Štorch (2006) although the lower limit of the *turriculatus* Biozone is hidden in the Prague Synform somewhere within the yellow-greenish mudstones of the lowermost Litohlavy Fm. (Štorch 2006 and Fig. 7). The upper limit is well defined by the incoming of *Str. crispus*, although the biozonal index *S. turriculatus* continues high into the *crispus* Biozone (Kříž 1992). The moderately diverse graptolite assemblage of the upper *turriculatus* Biozone (Fig. 13) includes the biozonal index species, *Parapetalolithus tenuis*, *Prist. variabilis*, *Prist. pristinus*, *Pristiograptus macrodon*, *M. marri*, *Streptograptus storchi*, rare *Streptograptus johnsonae*, *Torquigraptus proteus* (Fig. 12F), and *Rastrites distans*. *Streptograptus exiguus* (Fig. 12C) is particularly common just below the earliest *Str. crispus*. Most species of this assemblage continued well into the lower *crispus* Biozone (Fig. 13).

The service-railway cut opposite the Litohlavy water reservoir near Králův Dvůr (Litohlavy-railway cut) is the only outcrop of the richly fossiliferous upper part of the *turriculatus* Biozone. This biozone is represented by a 1 m thick alternation of graptolitic black shale and pale-coloured mudstones devoid of any macrofossils exposed above the principal mudstone bed at the base of the Litohlavy Formation (Kříž 1975, 1992). The same succession, 1.6 m thick, referable to the upper *turriculatus* Biozone, was studied in the pipeline trench in Velká Ohrada near Řeporyje (Štorch 2006, Fig. 6). An about 1.8 m thick *turriculatus* Biozone, with badly preserved graptolites, was temporarily exposed by building excavations at the Praha-Nové Butovice housing estate (Štorch 2006, Fig. 5), and a *ca* 0.2 m thick section occurs sandwiched between two basalt sills in the road cut south of Solopisky. Bouček (1953) reported this biozone from Barrande's Colony Lapworth near Zdice, from Modřany-

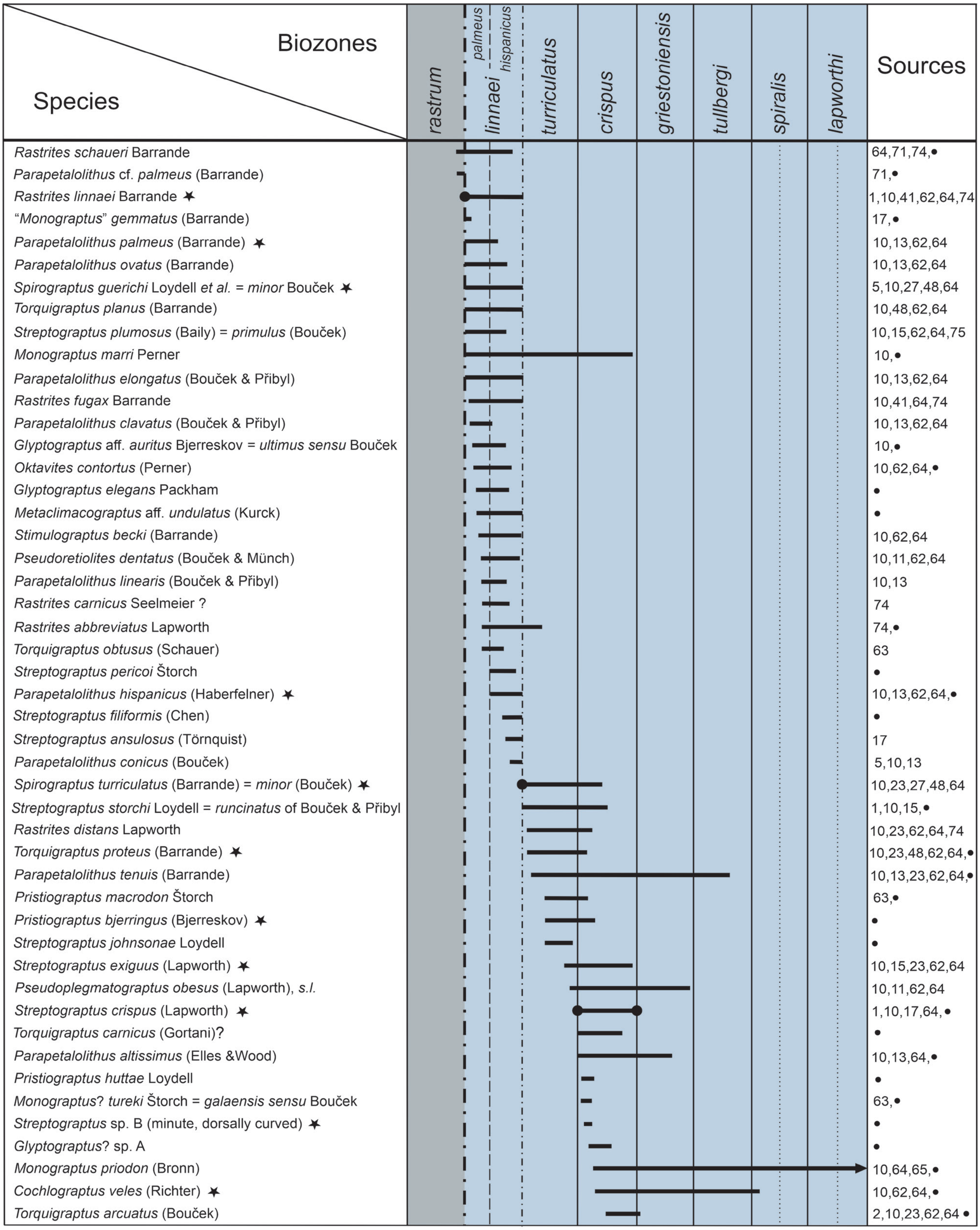


Figure 13. Stratigraphical ranges of lower Telychian graptolites in the Prague Synform, continued from Fig. 11. Dashed vertical line mark subzonal boundary, dash-and-dot vertical lines mark tentatively delineated boundaries, dotted vertical lines indicate subdivision of particularly long biozones into two or three subintervals of equal duration. Right-pointing arrow indicates continuation of the species range to the next range chart. See Fig. 5 for further explanation.

Vinice, Radotín-Lahovská, and Housina hillcrest near Želkovice, but none of these localities exhibits a stratigraphically useful section.

Streptograptus crispus Biozone

The *crispus* Biozone, established by Marr & Nicholson (1888) in England, was first identified in the Prague Synform by Bouček (1930). Bouček (1953) provided a brief description of this graptolite biozone and its assemblage. Štorch (in Kříž 1992) moved the lower limit of the *crispus* Biozone down to the lowest occurrences of the biozone index fossil based on detailed examination of the Litohlavy-railroad cut section.

This biozone is defined as an interval delineated by the stratigraphically lowest occurrences of *Streptograptus crispus* at the base and highest occurrences of this species at the top (Fig. 13). The lowermost part of the *crispus* Biozone is further characterized in Bohemia by the incoming of *Parapetalolithus altissimus*, *Monograptus*? *tureki*, uncommon *Pseudoplegmatograptus obesus*, *Pristiograptus huttae* and *Pristiograptus bjerringus* (Fig. 12G). *Streptograptus exiguus* proliferated in association with the first *Str. crispus* (Fig. 12D). *Pristiograptus macrodon* vanished in the lower *crispus* Biozone while *T. proteus* is replaced by *Torquigraptus carnicus*. The minute and short-lived *Streptograptus* sp. B (Fig. 12E) is confined to this level. Species continuing from the upper *turriculatus* Biozone are *Parapet. tenuis*, *Prist. pristinus*, *M. marri*, *Str. storchi*, *S. turriculatus* and *R. distans*. Minute but easily recognizable *Cochlograptus veles* (Fig. 12A), associated with reappearing *Str. crispus*, and closely followed by *Torquigraptus arcuatus* and *Pristiograptus initialis*, characterizes the middle part of the *crispus* Biozone. *Spirograptus turriculatus* has its highest occurrences here. The uppermost *crispus* Biozone is less well known due to unfavourable preservation of the graptolite fauna.

The total thickness of the *crispus* Biozone is up to 7 m in its classical reference section in Litohlavy. The black shales of this section are rich in well-preserved graptolites, pale-coloured mudstone intercalations become less common about mid-biozone. Another complete section through a 3.5 m thick *crispus* Biozone was temporarily exposed in the pipeline trench at Velká Ohrada. The first record of the biozone made by Bouček (1930) referred to Barrande's Colony Lapworth; Přibyl (1940a) identified this biozone in Modřany-Barrande's Colony Vinice, and a small part of the lower *crispus* Biozone was recorded between two basalt sills exposed by the road cut south of Solopisky. Prantl & Přibyl (1940) reported the *crispus* Biozone from a now recultivated brick pit in Praha-Stodůlky; Bouček (1953) noted outcrops along the local road from Radotín to Lahovská and at Housina hill-crest, along the road from Bykoš to Neumětely.

Monoclimacis griestoniensis Biozone

First recognized by Wood (1906) in Wales, this graptolite biozone was adopted into the Czech biozonal scheme by Bouček (1930). The only brief description of this interval and graptolite assemblage was provided by Bouček (1953) with reference to a well excavation in Praha-Pankrác. In the Pankrác syncline, however, the *griestoniensis* Biozone rests on the basal mudstone of the Litohlavy Formation (Kříž 1975), deposited after a long gap in sedimentation recognized by (Štorch 2006) and its lower strata are not graptolitic. Other records of well-preserved fauna referred to the *griestoniensis* Biozone came from incomplete drill cores. No permanent and complete sections have been accessible since the times of Bouček (1953).

The present concept of this unit follows Štorch (2006), who defined the *griestoniensis* Biozone as an interval between the stratigraphically highest occurrences of *Str. crispus* at the base and first appearances of *Torquigraptus tullbergi* at the top. Both species are biozone fossils of adjacent biozones. *Monoclimacis griestoniensis* s.l. (Fig. 12Q) and related monoclimacids with slender rhabdosomes are common in middle Telychian strata but their complete stratigraphical ranges are poorly known in the Prague Synform due to the lack of relevant sections and the taxonomic revision by Zalasiewicz *et al.* (1995), which has a significant impact on earlier records of *Mcl. griestoniensis*. The graptolite assemblage of the *griestoniensis* Biozone has been summarized from revision of the faunal list of Bouček (1953), unpublished records from temporary building excavations in Praha-Řepy housing estate, the Velká Ohrada-pipeline trench, Malá Ohrada, and several boreholes (Dufka *et al*. 1995). It is marked by common *Mcl. griestoniensis* s.l., *Monoclimacis woodae*, *Torquigraptus pragensis*, common *Torquigraptus australis*, *Streptograptus loydelli*, *Pristiograptus initialis*, "*Monograptus*" *drepanoformis* (Fig. 12N), *Pseudoplegmatograptus obesus* s.l., *Parapet. tenuis*, and *Parapet. altissimus*. *Torquigraptus arcuatus*, continuing from the underlying biozone, vanished in the lower part of the *griestoniensis* Biozone. Long-ranging taxa include *Retiolites angustidens*, *Monograptus priodon* and *Coch. veles*. Bouček (1953) reported also *Monoclimacis crenulata*.

Argillitic black shales with subordinate yellowish muddy intercalations referred to the middle and upper part of the *griestoniensis* Biozone crop out north of the entrance of the railway tunnel in Malá Chuchle; the lower part of the biozone was accessible along the local road from Radotín to Lahovská. Heavily weathered shales have been

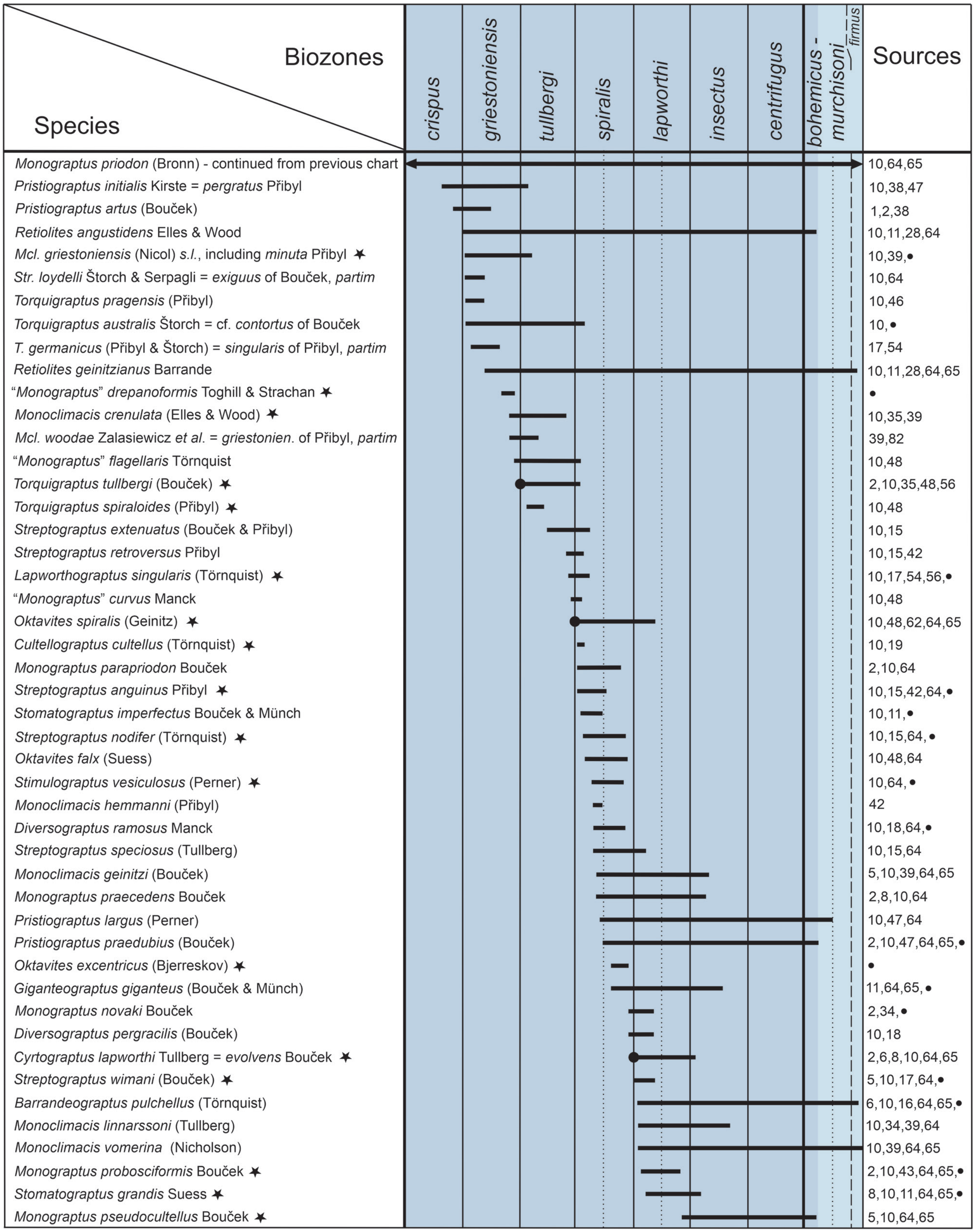


Figure 14. Stratigraphical ranges of Telychian graptolites in the Prague Synform, continued from Fig. 13. Dashed vertical line mark subzonal boundary, dotted vertical lines indicate subdivision of particularly long biozones into two or three subintervals of equal duration. Arrows indicate continuation of the species range to the next and/or preceding range chart. See Fig. 5 for further explanation.

also exposed along the road from Bykoš to Neumětely at Housina hill crest and in the now recultivated brick pit in Praha-Stodůlky (Prantl & Přibyl 1940). A complete, 1.6–1.7 m thick biozone was temporarily exposed by building excavations in the Praha-Řepy housing estate. (Štorch 1982) and the Velká Ohrada-pipeline trench.

Torquigraptus tullbergi Biozone

The *tullbergi* partial-range Biozone was established by Štorch (1994a) as a replacement for the less well-defined *Monoclimacis crenulata* Biozone, erected by Wood (1906) in Wales. The *crenulata* Biozone was formerly recognized by Prantl & Přibyl (1940) as a lower subzone of the *Spirograptus spiralis subconicus* Biozone and, indeed, it was based upon a graptolite association corresponding with the *Spirograptus spiralis* Biozone of subsequent authors, as already noted by Bouček (1953). A separate *crenulata* Biozone was recognized by Horný (1962), Kříž (1975, 1992) and Havlíček & Štorch (1990), with reference to the redefinition provided by Bouček (1953). Temporarily exposed middle-upper Telychian sections revealed significant overlaps of the stratigraphical range of *Mcl. crenulata* with the index species of the underlying *Mcl. griestoniensis* and overlying *Oktavites spiralis* biozones. *Monoclimacis crenulata* is relatively uncommon in the Prague Synform and specimens without a well-preserved proximal end are difficult to distinguish from *Monoclimacis vomerina* and *Monoclimacis geinitzi*; see Zalasiewicz *et al*. (2009) for further discussion. Abundant and easily identifiable *Torquigraptus tullbergi*, characteristic of this interval also in Germany (Schauer 1971), Bornholm (Bjerreskov 1975) and Spain (Gutiérrez-Marco & Štorch 1998) is a better index fossil of the Czech mid-Telychian strata below the first occurrence of *Oktavites spiralis.*

The *tullbergi* Biozone is formally redefined as an interval between the first occurrences of the biozone index graptolite and the incoming of *Oktavites spiralis*. The graptolite assemblage of this biozone is diverse, but the only incoming species, along with abundant *T. tullbergi* (Fig. 12M), are *Streptograptus extenuatus* and the rare, short-lived *Torquigraptus spiraloides* (Fig. 12J). *Monoclimacis griestoniensis*, *Mcl. woodae* and also *Mcl. crenulata* (Fig. 12P) continue from the underlying strata. Long-ranging taxa include *Pseudoplegm. obesus* s.l., *Ret. angustidens*, *Prist. initialis*, *M. priodon* and *Coch. veles*. Rare *Parapet. tenuis* represents the stratigraphically highest record of the genus. The *tullbergi–spiralis* Biozone boundary interval (Fig. 14) is marked by short-lived “*Monograptus*” *curvus*, *Lapworthograptus singularis*, *Streptograptus retroversus*, and rare *Giganteograptus* sp.

The best, although incomplete section of the *tullbergi* (at that time *crenulata*) Biozone was studied by Bouček (1953) in well excavations at Jinonice-Nová Ves and Praha-Pankrác. Přibyl & Prantl (1940) mistakenly reported *crenulata* Subzone from a former brick pit near Praha-Stodůlky based on faunal assemblage that corresponds with that of present *Oktavites spiralis* Biozone. Later (Prantl & Přibyl 1944) identified a graptolite assemblage corresponding with that of the present *tullbergi* Biozone from a borehole in Tachlovice. A complete 3.5–5.0 m thick *tullbergi* Biozone, developed in the typical alternation of black graptolitic shales and pale-coloured graptolite-barren mudstones, was temporarily accessible in building excavations in the Praha-Řepy housing estate (Štorch 1982), Velká Ohrada-building excavation (Štorch 1994b), Velká Ohrada-pipeline trench, and Malá Ohrada. Another complete section of the *tullbergi* Biozone, 3.7 m thick, crops out north of the railway-tunnel entrance in Malá Chuchle.

Oktavites spiralis Biozone

One of the first graptolite biozones recognized by Perner & Kodym (1919, 1922) was named after *Monograptus spiralis subconicus*, the preservational subspecies subsequently recognized by Přibyl (1945) to be a junior synonym of *Oktavites spiralis*. This biozone formerly embraced a stratigraphical interval much wider than today (*e.g*. Prantl & Přibyl 1940, 1944), including the present *Torquigraptus tullbergi* and lower *Cyrtograptus lapworthi* biozones. Bouček (1953) recognized three subzones in his invaluable description of the *spiralis* Biozone: those of *Monograptus parapriodon*, *Streptograptus anguinus* and *Monoclimacis geinitzi* in ascending order. The last named subzone is largely included herein in the *lapworthi* Biozone introduced in the biozonal scheme of the Prague Synform by Štorch (2006). The former two subzones are no longer recognized because their index species occur together through much of the *spiralis* Biozone.

The *spiralis* Biozone in its present stratigraphically restricted form is defined as an interval delimited by the lowest occurrence of the biozone index, *O. spiralis* (Fig. 15K), at the base and the lowest *Cyrtograptus lapworthi* at the top. The lowermost *spiralis* Biozone is marked by the stratigraphically highest occurrences of “*M.*” *curvus*, *Coch. veles* and *Lapw. singularis* (Fig. 15C) associated with the lowest occurrences of *O. spiralis.* The rich graptolite assemblage of the lower *spiralis* Biozone shown by Fig. 14 includes *Mcl. crenulata*, *Str. retroversus* and *Str. extenuatus*, continuing from the previous biozone, in association with the incoming of *M. parapriodon*, *Streptograptus anguinus* (Fig. 15D) and the short-lived and very distinctive *Cultellograptus* *cultellus* (Fig. 15A). Long-ranging elements are represented by *Retiolites geinitzianus*, *Ret. angustidens*, *M. priodon* and the first *Pristiograptus largus*. *Oktavites falx*, *Diversograptus ramosus*, *Streptograptus nodifer* (Fig. 15G), *Stimulograptus vesiculosus* (Fig. 15E), *Monograptus praecedens*, *Mcl. geinitzi*, rare *Oktavites excentricus* (Fig. 15F), *Giganteograptus giganteus* and *Stomatograptus imperfectus*, as well as the short-ranging *Monoclimacis hemmanni*, appear in the lower and middle part of the biozone. The uppermost part of the biozone sees the incoming of *Diversograptus pergracilis.*

This biozone, although stratigraphically restricted (Fig. 2) in comparison with the former concept of Bouček (1953), remains one of the thickest and temporally longest biostratigraphical intervals in the lower Silurian succession of the Prague Synform. It is represented by argillitic black shales with stratigraphically highest pale mudstone intercalations in its lowermost part. A complete profile was recorded by Bouček (1953) in temporary building excavations near the former railway station in Malá Chuchle. The present author studied a complete section, 7.5 m thick, in the pipeline trench at Malá Ohrada. An about 10 m thick *spiralis* Biozone was temporarily accessible in building excavations at Velká Ohrada (Štorch 1994b), and a 6 m thick *spiralis* Biozone was recorded in building excavations in the Praha-Řepy housing estate (Štorch 1982). A graptolite fauna from the lower part of the biozone came from a well excavation in Jinonice-Nová Ves (Bouček 1953) and from a sewerage tunnel near the brewery in Praha-Braník. Other records of the *spiralis* Biozone are from Řeporyje (Bouček 1937), the former Havlíčkův mill near Koněprusy, and nearby the entrance to the railway tunnel in Malá Chuchle.

Cyrtograptus lapworthi Biozone

The *lapworthi* Biozone, established by Tullberg (1883) in Scania, Sweden, has became one of the most widely recognized biozones in the upper Llandovery succession all over Europe (Bjerreskov 1975, Loydell & Cave 1996, Štorch *et al*. 2002, Loydell 2012), and is a standard biozone of the Silurian Time Scale (Melchin *et al*. 2020). In the Prague Synform, however, Bouček (1931a) established the *Monograptus probosciformis* and *Stomatograptus grandis* biozones for the graptolite assemblages distinguished between those of the underlying *Spirograptus spiralis subconicus* (now *O. spiralis*) Biozone and the overlying *Cyrtograptus insectus* Biozone. The *probosciformis* Biozone was also recognized by Schauer (1968) in Thuringia. Bouček (1953) incorporated the *probosciformis* Biozone as a “Band” within the *grandis* Biozone, which has been adopted by all subsequent Czech authors (Horný 1962; Kříž 1992; Havlíček & Štorch 1990; Štorch 1994a, b) until Štorch (2006) introduced the more widely correlatable *lapworthi* Biozone into the biozonal scheme of the Prague Synform. The *lapworthi* Biozone embraces both the former *grandis* Biozone of Bouček (1953) and much of the *geinitzi* Subzone recognized in Bouček’s upper *spiralis* Biozone (see Fig. 2).

The base of the *lapworthi* interval Biozone is defined by the incoming of *Cyrtograptus lapworthi* (Fig. 14) and its top is delineated by the lowest occurrence of *Cyrtograptus insectus*. *Cyrtograptus lapworthi* (Fig. 15B) co-occurs with *O. spiralis* in the lower part of the biozone and persists into the lowermost part of the *insectus* Biozone. The lower part of the *lapworthi* Biozone is marked by *Div. pergracilis, Streptograptus wimani* (Fig. 15N), *Streptograptus speciosus* and the rare, probably short-lived *Monograptus novaki*. Incoming *Monoclimacis linnarssoni*, *Mcl. vomerina* and *Barrandeograptus pulchellus* range from the lower *lapworthi* Biozone to the *insectus* Biozone as do the long-ranging *Ret. angustidens*, *Ret. geinitzianus*, *Pristiograptus praedubius*, *Prist. largus* and *M. priodon*. The very distinctive, but short-ranging *Monograptus probosciformis* (Fig. 15M) appears mid-biozone. *Stomatograptus grandis* (Fig. 15J), common in the upper part of the *lapworthi* Biozone, continues into the *insectus* Biozone.

Bouček (1953) described both the *geinitzi* Subzone of the *spiralis* Biozone and the *St. grandis* Biozone from above the basalt sill in an abandoned quarry beside the railway bridge at Praha-Hodkovičky, and below the basalt sill on the rocky slope at Malá Chuchle-Vyskočilka. The whole interval, which corresponds with the present *lapworthi* Biozone, is represented by graptolitic black shale, several metres thick. A more than 6 m thick succession of the *lapworthi* Biozone was temporarily exposed in building excavations in the Praha-Řepy housing estate (Štorch 1982), a *ca* 3 m thick *lapworthi* Biozone was recorded in building excavations at Velká Ohrada (Štorch 1994b), and an over 4 m thick succession was temporarily exposed in a pipeline trench near Malá Ohrada. The same interval, with few graptolites, is exposed at Karlštejn-Klučice, above the road to Hlásná Třebaň.

Cyrtograptus insectus Biozone

The *insectus* Biozone was established by Bouček (1931a) in the Prague Synform. After earlier confusion about the true biozonal succession on the poorly accessible rocky slope at Vyskočilka near Malá Chuchle, Bouček (1953) recognized the *grandis*, *insectus*, *centrifugus* and *murchisoni* biozones in the correct ascending order and the *Cyrtograptus insectus* Biozone became one of the most widely used graptolite biozones of the Silurian

System, adopted in Poland (Teller 1969), Bornholm (Bjerreskov 1975), Arctic Canada (Lenz & Melchin 1991), Wales (Loydell & Cave 1996, Zalasiewicz *et al*. 2009), Sardinia (Štorch & Piras 2009), China (Fu *et al*. 2000) and in the standard correlation charts by Loydell (2012), and Melchin *et al*. (2020).

The *insectus* Biozone is defined as an interval marked by the incoming of *Cyrtograptus insectus* at the base and the stratigraphically lowest occurrences of *Cyrtograptus centrifugus* at the top (Fig. 16). The first *Cyrt. insectus* (Fig. 15H) is accompanied by *Monograptus pseudocultellus* (Fig. 15I), *Monoclimacis basilica*, the short-lived *Monoclimacis chuchlensis* as well as *Monoclimacis kettneri*, *Mediograptus kolihai* and *Mediograptus kodymi* (Fig. 15L). Long-ranging elements of this diverse and characteristic graptolite assemblage include *Ret. angustidens*, *Ret. geinitzianus*, *Prist. praedubius*, *M. priodon*, *Mcl. vomerina* and *Barr. pulchellus*. *Stomatograptus grandis*, rare *Gig. giganteus*, *M. praecedens* and *Mcl. geinitzi*, continuing from the *lapworthi* Biozone, vanished within the *insectus* Biozone. Also, *Cyrt. lapworthi*, the index fossil of the underlying biozone, persists into the lowermost *insectus* Biozone. The upper part of the *insectus* Biozone is marked by the incoming of *Paraplectograptus* aff. *eiseli* (see Štorch 1994b, pl. 3, Fig. 4), *Mediograptus minor*, *Mediograptus flexuosus*, and the very rare *Cyrtograptus solaris*, with only two specimens known from the Prague Synform to date.

Bouček (1931a) identified, and later (Bouček 1953) described the *insectus* Biozone from the classical locality Malá Chuchle-Vyskočilka. Prantl & Přibyl (1940) recognized this biozone in the former brick pit in Praha-Stodůlky. The only other complete section, 1.7 m thick, was described by Štorch (1994b) from building excavations at Velká Ohrada.

Cyrtograptus centrifugus Biozone

Bouček (1931a) established the Cyrt. *centrifugus* Biozone in his preliminary study on graptolites from Vyskočilka near Malá Chuchle. The *centrifugus* Biozone has been recognized in Thuringia (Schauer 1971), Bornholm (Bjerreskov 1975), England (*e.g*. Rickards 1965), Wales (Loydell & Cave 1996, Zalasiewicz *et al*. 2009) and a combined *insectus–centrifugus* Biozone is recognized in Arctic Canada (Lenz & Melchin 1991). The upper Telychian *insectus*, *centrifugus* and probably also upper *lapworthi* biozones are missing in Spain (Loydell *et al*. 2009) and in some boreholes in the East Baltic area (Loydell *et al*. 2003, 2010) due to a stratigraphical gap ascribed to eustatic sea-level drawdown. However, the whole succession of *lapworthi*, *insectus* and *centrifugus* biozones is recorded in Kaliningrad district (Koren' & Suyarkova 2007, Suyarkova 2017).

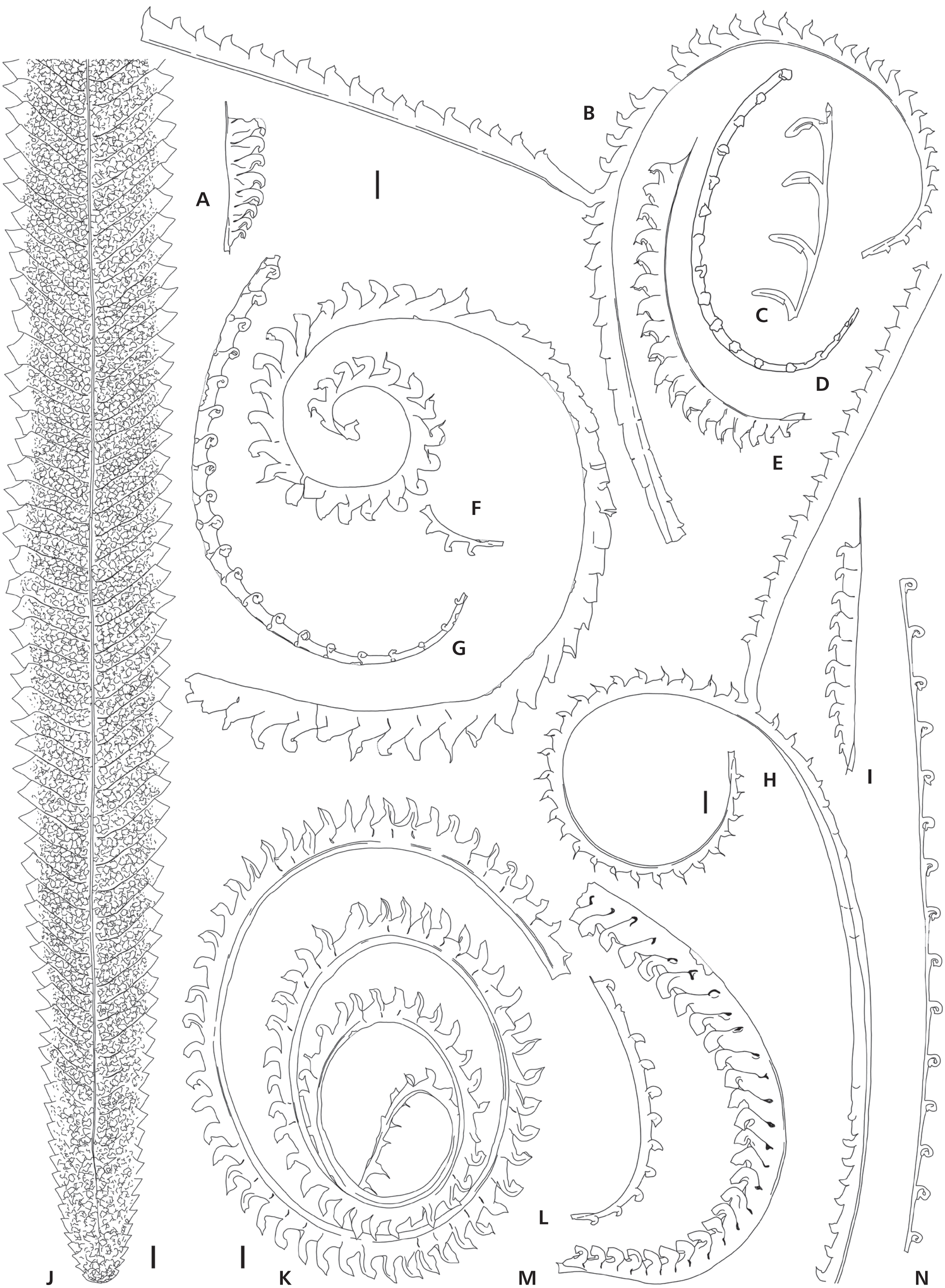
The base of this uppermost graptolite biozone of the Llandovery Series is delimited by the lowest occurrences of the biozone index fossil *Cyrt. centrifugus* (Fig. 17C) at the base and the first occurrences of *Cyrtograptus bohemicus* at the top (Fig. 16). *Mediograptus inconspicuus* first appears in the upper part of the *centrifugus* Biozone. Biostratigraphically important graptolites continuing from the previous biozone include *M. pseudocultellus*, *Med. kolihai* (Fig. 17F), and *Med. minor*. *Cyrtograptus insectus* vanished in the lowermost part of the *centrifugus* Biozone; *Med. kodymi* disappeared mid-biozone. Long-ranging elements of the biozone assemblage include *Ret. geinitzianus*, *Ret. angustidens*, *Paraplect.* aff. *eiseli*, *Prist. largus*, *Prist. praedubius*, *Mcl. vomerina*, *Monoclimacis basilica*, *M. priodon* and *Barr. pulchellus*.

The *centrifugus* Biozone is represented by black shales with local intercalations of dark-grey micritic limestone and is a relatively thin unit in the Prague Synform. Bouček (1953) reported 0.4 m from the classical outcrop at Malá Chuchle-Vyskočilka. Štorch (1994b) described a 0.8 m thick *centrifugus* Biozone from building excavations at Velká Ohrada. Prantl & Přibyl (1940) recorded this biozone in the former brick pit in Praha-Stodůlky.

Cyrtograptus bohemicus–Cyrtograptus murchisoni Biozone

The *murchisoni* Biozone, first recognized by Lapworth (1879–1880) in Wales, appeared among the primary

Figure 15. Age-diagnostic upper Telychian graptolites. • A – *Cultellograptus cultellus* (Törnquist), BB 6982, lower *spiralis* Biozone. • B – *Cyrtograptus lapworthi* Tullberg, PŠ536, *lapworthi* Biozone. • C – *Lapworthograptus singularis* (Törnquist), L59250, lower *spiralis* Biozone. • D – *Streptograptus anguinus* Přibyl, holotype L30966, lower *spiralis* Biozone. • E – *Stimulograptus vesiculosus* (Perner), BB 6993, middle *spiralis* Biozone. • F – *Oktavites excentricus* (Bjerreskov), PŠ 4360a, upper *spiralis* Biozone. • G – *Streptograptus nodifer* (Törnquist), BB 6985, middle *spiralis* Biozone. • H – *Cyrtograptus insectus* Bouček, PŠ 571, *insectus* Biozone. • I – *Monograptus pseudocultellus* Bouček, PŠ 480, *insectus* Biozone. • J – *Stomatograptus grandis* Suess, proximal and mesial part of mature specimen PŠ 574, *lapworthi* Biozone. • K – *Oktavites spiralis* (Geinitz), PŠ 4359, upper *spiralis* Biozone. • L – *Mediograptus kodymi* (Bouček), PŠ 599/1, *insectus* Biozone. • M – *Monograptus probosciformis* Bouček, PŠ 590, *lapworthi* Biozone. • N – *Streptograptus wimani* (Bouček), PŠ 4399, lower *lapworthi* Biozone. A – Malá Chuchle-former railway station; B, D, F, K, N – Malá Chuchle-Vyskočilka; C – Praha-Pankrác, Na Strži, borehole; E, G – Praha-Braník, sewerage gallery; H–J, L – Velká Ohrada-building excavation; M – Koledník, borehole B48. All figures × 5, except for H, J, K × 4. Scale bars represent 1 mm.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graptolite biozones recognized in the Silurian succession of central Bohemia by Perner & Kodym (1919, 1922). Bouček (1953) based his description of the *murchisoni* Biozone and its graptolite assemblage on samples and data from Malá Chuchle-Vyskočilka. The almost complete overlap of the stratigraphical ranges of *Cyrtograptus murchisoni* (Fig. 17B) and *Cyrtograptus bohemicus* (Fig. 17G), along with more abundant occurrence of the latter species in all sections studied in the Prague Synform, prompted the present definition of a combined *murchisoni–bohemicus* Biozone. A separate *Monograptus firmus* Biozone, established by Bouček (1931a) below the *Monograptus riccartonensis* Biozone and later adopted by Zalasiewicz *et al*. (2009) in Britain and Loydell *et al*. (2003) in the East Baltic, is no longer recognized as a separate biozone in the present biozonal scheme. It is downgraded to a subzone confined to the upper part of the *bohemicus–murchisoni* Biozone. Its base is delineated by the lowest occurrence of *M. firmus*. The Velká Ohrada-building excavation section and new study at Malá Chuchle-Vyskočilka have revealed that *M. firmus* (Fig. 17E) is restricted to the uppermost part of the *bohemicus–murchisoni* Biozone, still within the range of *Cyrt*. *bohemicus.* Less well-preserved rhabdosomes are hard to tell apart from *M. riccartonensis*, and those without a proximal end are impossible.

The *bohemicus-murchisoni* Biozone comprises an interval delineated by the lowest occurrences of *Cyrtograptus bohemicus* at the base and the incoming of *Monograptus riccartonensis* at the top (Fig. 16). The uncommon *Cyrt. murchisoni* made its lowest occurrence slightly above *Cyrt. bohemicus* and disappears again in the upper part of the biozone, below the highest *Cyrt. bohemicus*. *Mediograptus vittatus* appears in the lower part of the biozone, whereas *Prist. largus*, *Mcl. basilica*, *M. pseudocultellus*, *Med. kolihai*, *Med. minor* and *Cyrt. centrifugus* vanished. *Mediograptus remotus* (Fig. 17H) joins the assemblage mid-biozone. The upper part of the biozone is marked by the relatively short-lived *Euroclimacis adunca* (Fig. 17D), shortly associated by *Euroclimacis radotinensis*, *Monoclimacis deflexa* and highest occurrences of *Streptograptus flexuosus*. The uppermost *bohemicus–murchisoni* Biozone yields *Monograptus firmus* and rare *Monograptus solitarius* (Fig. 17A). The boundary interval with the overlying *Monograptus riccartonensis* Biozone sees several extinctions (Štorch 1995b and Fig. 16), including long-ranging taxa: *Ret. geinitzianus*, *Paraplect.* aff. *eiseli*, *Mcl. vomerina*, *Monograptus latus*, *M. priodon*, *Barr. pulchellus*, the biozone-index cyrtograptids, and the short-ranging *Med. vittatus* and *Med. remotus*.

The *bohemicus-murchisoni* Biozone is largely represented by calcareous black shales with several intercalations of thin-bedded muddy limestones. The classical, *ca* 3 m thick succession assigned to this biozone by Bouček (1931a, 1933) and Přibyl (1938) at Malá Chuchle-Vyskočilka is barely accessible without climbing using a rope. This is why the correct biozonal succession across the Llandovery–Wenlock boundary interval was not revealed until thorough examination of the section by Bouček (1953). The only other complete section of this biozone, 2.4 m thick, was studied in detail by Štorch (1994b) in the building excavation at Velká Ohrada. A partial section was exposed along the road in Praha-Motol. Alternating calcareous shales and biodetrital limestones with abundant brachiopods (*Niorhynx niobe*) and other benthic fauna (Havlíček & Štorch 1990) crop out in Řeporyje along cart track to Velká Ohrada (Bouček 1937) and in Beroun-Lištice (Kříž 1992).

Monograptus riccartonensis Biozone

The *riccartonensis* Biozone was originally recognized by Elles (1900) in Wales and subsequently adopted by Perner & Kodym (1919, 1922) in their early graptolite biozonal scheme of the Czech Silurian succession.

The base of *riccartonensis* Biozone is marked by the appearance and the top by the highest occurrence of the name-giving *Monograptus riccartonensis* (Fig. 18G). The graptolite assemblage is significantly impoverished in the aftermath of the upper *murchisoni* mass-extinction Event (Štorch 1995b). *Monoclimacis* ex gr. *vomerina*, *M. priodon* and *M. firmus* survived into the lower part of the biozone from the previous *murchisoni* Biozone. *Monograptus firmus* is limited to the relatively narrow *murchisoni–riccartonensis* boundary interval in Bohemia. The long-ranging *Pristiograptus dubius* accompanies the abundant index species *M. riccartonensis* through the whole interval, which is also marked by a number of bedding planes crowded with siculae. *Pseudoplegmatograptus*? *wenlockianus* has been recorded (Štorch 1992) mid-biozone. Bouček (1953) reported the minute *M. solitarius* from this low diversity assemblage. The upper part of the biozone witnessed the incoming of *Pristiograptus latus* and, according to Bouček (1953), also *Mediograptus antennularius.* The latter occurrence has not been confimed by new data. The whole thickness of the biozone, 2.0–2.5 m at Malá Chuchle-Vyskočilka (Bouček 1953), 2.2 m at Velká Ohrada and 2.0 m at Malá Ohrada, is represented by very calcareous shale.

The only complete and readily accessible section through the *riccartonensis* Biozone crops out on a steep slope at Malá Chuchle-Vyskočilka described by Bouček (1953). Temporary sections were studied in building excavations at Velká Ohrada (Štorch 1994b) and a pipeline trench near Malá Ohrada.

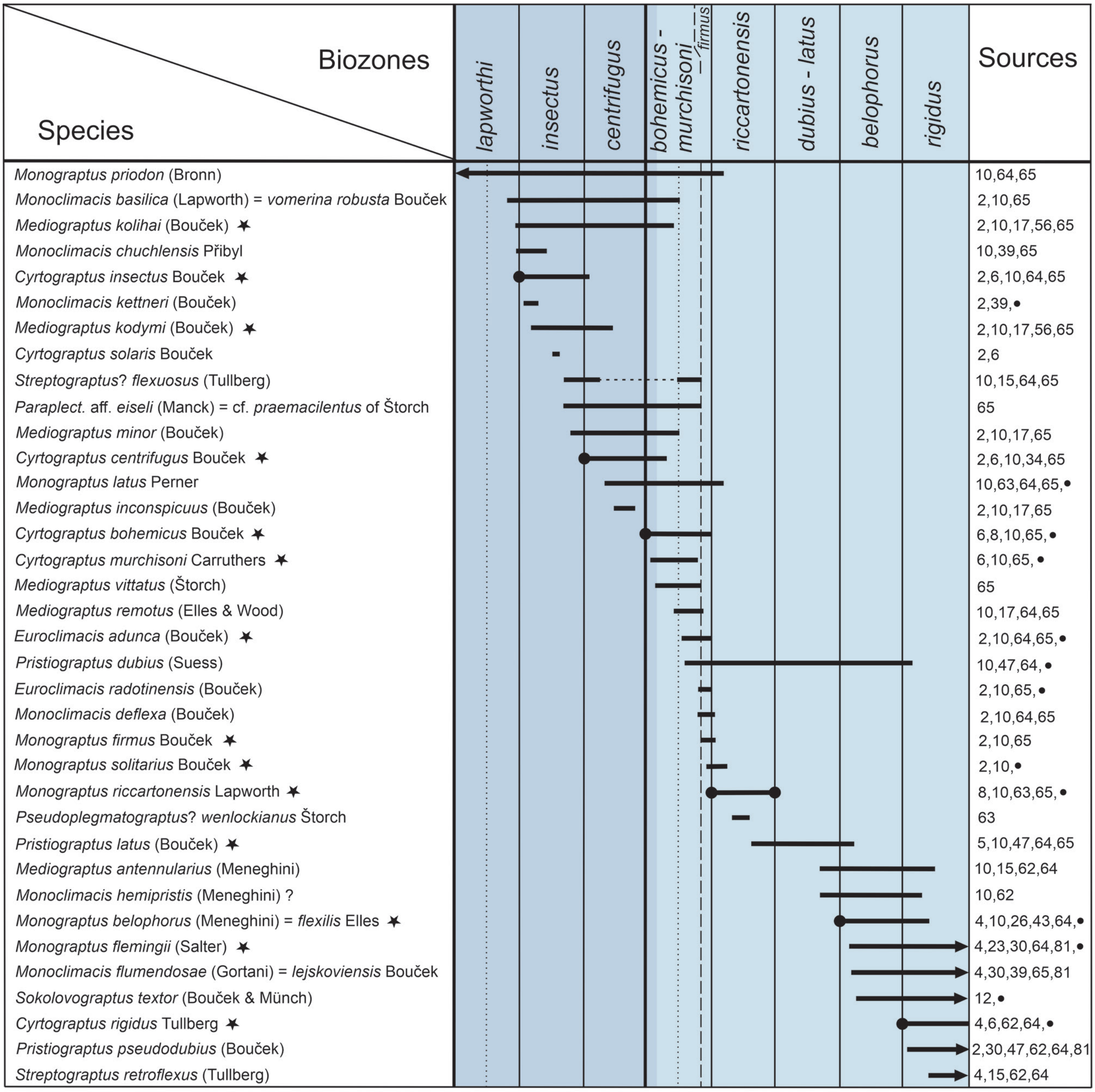


Figure 16. Stratigraphical ranges of upper Telychian and Sheinwoodian graptolites in the Prague Synform. See Figs 5 and 14 for further explanation.

Pristiograptus dubius–Pristiograptus latus Biozone

This biozone was originally recognized by Bouček (1953) and named after the long ranging *Pristiograptus dubius*. It encompasses an interval between the highest occurrence of *M. riccartonensis* and the lowest occurrence of *Monograptus belophorus*. Zalasiewicz & Williams (1999) recognized an equivalent *dubius* Biozone in Wales and Loydell *et al*. (2017) identified this interval on Bornholm. Bouček's index species has been supplemented in this paper by the similar *Pristiograptus latus* (Fig. 18F), which is better taxonomically defined by its type specimen and more characteristic of this low diversity interregnum (see Štorch 1994b).

The *dubius–latus* Biozone is delineated in the same way as the original *dubius* Biozone recognized by Bouček (1953), Štorch (1994a) and Zalasiewicz *et al*. (2009). The low diversity graptolite assemblage comprises abundant *Prist. dubius* and *Prist. latus*. *Monoclimacis hemipristis*? appears in the upper part of this 1.2–3.0 m thick succession of calcareous shales. The presence of *Med. antennularius* has not been proven except in the Malá Ohrada-pipeline trench section.

An easily accessible reference section of the *dubius–latus* Biozone is exposed on the steep rocky slope at Malá Chuchle-Vyskočilka described by Bouček (1953). Other sections have been studied in the building excavation at Velká Ohrada (Štorch 1994b) and Malá Ohrada-pipeline trench.

Monograptus belophorus Biozone

Bouček (1931a, 1934, 1953) originally referred to this biozone, placed between his *Cyrtograptus rigidus* Biozone below and *Cyrtograptus ramosus* Biozone above, as the *Monograptus flexilis* Biozone. The reverse biozonal sequence, with the *flexilis* Biozone below the *rigidus* Biozone, was documented by Kříž (1992). Štorch (1994a) renamed this unit after the senior synonym index fossil *M. belophorus* (Fig. 18B). The mid-Sheinwoodian graptolite biozonation of the Euro-Atlantic realm is still seeking more stability in the interval comprising the *M. belophorus* (= *flexilis*) and *Cyrt. rigidus* biozones, in part due to low graptolite diversity but also taxonomic uncertainties about the index taxa and their significant stratigraphical overlap recorded in many sections (Barca & Jaeger 1990, Zalasiewicz & Williams 1999, Zalasiewicz *et al*. 2009). However, the two biozones can be distinguished in all sections studied in the Prague Synform to date. Zhang *et al*. (2014) recognized separate *flexilis* (*belophorus*) and *rigidus* biozones in southwestern China (Sibumasu Plate of NE Gondwana).

The *belophorus* Biozone is defined as an interval delineated by the appearance of its distinctive index species at the base and lowest occurrence of *Cyrtograptus rigidus* at the top. Species diversity is still relatively low in the *belophorus* Biozone, although greater than that of the underlying *dubius–latus* Biozone interregnum, and includes *M. belophorus*, *Med. antennularius*, *Mcl. hemipristis*?, *Prist. dubius*, *Sokolovograptus textor* and the poorly documented *Paraplectograptus* sp. *Monograptus flemingii* and *Monoclimacis flumendosae* appear in the lower part of the *belophorus* Biozone whereas *Prist. latus* disappears from the fossil record in this level.

The *belophorus* Biozone is represented by calcareous black or dark-grey graptolitic shales, about 4 m thick across a large part of the Prague Synform. A local *Miraspis* limestone facies, a *ca* 8 m thick succession of alternating tuffitic calcareous shales and thin bedded limestones with mixed graptolite, trilobite and shelly fauna, is developed in the Svatý Jan volcanic centre between Loděnice and Svatý Jan pod Skalou.

The only complete section through graptolitic shales of the *belophorus* Biozone, 3.9 m thick, has been recorded in the pipeline trench at Malá Ohrada. A partial section was temporarily exposed in the Praha-Zličín housing estate; the upper part of the biozone, with significant stratigraphical overlap between *M. belophorus* and *Cyrtograptus rigidus*, was temporarily accessible in the lowest, now covered, 5th level of Kosov quarry. The *Miraspis* limestone facies with common *M. belophorus* and other, uncommon elements of the biozone assemblage is exposed in a roadcut at Loděnice-Černidla (Libertín *et al*. 2018) and in several outcrops along the east side of the Loděnice stream valley between Loděnice and Svatý Jan pod Skalou (U elektrárny, Sedlec).

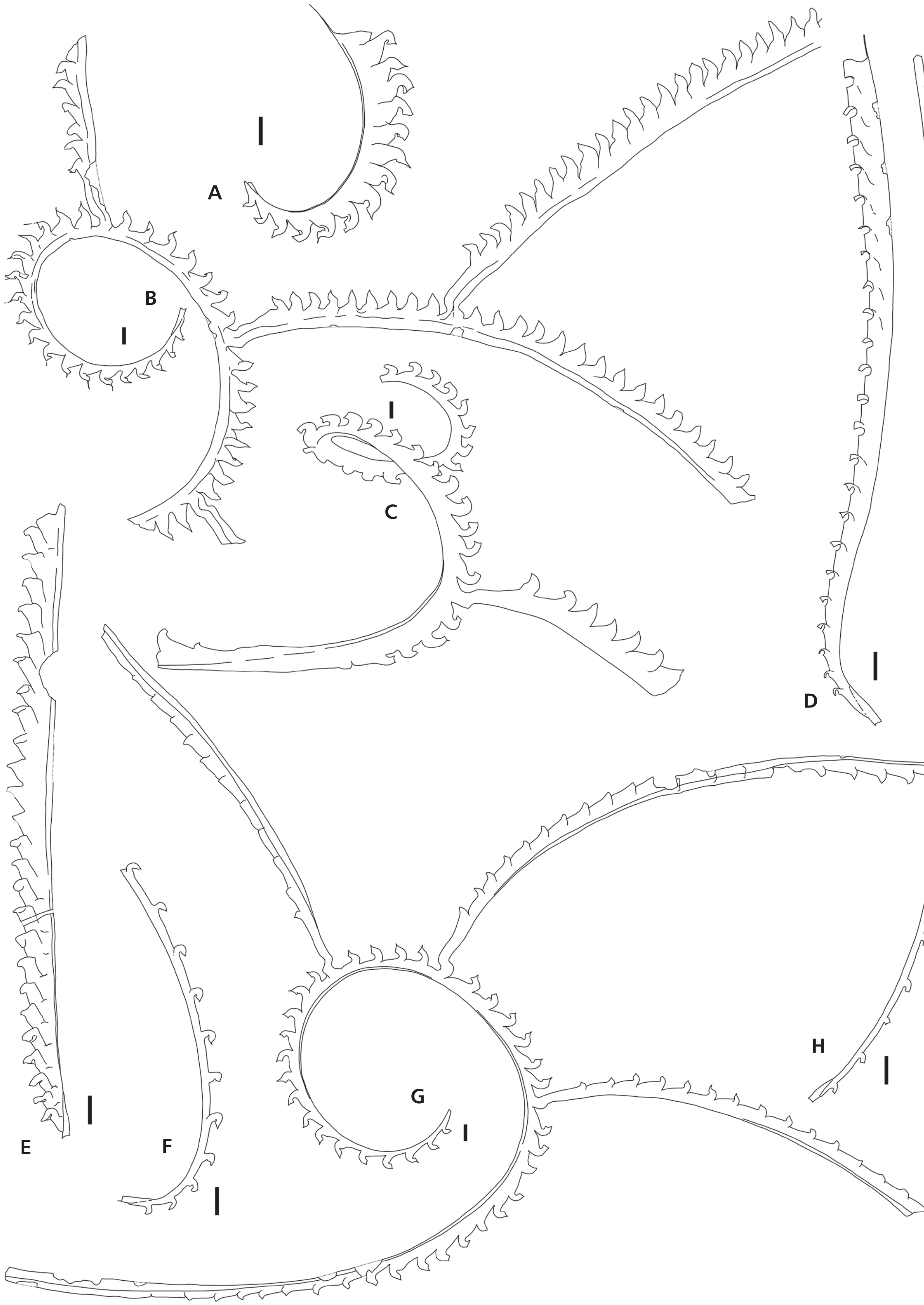
Cyrtograptus rigidus Biozone

The *Cyrtograptus rigidus* Biozone, established by Tullberg (1883) in Sweden, was first identified by Bouček (1932a) in the western part of the Silurian outcrop area of Central Bohemia. Since then the unit became an integral part of the mid-Sheinwoodian graptolite biozonal scheme of the Prague Synform (Bouček 1934, Přibyl 1948, Štorch 1994a).

The base of this interval biozone is defined by incoming biozone fossil *Cyrtograptus rigidus* (Fig. 18C) and the top is marked by the lowest occurrence of *Cyrtograptus ramosus*. No overlap was recorded of the two index taxa. The only other species to appear in the lower part of the *rigidus* Biozone is *Pristiograptus pseudodubius*. The lowest occurrence of *Streptograptus retroflexus* is recorded in the middle part of the biozone. *Pristiograptus dubius*, *M. belophorus* and *Med. antennularius* range from the previous biozone up to the lower–middle part of this biozone. Some elements of the moderately diverse assemblage, such as *Sok. textor*, *M. flemingii*, and *Mcl. flumendosae*, are truly long-ranging species.

The only reference section of the *rigidus* Biozone was exposed in the two lower levels of Kosov quarry near Beroun (Turek 1990, and personal observation). A basalt

Figure 17. Age-diagnostic graptolites of the Telychian–Sheinwoodian boundary biozones. • A – *Monograptus solitarius* Bouček, BB 6989, upper *bohemicus–murchisoni* Biozone. • B – *Cyrtograptus murchisoni* Carruthers, BB 6987, *bohemicus–murchisoni* Biozone. • C – *Cyrtograptus centrifugus* Bouček, PŠ 572, *centrifugus* Biozone. • D – *Euroclimacis adunca* (Bouček), PŠ 475, upper *bohemicus–murchisoni* Biozone. • E – *Monograptus firmus* Bouček, BB 6994, uppermost *bohemicus–murchisoni* Biozone. • F – *Mediograptus kolihai* (Bouček), PŠ 477/1, *centrifugus* Biozone. • G – *Cyrtograptus bohemicus* Bouček, PŠ 549, *bohemicus–murchisoni* Biozone. • H – *Mediograptus remotus* (Elles Wood), PŠ 586/1, *bohemicus–murchisoni* Biozone. A – Karlštejn-Klučice; B, E – Malá Chuchle-Vyskočilka; C, D, F, H – Velká Ohrada-building excavation; G – Praha-Motol. A, D–F, H × 5, figures B, C, G × 3, scale bars represent 1 mm.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sill, *ca* 2.5 m thick, divides the 4.5 m thick succession of slightly calcareous graptolitic black shales into two almost equal parts. Another complete section was studied in the pipeline trench at Malá Ohrada. Partial sections referred to by Bouček (1932a) crop out near Lounín and Malkov.

Cyrtograptus ramosus–Cyrtograptus perneri Biozone

The *ramosus* Biozone was established by Bouček (1931b) and the *perneri* Biozone appeared in the biozonal scheme two years later (Bouček 1933). Turek (1990) combined the two into one *ramosus–perneri* Biozone based on the almost complete overlap of the two cyrtograptid species. Štorch (1994a) defined this unit as a partial couple-range biozone. This particular interval is not represented by a specific graptolite biozone in the graptolite biozonal chart used by Melchin *et al*. (2020), although roughly corresponding late Sheinwoodian units with *Cyrtograptus perneri* as a biozone fossil were recognized in Arctic Canada (Lenz *et al*. 2012) and in the graptolite biozone correlation charts compiled by Loydell (2012). In the Prague Synform, neither *Cyrt. rigidus*, *Med. antennularius*, nor *M. belophorus* range close to the lowest occurrence of *Cyrtograptus lundgreni* (Fig. 19).

Following recent restudy of the Kosov quarry section, the *ramosus–perneri* Biozone is defined as an interval bounded by the lowest occurrence of *Cyrtograptus perneri* at the base and lowest *Cyrtograptus lundgreni* at the top (Fig. 19). *Cyrtograptus ramosus* (Fig. 18E) is rather common in the lower part of the biozone and does not reach the top, whereas *Cyrt. perneri* (Fig. 18D) proliferated in the middle and upper part and continued well into the lower *lundgreni* Biozone. *Cyrtograptus*? *gracilis* is one of only two other species incoming in the lower part of the biozone, the other being *Med.* cf. *antennularius*, which is confined to this short interval. *Pristiograptus pseudodubius*, *Mcl. flumendosae* and *M. flemingii* are abundant, long-ranging elements of this moderately diverse assemblage. *Streptograptus retroflexus* vanished mid-biozone, *Sok. textor* is rarely seen in black calcareous shales but may be actually more commonly observed in bleached rocks. Lowest occurrences of rare *Cyrtograptus radians* have been recorded in the uppermost *ramosus–perneri* Biozone at 5th level of the Kosov quarry. *Cyrtograptus multiramis* (Fig. 18A), which is confined to the upper part of the biozone in Kosov quarry, Malá Chuchle-former railway station (Bouček & Přibyl 1952a), Rovina near Lety and Praha-Nové Butovice housing estate, could be a potential tool for finer subdivision of this unit with respect to high-resolution correlation of the Sheinwoodian–Homerian boundary interval.

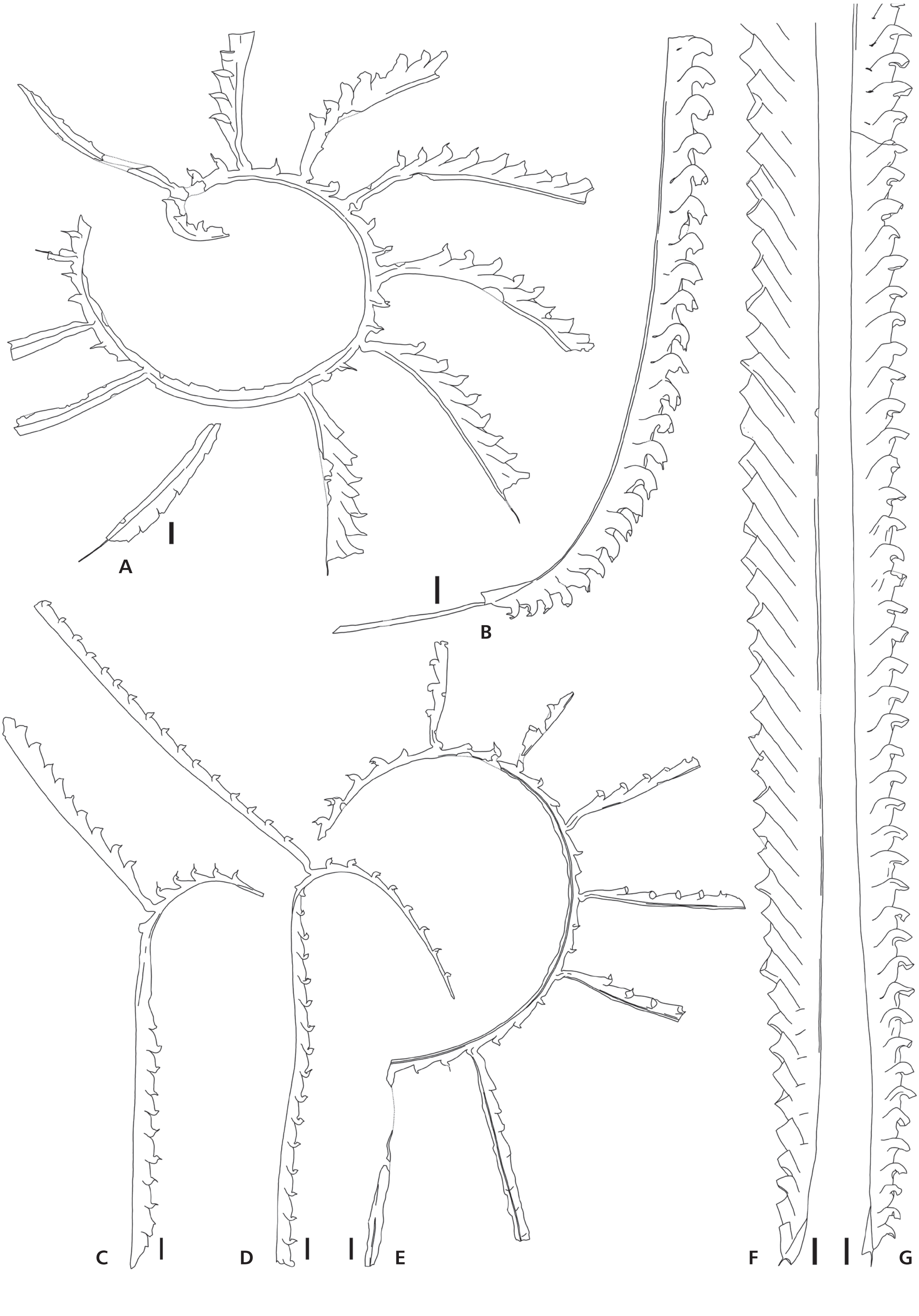
The *ramosus–perneri* Biozone is represented by a 6.5 m thick succession of black calcareous shales in the reference Kosov quarry section. Other occurrences were recorded in building excavations in the Praha-Nové Butovice housing estate, Malá Ohrada-pipeline trench and at Rovina near Lety (Štorch 1994a). Bouček & Přibyl (1952a) described the biozonal assemblage from a temporary exposure in building excavations near the former railway station at Malá Chuchle, with further reference to the classical locality Lejškov near Suchomasty (Bouček 1933).

Cyrtograptus lundgreni Biozone

The first biozonal scheme introduced by Perner & Kodym (1919, 1922) established a *Testograptus testis* Biozone in the lower Homerian succession of the Prague Synform. Their concept was modified by Bouček (1934) who recognized a *Cyrtograptus radians* Biozone between his *perneri* and *testis* biozones. Přibyl (1948) distinguished another biozone, characterized by *Cyrt. lundgreni*, between the *testis* and *radians* biozones. The co-occurrence of *Cyrt. lundgreni* with both *Cyrt. radians* and *Testograptus testis* was recorded by Bouček & Přibyl (1952a). New graptolite data from the 5th level of Kosov quarry, showing major stratigraphical range overlaps among the biozonal index species, prompted Turek (1990) to merge the three biozones of Přibyl (1948) into one *Cyrt. lundgreni* Assemblage Biozone with broader correlation potential. Štorch (1994a) defined this biozone by the full stratigraphical range of the biozone fossil and included the *radians* Subzone at the base and the *testis* Subzone in the upper part. A new detailed study carried out on the Kosov section has questioned recognition of the *radians* Subzone due to intermittent occurrences of the index graptolite from the uppermost *ramosus–perneri* Biozone high into the lower part of the *testis* Subzone.

The *lundgreni* Biozone is defined as an interval between the stratigraphically lowest occurrence of the biozone index *Cyrtograptus lundgreni* (Fig. 20C) and

Figure 18. Age-diagnostic Sheinwoodian graptolites (continued). • A – *Cyrtograptus multiramis* Törnquist, PŠ 241a, upper *ramosus–perneri* Biozone. • B – *Monograptus belophorus* (Meneghini), PŠ 1356, *belophorus* Biozone. • C – *Cyrtograptus rigidus* Tullberg, PŠ 565, *rigidus* Biozone. • D – *Cyrtograptus perneri* Bouček, PŠ 561, *ramosus–perneri* Biozone. • E – *Cyrtograptus ramosus* Bouček, PŠ 4358a, *ramosus–perneri* Biozone. • F – *Pristiograptus latus* (Bouček), PŠ 4361, *dubius–latus* Biozone. • G – *Monograptus riccartonensis* Lapworth, PŠ 4355, *riccartonensis* Biozone. Figures A, C–E × 4, B, F, G × 5, scale bars represent 1 mm. A – Praha-Nové Butovice; B–E – Kosov quarry, 5th level; F, G – Velká Ohrada-building excavation.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the last occurrence of the genus *Cyrtograptus* (Manda *et al*. 2019 and Fig. 19). The name-giving graptolite is common throughout this interval except for the uppermost part, presumably being affected by the beginning of the *lundgreni* mass-extinction Event (Manda *et al*. 2019). The graptolite assemblage of the lower part of the *lundgreni* Biozone is dominated by the long-ranging *Prist. pseudodubius*, *Mcl. flumendosae* and *M. flemingii*, accompanied by *Cyrt. lundgreni*. *Cyrt. perneri* and *Cyrt*.? *gracilis* continued from the underlying biozone. The retiolitid fossil record is limited to rare *Sok. textor*, presumably due to the low colour contrast of the delicate retiolitid rhabdosomes in calcareous black shales. *Cyrtograptus radians* (Fig. 20L) is known from several separate levels up to the middle part of the biozone. *Testograptus testis* (Fig. 20E), index graptolite of the *testis* Subzone, appears mid-biozone along with *Cyrtograptus hamatus* and the retiolitids *Pseudoplectograptus praemacilentus*, *Paraplectograptus eiseli* and rare *Cometograptus* sp. A. Retiolitids are particularly easily seen in bleached calcareous-tuffitic laminae. The upper part of the *lundgreni* Biozone, herein assigned to the *testis* Subzone, displays a distinct assemblage enriched by the incoming of *Gothograptus kozlowskii*, *Gothograptus domeyki* and *Monograptus subflexilis*. The *testis* Subzone has good potential for further biostratigraphical subdivision since the uppermost strata are marked by occurrences of *Cyrtograptus mancki*, *Cyrtograptus hemmanni* and "*Monograptus*" *ambiguus* (Fig. 20D), along with the demise of *Cyrt. lundgreni* and retiolitids.

This is one of the thickest graptolite biozones of the Prague Synform even in its relatively condensed graptolitic shale facies. A reference section representing the complete *lundgreni* Biozone is exposed in the 5th and 4th level of the now abandoned Kosov quarry (Turek 1990, Štorch 1991, Manda *et al*. 2019). A nearly 22 m thick succession of graptolite-rich calcareous shales with a number of thin tuffitic intercalations is divided in Kosov quarry into two parts by a 4 m thick doleritic basalt sill. Another black-shale section is accessible along the cart track northwest of Všeradice (Kříž 1992). Bouček (1933) collected well-preserved graptolites of the *testis* Subzone at Lejškov near Suchomasty. The lower part of the *lundgreni* Biozone with *Cyrt. radians* crops out along an unpaved road from Karlštejn-Budňany to Hlásná Třebaň (Bouček 1931b); temporary excavations with a rich graptolite assemblage were studied by Bouček & Přibyl (1952a) at Malá Chuchle-former railway station.

Monograptus flemingii Biozone

The relatively thin and presumably short interval between the highest *Cyrt. hamatus* and highest *M. flemingii* was assigned to the *flemingii* Biozone by Manda *et al*. (2019). It is an equivalent to the *flemingi–dubius* Biozone of Porębska *et al*. (2004). Its base is coincident with a major drop in graptolite species richness and the disappearance of *Testograptus*, *Cyrtograptus* (see Porębska *et al*. 2004) and "*M*." *ambiguus*. The biozonal assemblage is limited to the long-ranging *M. flemingii* (Fig. 20M) and *Prist. pseudodubius* which both vanished at the top of this interval. The *flemingii* Biozone, 0.4 m thick, is exposed at the 4th level in Kosov quarry (Manda *et al*. 2019). A similar interval has been recently documented in a trench along the field track northwest of Všeradice but application of this unit in interregional correlation needs to be verified in some further sections.

Pristiograptus parvus Biozone

Ulst (1974) distinguished *Pristiograptus parvus–Pristiograptus piltenensis* Biozone above the *testis* (*lundgreni*) Biozone in Latvia. Jaeger (1991) established the *Monograptus dubius parvus* Biozone to designate and correlate the most critical interval of his "Grosse Krise" (referred to as the *lundgreni* Event by most subsequent authors), which resulted in almost the complete eradication of the planktic graptolites. The *parvus* Biozone was soon recognized in the Prague Synform by Kříž (1992) and Kříž *et al*. (1993) and adopted in the lower Silurian biozonal scheme by Štorch (1994a). Kozłowska-Dawidziuk *et al*. (2001) preferred to use a combined *Pristiograptus parvus–Gothograptus nassa* Biozone in the Všeradice section but Manda *et al*. (2019) returned to the original usage. Kozłowska-Dawidziuk *et al*. (2001) did not report pristiograptids other than *Prist. parvus* in the Všeradice section. However, new examination of the graptolite samples has revealed that *Pristiograptus frequens* is actually common in the upper part of the *parvus–nassa* interval of Kozłowska-Dawidziuk *et al*. (2001) in the Všeradice section. Recent study of the Kosov section indicates that the *parvus* Biozone as used herein corresponds with the *parvus* Biozone in Lithuania (Radzevičius 2006), the lower part of the *Gothograptus nassa* Biozone in Britain (Zalasiewicz *et al*. 2009) and Kyrgyzstan (Koren' 1991), the lower part of the *parvus–nassa* Biozone adopted by Melchin *et al.* (2020), and most likely also the lower part of the *dubius–nassa* Biozone recognized by Lenz *et al*. (2006) in Arctic Canada.

The *parvus* Biozone in the present biozonal scheme for the Prague Synform is defined as an interval delineated by the stratigraphically lowest and highest occurrences of *Prist. parvus* (Fig. 20A). The biozone index taxon is common, *Gothograptus nassa* appears and proliferates in the upper part of this interval, but continues through the two subsequent upper Homerian graptolite biozones.

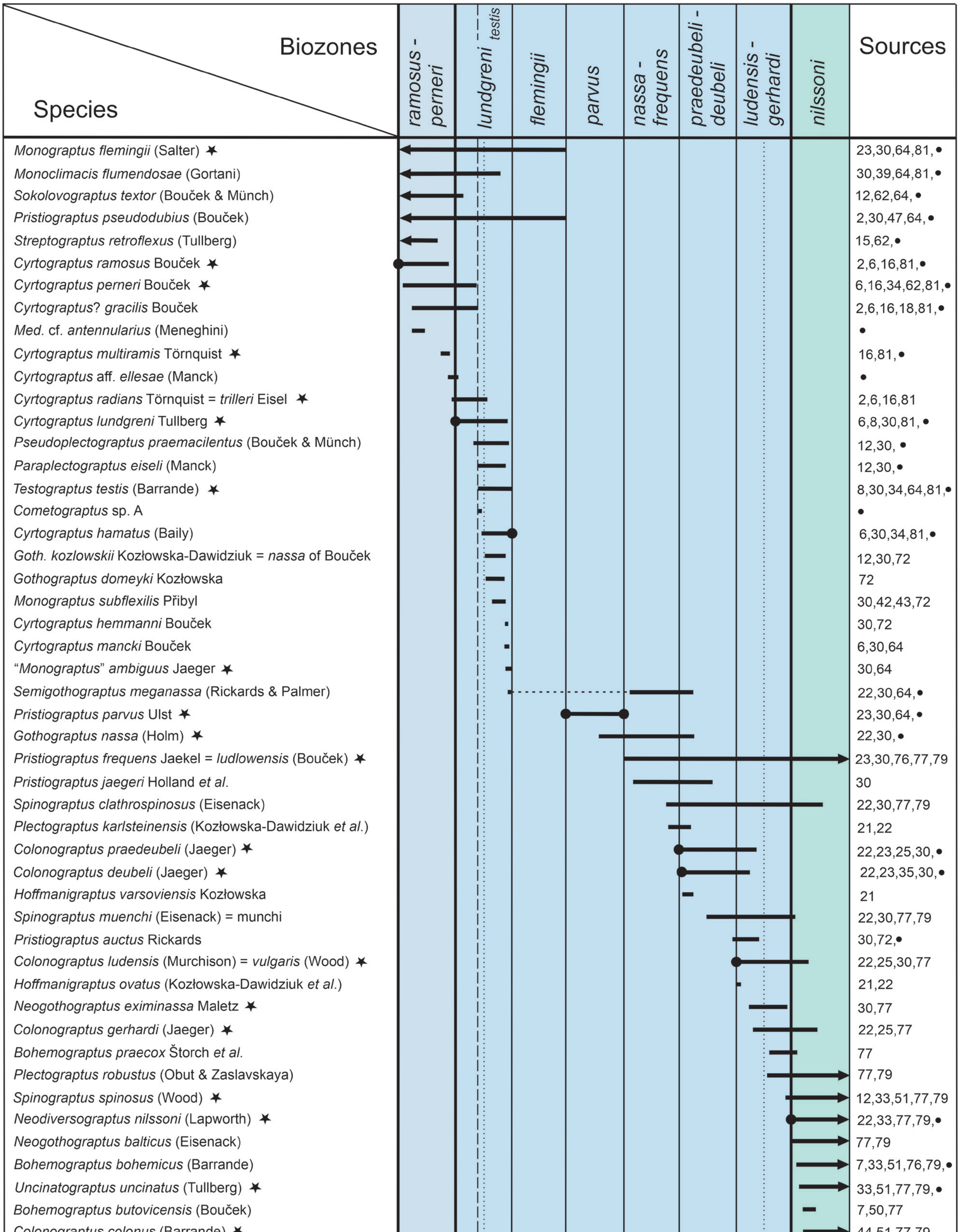


Figure 19. Stratigraphical ranges of upper Sheinwoodian, Homerian and lower Gorstian graptolites in the Prague Synform. See Figs 5 and 14 for further explanation.

This biozone encompasses a 0.7 m thick interval in the reference Kosov section (Manda *et al*. 2019). Shale, 1.2 m thick, between the stratigraphically lowest and highest occurrences of the index species, was recorded in the trench along field tract northwest of Všeradice (Kříž *et al*. 1993). Other relevant sections with *Prist. parvus*, namely the road cut southeast of Koněprusy, and Praha-Braník, were described by Kříž *et al*. (1993).

Gothograptus nassa–Pristiograptus frequens Biozone

Jaeger (1991) recognized a *Monograptus dubius frequens–Gothograptus nassa* Interregnum above his *parvus* Biozone in Thuringia. Kříž (1992) and Kříž *et al*. (1993) recognized this combined biozone in the Prague Synform. Their *nassa–frequens* Biozone, adopted by Štorch (1994a), corresponds to the upper part of *parvus–nassa* Biozone recognized by Kozłowska-Dawidziuk *et al*. (2001) in the trench northwest of Všeradice. Manda *et al*. (2019) renamed this interval of generally low diversity without specific taxa as the *Pristiograptus frequens* Biozone. The present study returns to the original concept of a combined *nassa–frequens* Biozone characterized by the abundant co-occurrence of the two long-ranging index taxa and delineated by bounding horizons defined by the index species of adjacent biozones (Fig. 19). This interval corresponds with the *dubius–nassa* Biozone recognized by Porębska *et al*. (2004) in the Polish part of the East European Platform, or the upper part of *nassa* Biozone of the East Baltic (Radzevičius & Paškevičius 2005), but otherwise is rarely formally distinguished outside peri-Gondwanan Europe.

The base of the *nassa–frequens* Biozone is defined by the disappearance of *Prist. parvus*, associated with the reappearance of normal-sized pristiograptid rhabdosomes assigned to the long-ranging *Prist. frequens* (Fig. 20J), one of the name-giving species of this biozone. Its upper limit coincides with the lowest occurrence of *Colonograptus praedeubeli*. Common *Goth. nassa* (Fig. 20K) continues from the previous biozone through to the lower part of the overlying *Colonograptus praedeubeli–Colonograptus deubeli* Biozone. Incoming taxa include *Pristiograptus jaegeri*, *Hoffmanigraptus karlsteinensis* and *Spinograptus clathrospinosus*, along with the reappearance of *Semigothograptus meganassa*.

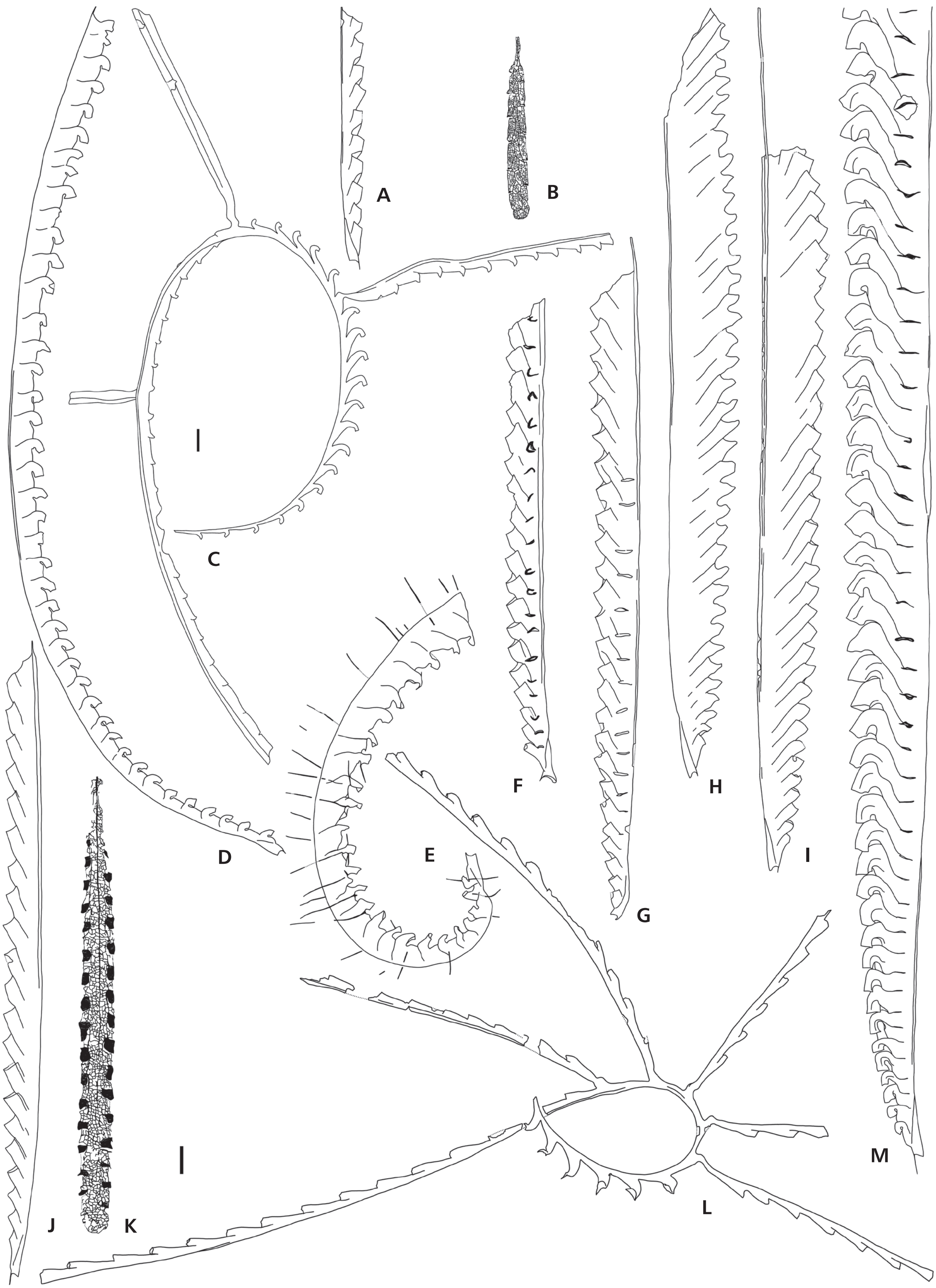
The calcareous shales of this biozone alternate with several thin beds of laminated tuffites. A complete section, 1.7 m thick, is easily accessible in 4th level of Kosov quarry (Manda *et al*. 2019). Other complete sections, studied by Kříž *et al*. (1993) and Kozłowska-Dawidziuk *et al.* (2001), occur in the road cut southeast of Koněprusy and the trench northwest of Všeradice.

Colonograptus praedeubeli–Colonograptus deubeli Biozone

The *praedeubeli* and *deubeli* biozones established by Jaeger (1991) in Thuringia and soon after recognized by Kříž (1992) and Kříž *et al*. (1993) in the Prague Synform have been combined into the *praedeubeli–deubeli* Partial couple-range Biozone by Štorch (1994a) based on the almost complete stratigraphical range overlap of the two index taxa (the amount of overlap varies from section to section). This approach was adopted by Kozłowska-Dawidziuk *et al*. (2001) and Manda *et al*. (2019). A combined *praedeubeli–deubeli* Biozone was also recognized in Iberia (Gutierrez-Marco *et al*. 1996), Arctic Canada (Lenz 1995, Lenz & Kozłowska-Dawidziuk 2002), in the correlation charts of Loydell (2012) and in the Silurian Time Scale of Melchin *et al.* (2020).

Manda *et al*. (2019) defined the *Colonograptus praedeubeli–Colonograptus deubeli* Biozone as an interval between the lowest occurrence of either *Colonograptus praedeubeli* or *Colonograptus deubeli* and the lowest occurrence of *Colonograptus ludensis*, which is the biozonal index species of the overlying biozone. Their definition is adopted in this study (Fig. 19). *Colonograptus praedeubeli* (Fig. 20G) and *Col. deubeli* (Fig. 20F) are common and co-occur in the vast majority of samples. The former taxon usually appears first and is more abundant in the lower part of the biozone than the latter which is more common in the upper part. The two biozone fossils both continue well into the overlying biozone and occur in the *praedeubeli–deubeli* Biozone with the long-ranging *Prist. frequens* and rare *Sp. clathrospinosus*. *Gothograptus*

Figure 20. Age-diagnostic Homerian graptolites. • A – *Pristiograptus parvus* Ulst, PŠ 4373, *parvus* Biozone. • B – *Neogothograptus eximinassa* Maletz, PŠ 3724, *ludensis–gerhardi* Biozone. • C – *Cyrtograptus lundgreni* Tullberg, PŠ 541, *lundgreni* Biozone. • D – "*Monograptus*" *ambiguus* Jaeger, PŠ 3866, upper *lundgreni* Biozone. • E – *Testograptus testis* (Barrande), PŠ 3887b, upper *lundgreni* Biozone. • F – *Colonograptus deubeli* (Jaeger), PŠ 4369, *praedeubeli–deubeli* Biozone. • G – *Colonograptus praedeubeli* (Jaeger), PŠ 4370, *praedeubeli–deubeli* Biozone. • H – *Colonograptus gerhardi* (Kühne), PŠ 3718, upper *ludensis–gerhardi* Biozone. • I – *Colonograptus ludensis* (Murchison), PŠ 4371/2, *ludensis–gerhardi* Biozone. • J – *Pristiograptus frequens* Jaekel, PŠ 3738, upper *ludensis–gerhardi* Biozone. • K – *Gothograptus nassa* (Holm), PŠ 4375/1, upper *parvus* Biozone. • L – *Cyrtograptus radians* Törnquist, PŠ 4396, lower *lundgreni* Biozone. • M – *Monograptus flemingii* (Salter), proximal portion of mature rhabdosome, PŠ 4357, upper *lundgreni* Biozone. All figures × 5 except for C × 4, scale bars represent 1 mm. A, F, G, K – Všeradice-trench; B, H, J – Nesvačily-trench; C–E, L, M – Kosov quarry, 4th level; I – Bykoš-trench.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nassa and *Hoffmanigraptus karlsteinensis* associated with short-ranging *Hoffmanigraptus varsoviensis* vanished in the lower part of the *praedeubeli–deubeli* Biozone. *Pristiograptus jaegeri* seems to disappear mid-biozone. *Spinograptus muenchi* appears in the same bed whereas lowest occurrences of *Pristiograptus auctus* came in the uppermost *praedeubeli–deubeli* Biozone.

A very good reference section of the *praedeubeli–deubeli* Biozone was described by Manda *et al*. (2019) from the 4th level of Kosov quarry. It is represented by a 3.3 m thick succession of calcareous graptolitic shales with several thin intercalations of tuffites and argillitic limestones. Another complete section, formed by graptolitic shales 7.2 m thick, was described from the trench along the field track northwest of Všeradice by Kříž (1992) and Kozłowska-Dawidziuk *et al*. (2001).

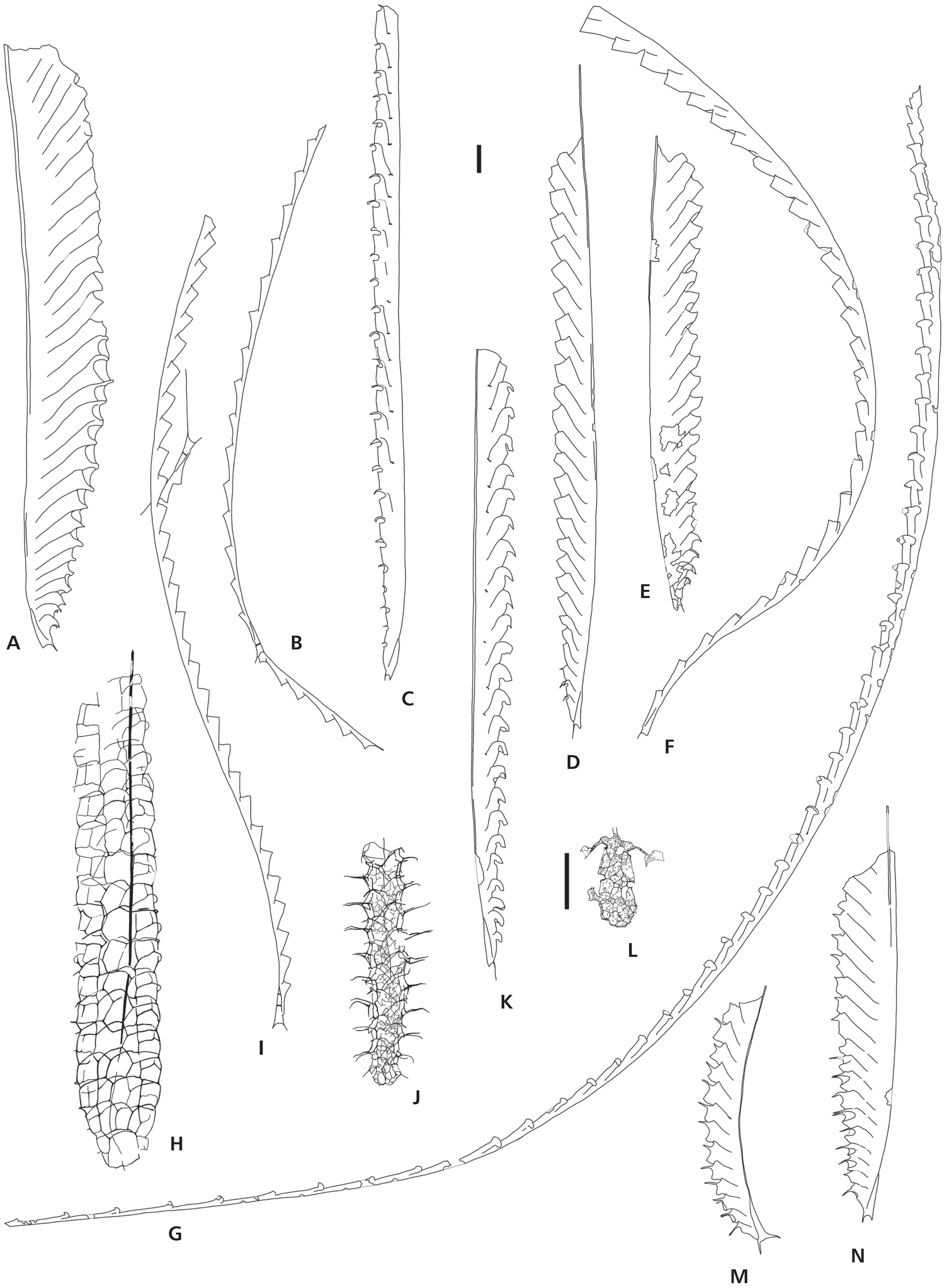
Colonograptus ludensis–Colonograptus gerhardi Biozone

This biozone was established by Jaeger (1991) in the uppermost Wenlock of Thuringia as the *Monograptus vulgaris–Monograptus gerhardi* Biozone instead of the *Pristiograptus vulgaris* Biozone that some earlier Czech authors assigned to the lowermost Ludlow (Bouček 1960, Horný 1962). Kříž (1992) and Kříž *et al*. (1993) referred the *vulgaris* Biozone to the uppermost Wenlock but retained the incorrect junior synonym of the species. The renamed *Pristiograptus ludensis* Biozone was adopted in the uppermost Wenlock of the Prague Basin by Přibyl (1983) and Štorch (1994a). Kozłowska-Dawidziuk *et al*. (2001) returned to a combined *ludensis–gerhardi* Biozone, previously introduced also in the East European Platform (Koren' *et al*. 2009). The present study follows the latter concept, which reflects the great overlap of the stratigraphical ranges of the two species. This unit is readily correlatable with the more widely used *ludensis* Biozone (*e.g.* Loydell 2012, Melchin *et al*. 2020).

The base of the *ludensis–gerhardi* Interval Biozone is defined by the lowest occurrence of *Col. ludensis*; the top is marked by the incoming of *Neodiversograptus nilssoni*, index species of the lowermost Ludlow *nilssoni* Biozone (Fig. 19). *Colonograptus ludensis* (Fig. 20I) is more abundant in the lower part of this combined biozone, whereas *Col. gerhardi* (Fig. 20H) prevails in the upper part. Both the former and, in particular, the latter taxon range through to the middle *nilssoni* Biozone. *Colonograptus deubeli* and *Col. praedeubeli* vanished within the lower part of the *ludensis–gerhardi* Biozone, which is also marked by *Prist. auctus* and rare occurrences of *Hoffmanigraptus ovatus*. *Neogothograptus eximinassa* (Fig. 20B) is a characteristic and common element in the middle and upper part of the biozone, which also sees the incoming of *Bohemograptus praecox* and *Plectograptus robustus*. *Spinograptus muenchi*, *Sp. clathrospinosus* and the long-lived *Prist. frequens* range from underlying biozone through to the overlying one. *Spinograptus spinosus* joined the assemblage in the uppermost *ludensis–gerhardi* Biozone.

A complete section of the *ludensis–gerhardi* Biozone was described from the trench along the field track northwest of Všeradice (Kříž 1992, Kříž *et al*. 1993, Kozłowska-Dawidziuk *et al*. 2001). Kříž (1992) and Kříž *et al*. (1993) recorded a total thickness of 4.2 m and only the index taxon – *Col. ludensis* (= *M. vulgaris*). Kozłowska-Dawidziuk *et al*. (2001), however, identified both *Col. ludensis* and *Col. gerhardi* and reduced the biozone thickness to about half due to the low appearance of *Neodiv. nilssoni*, index fossil of the overlying biozone. The upper part of the *ludensis–gerhardi* Biozone, 2.2 m thick, has been studied in the trench near Nesvačily (Štorch *et al*. 2016). The sedimentary succession, rich in well-preserved graptolites, continues through the Wenlock–Ludlow boundary, delineated by the incoming of *Neodiv. nilssoni.* Only the lower and middle parts of the *ludensis–gerhardi* Biozone are preserved in the uppermost 2.9 m of the Kosov quarry section (Manda *et al*. 2019) as indicated by the absence of *Col. gerhardi* and some other taxa abundant in the upper part of the biozone in the Nesvačily-trench section. An about 5 m thick *dubius-gerhardi* Biozone, with *Col. ludensis* in the lower part and *Col. gerhardi* in the upper part, has been recorded in pipeline excavations near Lištice. Other records of the biozone are from Braník Rocks in Praha-Braník (Kříž *et al*. 1993) and a trench east of Bykoš.

Figure 21. Age-diagnostic Gorstian graptolites. • A – *Colonograptus*? *heathcotensis* Rickards & Sandford, PŠ 3045, *chimaera–scanicus* Biozone. • B – bipolar *Neodiversograptus nilssoni* (Lapworth), PŠ 3804, *nilssoni* Biozone. • C – *Heisograptus micropoma* (Jaekel), PŠ 3311, upper *progenitor* Biozone (*fritschi* Subzone). • D – *Saetograptus varians* (Wood), PŠ 3306, *progenitor* Biozone. • E – *Colonograptus colonus* (Barrande), PŠ 3828, *nilssoni* Biozone. • F – *Lobograptus progenitor* Urbanek, PŠ 3371, *progenitor* Biozone. • G – *Lobograptus scanicus* (Tullberg), PŠ 3158, uppermost *chimaera–scanicus* Biozone. • H – *Plectograptus macilentus* (Törnquist), PŠ 3318, upper *progenitor* Biozone. • I – unipolar *Neodiversograptus nilssoni* (Lapworth), PŠ 3833b, *nilssoni* Biozone. • J – *Spinograptus spinosus* (Wood), PŠ 3353, *progenitor* Biozone. • K – *Uncinatograptus uncinatus* (Tullberg), PŠ 3361, uppermost *nilssoni* Biozone. • L – *Neogothograptus alatiformis* Lenz *et al*., PŠ 3391, *progenitor* Biozone. • M – *Saetograptus fritschi* (Perner), PŠ 3230, *chimaera–scanicus* Biozone. • N – *Saetograptus chimaera* (Barrande), PŠ 3193, upper *chimaera–scanicus* Biozone. A, G, M, N – Všeradice-trench; B, E, I – Nesvačily-trench; C, D, F, H, J–L – Bykoš-trench. All figures × 5 except for L × 10, scale bars represent 1 mm.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Neodiversograptus nilssoni Biozone

Perner & Kodym (1919, 1922) recognized a *Monograptus colonus* Biozone at the top of their graptolite biozonal scheme. Bouček (1937) renamed this unit the *Monograptus nilssoni* Biozone despite the continuing problems with the taxonomic definition of the species. Lack of well-preserved material collected *in situ* in the Prague Synform resulted in the preferred application of either a *Lobograptus scanicus* Biozone *sensu lato* (Horný 1955) or a combined *nilssoni–scanicus* Biozone (Prantl & Přibyl 1948). At that time, *Neodiv. nilssoni* had not been properly distinguished from *Lobograptus progenitor*, described by Urbanek (1966). Jaeger *in* Kříž *et al*. (1993) returned to use of the *colonus* Biozone, although Přibyl (1983) correctly identified the *nilssoni* Biozone in a few localities including the road cut southeast of Bykoš and classical Barrande's locality Butovice-Na Břekvici (see Kříž 1961). Subsequent field work has recorded an easily recognizable *nilssoni* Biozone with the index species fairly common in several sections in southwestern part of the Prague Synform (Štorch *et al*. 2016, unpublished data). The present study adopts the almost globally recognized index species *Nd. nilssoni* as defined by Palmer (1971) and thus avoids the rather problematical differentiation between less well-preserved *Col. colonus* and *Saetograptus varians*, which is a typical element of the *Lobograptus progenitor* Biozone assemblage.

The *nilssoni* Biozone is an interval between the lowest occurrence of the biozone fossil *Neodiv. nilssoni* and the incoming of *L. progenitor*, index species of the overlying biozone. The base of the *nilssoni* Biozone formally equates with that of the Ludlow Series (Holland & Bassett 1989, Melchin *et al*. 2020). *Neodiversograptus nilssoni* occurs in two different morphotypes. Unipolar rhabdosomes (Fig. 21I) are common through most of the biozone, whereas bipolar specimens (Fig. 21B) appear about mid-biozone and continue up to the *progenitor* Biozone. The lower part of the biozone is further characterized by the incoming of *Neogothograptus balticus* and *Uncinatograptus uncinatus* (Fig. 21K), and further proliferation of *Sp. spinosus* (Fig. 21J). The long-ranging *Bohemograptus bohemicus* replaced the short-lived *Boh. praecox*. *Plectograptus macilentus* (Fig. 21H), *Kirkigraptus*? aff. *inexpectans*, *Col. colonus* (Fig. 21E) and the enigmatic, short-lived *Bohemograptus butovicensis* (Štorch *et al*. 2016, figs 4n, q, w; 5a, c) appear mid-biozone. *Colonograptus roemeri* made its lowest occurrence in the upper part of the biozone whereas *Plect. robustus* and *U. uncinatus* vanished within the *nilssoni–progenitor* Biozone boundary interval.

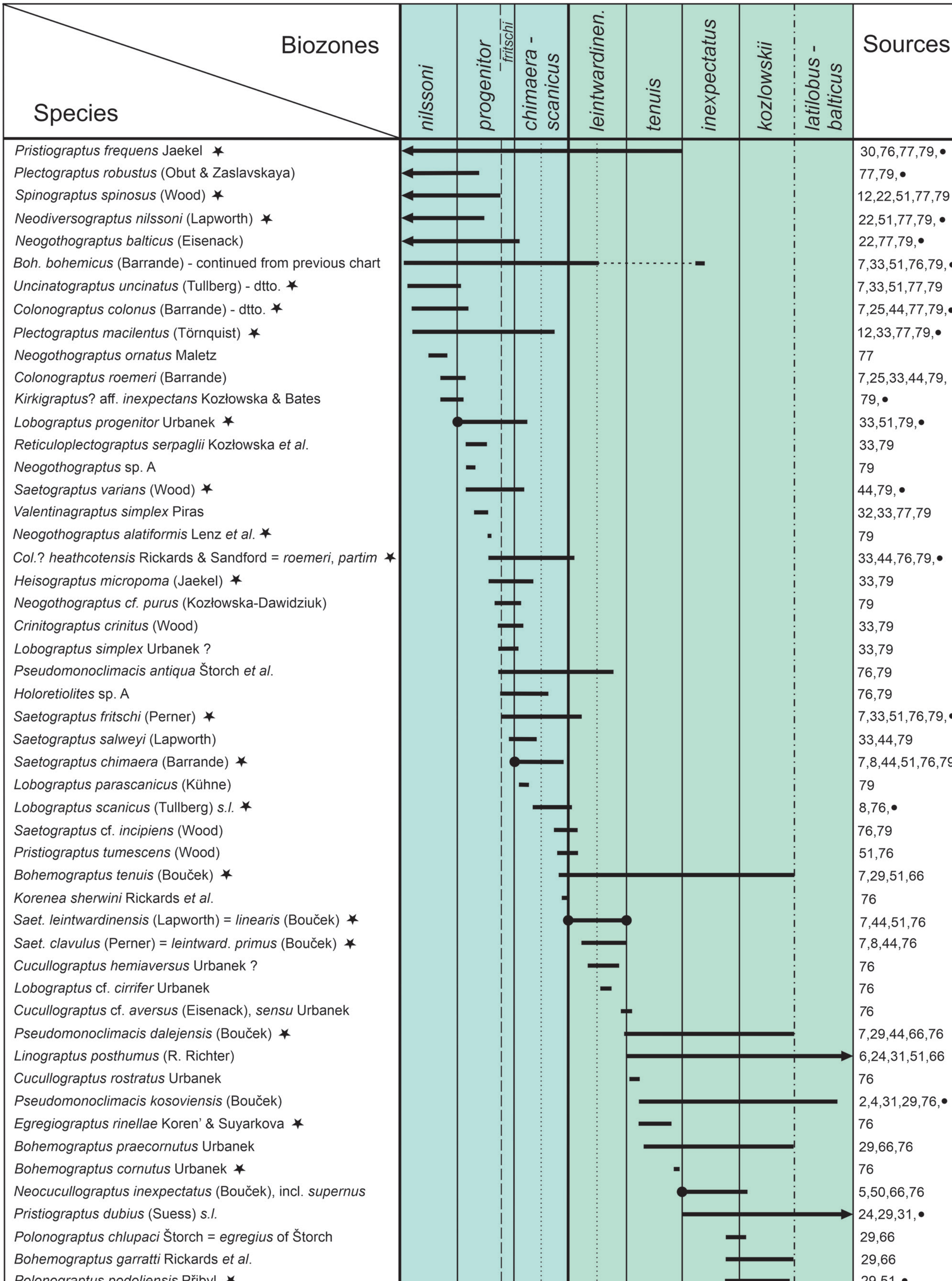
Basin-wide revival of intermittent synsedimentary alkaline basalt volcanism is particularly well recorded in the Wenlock–Ludlow boundary strata. In addition to volcanic-carbonate facies developed around largely submarine volcanoes (Horný 1960, Kříž 1991), pyroclastic layers spread across hemipelagic shale facies far from the volcanic vents. Shaly successions with a limited number of relatively thin pyroclastic layers, limestone nodules and lenses have been found in the southwestern part of the Prague Synform. The graptolite-rich lower and middle part of the *nilssoni* Biozone, 5 m thick, was studied in the trench north of Nesvačily (Štorch *et al*. 2016). The upper part of the biozone, 2.2 m thick, was exposed in a trench east of Bykoš above a *ca* 1.5 m thick pyroclastic layer. A complete, more than 3 m thick *nilssoni* Biozone is developed in the Všeradice section (Kozłowska-Dawidziuk *et al*. 2001; Piras 2006a, b), although with pyroclastics in the middle part, limestone nodules and graptolites less common in the tuffitic shales.

Lobograptus progenitor Biozone

The *Lobograptus progenitor* Biozone, established by Urbanek (1966) in the Polish part of the East European Platform, was adopted in the Prague Synform by Přibyl (1983). Since then, the unit has been applied nearly worldwide (Loydell 2012, Melchin *et al*. 2020). This biozone represents the lowest Ludlow graptolite biozone in the Canadian Arctic Islands, in the absence of *Neodiv. nilssoni* (Lenz & Kozłowska-Dawidziuk 2004). It is correlatable with lower part of the *Lobograptus scanicus* Biozone, which immediately succeeds the *nilssoni* Biozone in the generalized biozonal scheme of Melchin *et al*. (2020). Urbanek (1966) has shown that *Lobograptus scanicus* is a highly advanced lobograptid limited to the upper Gorstian and separated from the graptolite assemblage of the *nilssoni* Biozone by strata characterized by less advanced lobograptids, such as *Lobograptus progenitor*, *Lobograptus simplex* and *Lobograptus parascanicus*.

The *progenitor* Biozone is defined as an interval between the lowest occurrence of the index species and the lowest occurrence of *Saetograptus chimaera*, one of the two index taxa of the overlying *Saetograptus chimaera–Lobograptus scanicus* Biozone (Fig. 22). The stratigraphical range of *L. progenitor* (Fig. 21F) extends into the lower part of the latter biozone. The *progenitor* Biozone displays a diverse and distinctive graptolite assemblage, with significant faunal change mid-biozone.

Figure 22. Stratigraphical ranges of Gorstian and Ludfordian graptolites in the Prague Synform. Dash-and-dot vertical line indicates tentatively delineated zonal boundary. See Figs 5 and 14 for further explanation.


Biozones
Species
nilssoni
progenitor
– fritschi
chimaera - scanicus
leintwardinen.
tenuis
inexpectatus
kozlowskii
latilobus - balticus
Sources
Pristiograptus frequens Jaekel ✶ 30,76,77,79,•
Plectograptus robustus (Obut & Zaslavskaya) 77,79,•
Spinograptus spinosus (Wood) ✶ 12,22,51,77,79
Neodiversograptus nilssoni (Lapworth) ✶ 22,51,77,79,•
Neogothograptus balticus (Eisenack) 22,77,79,•
Boh. bohemicus (Barrande) - continued from previous chart 7,33,51,76,79,•
Uncinatograptus uncinatus (Tullberg) - dtto. ✶ 7,33,51,77,79
Colonograptus colonus (Barrande) - dtto. ✶ 7,25,44,77,79,•
Plectograptus macilentus (Törnquist) ✶ 12,33,77,79,•
Neogothograptus ornatus Maletz 77
Colonograptus roemeri (Barrande) 7,25,33,44,79,
Kirkigraptus? aff. inexpectans Kozłowska & Bates 79,•
Lobograptus progenitor Urbanek ✶ 33,51,79,•
Reticuloplectograptus serpaglii Kozłowska et al. 33,79
Neogothograptus sp. A 79
Saetograptus varians (Wood) ✶ 44,79,•
Valentinagraptus simplex Piras 32,33,77,79
Neogothograptus alatiformis Lenz et al. ✶ 79
Col.? heathcotensis Rickards & Sandford = roemeri, partim ✶ 33,44,76,79,•
Heisograptus micropoma (Jaekel) ✶ 33,79
Neogothograptus cf. purus (Kozłowska-Dawidziuk) 79
Crinitograptus crinitus (Wood) 33,79
Lobograptus simplex Urbanek ? 33,79
Pseudomonoclimacis antiqua Štorch et al. 76,79
Holoretiolites sp. A 76,79
Saetograptus fritschi (Perner) ✶ 7,33,51,76,79,•
Saetograptus salweyi (Lapworth) 33,44,79
Saetograptus chimaera (Barrande) ✶ 7,8,44,51,76,79
Lobograptus parascanicus (Kühne) 79
Lobograptus scanicus (Tullberg) s.l. ✶ 8,76,•
Saetograptus cf. incipiens (Wood) 76,79
Pristiograptus tumescens (Wood) 51,76
Bohemograptus tenuis (Bouček) ✶ 7,29,51,66
Korenea sherwini Rickards et al. 76
Saet. leintwardinensis (Lapworth) = linearis (Bouček) ✶ 7,44,51,76
Saet. clavulus (Perner) = leintward. primus (Bouček) ✶ 7,8,44,76
Cucullograptus hemiaversus Urbanek ? 76
Lobograptus cf. cirrifer Urbanek 76
Cucullograptus cf. aversus (Eisenack), sensu Urbanek 76
Pseudomonoclimacis dalejensis (Bouček) ✶ 7,29,44,66,76
Linograptus posthumus (R. Richter) 6,24,31,51,66
Cucullograptus rostratus Urbanek 76
Pseudomonoclimacis kosoviensis (Bouček) 2,4,31,29,76,•
Egregiograptus rinellae Koren' & Suyarkova ✶ 76
Bohemograptus praecornutus Urbanek 29,66,76
Bohemograptus cornutus Urbanek ✶ 76
Neocucullograptus inexpectatus (Bouček), incl. supernus 5,50,66,76
Pristiograptus dubius (Suess) s.l. 24,29,31,•
Polonograptus chlupaci Štorch = egregius of Štorch 29,66
Bohemograptus garratti Rickards et al. 29,66
Polonograptus podoliensis Přibyl ✶ 29,51,•

The lower part of the biozone sees the last appearance of *U. uncinatus*. *Colonograptus colonus* and *Col. roemeri* were replaced by *Saet. varians* (Fig. 21D). *Spinograptus spinosus*, the short-ranging *Valentinagraptus simplex*, and the bipolar *Neodiv. nilssoni* disappear mid-biozone. Incoming taxa include *Lobograptus simplex*? and the robust *Colonograptus*? *heathcotensis*, easily misidentified as the earlier *Col. roemeri*. Tiny, but relatively common *Neogothograptus alatiformis* (Fig. 21L) was found in a very limited, 0.3 m thick interval in the middle of the biozone. *Neogothograptus balticus* and the long-ranging generalists, *Plect. macilentus*, *Prist. frequens* and *Boh. bohemicus*, continue through the whole interval. The upper part of the biozone, marked by the incoming of *Saetograptus fritschi* (Fig. 21M), *Saetograptus salweyi*, *Neogothograptus* cf. *purus*, *Heisograptus micropoma* (Fig. 21C), *Pseudomonoclimacis antiqua* and *Crinitograptus crinitus*, is proposed as a distinct subzone with its base delineated by the lowest occurrence of the subzone index *Saet. fritschi*.

The *progenitor* Biozone, 1–2 m thick, was reported by Přibyl (1983) from Praha-Konvářka, the southeastern slope of Lejškov near Suchomasty, and the roadcut southeast of Bykoš. A new detailed study of the shale-dominated lower Ludlow succession has revealed a total thickness of more than 11 m in the proposed reference section east of Bykoš, not including a 3 m thick basalt sill. The Všeradice-trench section includes a complete *progenitor* Biozone 8.5 m thick.

Saetograptus chimaera–Lobograptus scanicus Biozone

The *Monograptus scanicus* Biozone, established by Wood (1900) in England, was incorporated into the graptolite biozonal scheme of the Prague Synform by Bouček (1934). Since then, the *scanicus* Biozone became an integral, but rather problematical part of the biozonal scheme. Diverse, but closely similar species of the genera *Lobograptus* and *Cucullograptus* are uncommon and hard to distinguish except for the abundant and highly distinctive *L. progenitor*. *Lobograptus scanicus*, in particular, is an uncommon and relatively short-ranging element in the graptolite fauna of the Prague Synform. In order to get a full biostratigraphical coverage of the upper Gorstian succession, prominent *Saetograptus chimaera*, that appeared significantly lower than *L. scanicus*, is chosen to define the base of the combined *chimaera–scanicus* Biozone. The *scanicus–chimaera* Biozone has been preferred by Koren' (1983, 1986, 1993) in Central Asia and Koren'& Suyarkova (2007) in the Kaliningrad area, whereas Jaeger (1959) and Kříž (1992) named this interval the *chimaera* Biozone. The lower limit of the *chimaera–scanicus* Biozone is probably at a somewhat stratigraphically lower level than that of the British *scanicus* Biozone of Zalasiewicz *et al*. (2009). It is, however, higher than the lower limit of the *scanicus* Biozone, which immediately overlies the *nilssoni* Biozone in the Silurian Time Scale (Melchin *et al*. 2020).

The *chimaera–scanicus* Biozone comprises an interval between the first appearance of *Saet. chimaera* and the first *Saetograptus leintwardinensis*, the index species of the overlying biozone (Fig. 22). *Saetograptus chimaera* (Fig. 21N) is relatively common in the lower part of the combined biozone and continues up to nearly the base of the overlying biozone. *Lobograptus scanicus* (Fig. 21G) has its lowest occurrence mid-biozone and vanished in the lower part of the overlying biozone. Other incoming taxa include *Saet. salweyi*, *Saet.* cf. *incipiens*, *Holoretiolites* sp. A, rare *Korenea sherwini* and *L. parascanicus*, which is common in the lower part of the biozone. *Pristiograptus tumescens* and the long-ranging *Bohemograptus tenuis* first appear in the upper *chimaera–scanicus* Biozone. Other long-ranging taxa present include *Prist. frequens*, *Pseudomcl. antiqua*, *Saet. fritschi* and *Boh. bohemicus*. *Neogothograptus balticus*, *Cr. crinitus*, *L. simplex*? and *L. progenitor* disappear in the lower part of the biozone, being followed by *Plect. macilentus* and *H. micropoma* mid-biozone, and *Col.*? *heathcotensis* (Fig. 21A) in the upper part.

A complete section through the 13.6 m thick *chimaera–scanicus* Biozone, developed in shale-dominated offshore facies, was studied in detail by Štorch *et al*. (2014, unpublished data) in the trench along the field tract northwest of Všeradice. Other significant outcrops have been reported from Praha-Konvářka (Přibyl 1983), the hillslope west of the Mušlovka quarry near Řeporyje (Bouček 1937, Kříž 1992), the cut before the entrance to Na Požárech quarry near Řeporyje (Přibyl 1983, Kříž 1992), the westernmost part of Kosov quarry (Přibyl 1983), and high on the rocky slope at Malá Chuchle-Vyskočilka.

Saetograptus leintwardinensis Biozone

The *leintwardinensis* Biozone was first defined by Marr (1892) in the Lake District of England. In the Prague Synform, Bouček (1936) recognized this interval in the Prague Synform where he named it after the proposed biozone fossil *Monograptus leintwardinensis primus*. Jaeger (1959) came to the conclusion that *M. leintwardinensis primus* is conspecific with the associated *Monograptus fritschi linearis* described by Bouček (1936) in the same paper. Later on the *linearis* Biozone became an integral part of the Silurian graptolite biozonal scheme in Bohemia (Horný 1962, Přibyl 1983, Havlíček & Štorch

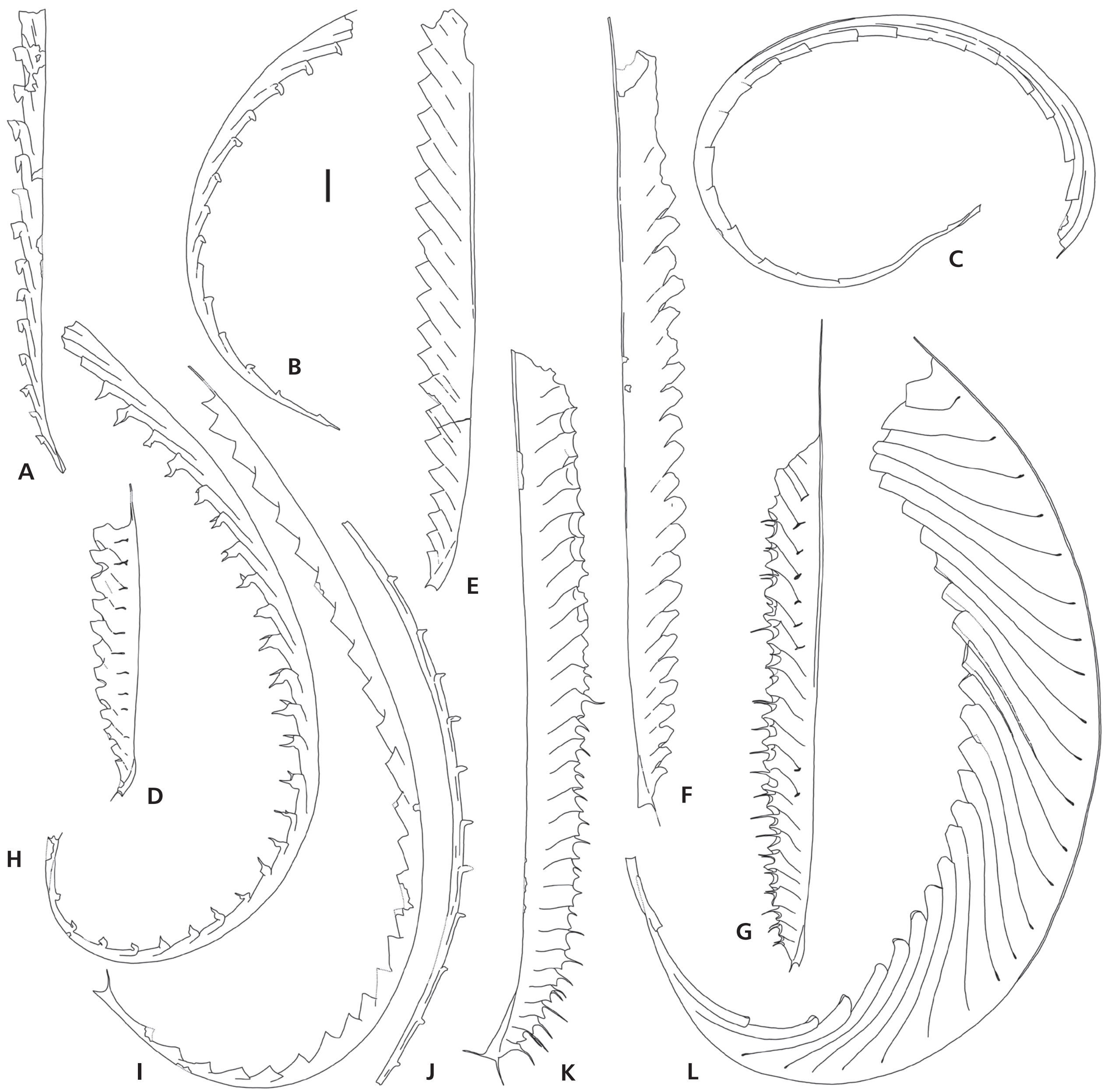


Figure 23. Age-diagnostic Ludfordian graptolites. • A – *Slovinograptus balticus* (Teller), PŠ 2018, *latilobus–balticus* Biozone. • B – *Neocucullograptus inexpectatus* (Bouček), PŠ 2100, *inexpectatus* Biozone. • C – *Egregiograptus rinellae* Koren' & Sujarkova, PŠ3060, *tenuis* Biozone. • D – *Pseudomonoclimacis dalejensis* (Bouček), PŠ 3049, *tenuis* Biozone. • E – *Pristiograptus fragmentalis* (Bouček), PŠ 2309, *fragmentalis* Biozone. • F – *Pseudomonoclimacis latilobus* (Tsegelnyuk), PŠ 2006, *latilobus–balticus* Biozone. • G – *Saetograptus leintwardinensis* (Lapworth), PŠ 3252, *leintwardinensis* Biozone. • H – *Neocucullograptus kozlowskii* Urbanek, PŠ 670/1, *kozlowskii* Biozone. • I – *Bohemograptus tenuis* (Bouček), PŠ 3134, *tenuis* Biozone. • J – *Crinitograptus*? sp., PŠ 2308, *latilobus–balticus* Biozone. • K – *Saetograptus clavulus* (Perner), PŠ 3174, upper *leintwardinensis* Biozone. • L – *Polonograptus podoliensis*, PŠ 620/1, *kozlowskii* Biozone. A–G, I–K – Všeradice-trench; H, L – Kosov quarry, 3rd level. All figures × 5, scale bar represents 1 mm.

1990, Kříž 1992) in a similar way as the *leintwardinensis* Biozone became part of the standard graptolite biozonal schemes of the Ludlow Series worldwide (Koren' *et al*. 1996, Loydell 2012, Melchin *et al*. 2020). Subsequently Štorch *et al*. (2014) renamed the former *Saetograptus linearis* Biozone as the *Saetograptus leintwardinensis* Biozone resulting from their taxonomic revision of the species that put *Saetograptus linearis* into synonymy of the senior name *Saetograptus leintwardinensis*. The lower part of the Czech *leintwardinensis* Biozone, with common *Prist. tumescens*, may be tentatively compared with the upper part of the imprecisely-defined *Pristiograptus tumescens* Biozone of the British biozonal scheme (Zalasiewicz *et al*. 2009).

This biozone is recognized in the Prague Synform as an interval bounded by the lowest and highest occurrences of the eponymous graptolite (Fig. 22). *Saetograptus clavulus* (Fig. 23K) is another prominent species appearing in the lower part of the *leintwardinensis* Biozone. *Pristiograptus frequens* and *Boh. tenuis* are common, long-ranging elements of the biozone assemblage. Several species that continue from the previous biozone, including *Prist. tumescens*, *Saet. fritschi* and *Saet.* cf. *incipiens*, vanished in the lower part of this biozone, *Pseudomonoclimacis antiqua* vanished in the upper part, whereas *Col.*? *heathcotensis* and *L. scanicus* disappear shortly after the stratigraphically lowest occurrence of the biozone index *Saet. leintwardinensis* (Fig. 23G). Typical *Boh. bohemicus* vanished, at least temporarily, from the fossil record mid-biozone, whereas probable *Cucullograptus hemiaversus* and *Lobograptus* cf. *cirrifer* appear in this level, followed by *Cucullograptus* cf. *aversus* in the upper part of the biozone. The relatively long-ranging *Pseudomonoclimacis dalejensis* (Fig. 23D) first occurs in the uppermost part of the *leintwardinensis* Biozone. The top of the *leintwardinensis* Biozone is marked by the abrupt demise of spinose saetograptids as part of the lower Ludfordian *leintwardinensis* graptolite Extinction Event (Štorch *et al*. 2014), which is otherwise manifested by stepwise turnover of the graptolite fauna.

The only complete section of the *leintwardinensis* Biozone in graptolitic off-shore facies, 11.6 m thick including subordinate and thin limestone intercalations, was described by Štorch *et al*. (2014) from the trench along the field track northwest of Všeradice. Shale beds alternating with biodetrital limestones referred to the *leintwardinensis* Biozone (formerly *Saetograptus linearis* or *fritschi linearis* Biozone) have been known from the southwestern periphery of Prague (Řeporyje-Mušlovka and Na Požárech quaries, water-supply gallery in Praha-Podolí) and from Kosov quarry-behind the canteen (Bouček 1937, Přibyl 1983, Kříž 1992).

Bohemograptus tenuis Biozone

A *Bohemograptus* proliferation Biozone marked by a monospecific assemblage of *Bohemograptus tenuis* was originally recognized by Holland & Palmer (1974) above the *leintwardinensis* Biozone in the Welsh Borderland (UK) and later adopted by Melchin *et al*. (2020) in the Silurian Time Scale. The *Bohemograptus tenuis* Biozone was recognized by Koren' & Suyarkova (2004) in Central Asia, by Radzevičius *et al*. (2023) in East Baltic region and, combined with that of *Bohemograptus praecornutus*, used by Lenz & Kozłowska-Dawidziuk (2004) in Arctic Canada. The *tenuis* Biozone can be tentatively correlated with the *Bohemograptus praecornutus*, *Bohemograptus cornutus* and *Neolobograptus auriculatus* biozones recognized by Urbanek & Teller (1997) in the subsurface Silurian of the Polish part of the East European Platform. The *tenuis* Biozone adopted by Manda *et al*. (2012) and Štorch *et al*. (2014) corresponds with the earlier *Pristiograptus longus* Biozone and overlying unnamed interval with abundant bohemograptids (Fig. 2) reported from the Prague Basin by Přibyl (1983). Přibyl's *longus* Biozone, defined by a locally recognized derivative from the pristiograptid stem-lineage, is abandoned due to the unclear systematic status and stratigraphical range of the biozone fossil.

This biozone is one of the interval biozones following mass extinction events and designated as interregna by Jaeger (1991) and Zalasiewicz *et al*. (2009). The *tenuis* Biozone, defined by Manda *et al*. (2012) and Štorch *et al*. (2014), is characterized by the abundant occurrence of the long-ranging, probably generalist *Boh. tenuis* (Fig. 23I) and delineated by the extinction of saetograptids (*Saet. leintwardinensis* and *Saet. clavulus*) at the biozone base and appearance of *Neocucullograptus inexpectatus* at the top (Fig. 22). Robust rhabdosomes of the relatively long-ranging *Pseudomonoclimacis kosoviensis* first occur in the lower *tenuis* Biozone. The short-lived *Cucullograptus* cf. *aversus* and *Cucullograptus rostratus* occur in the lower part of the biozone, whereas *Egregiograptus rinellae* (Fig. 23C) is common mid-biozone. Long-lived *Boh. praecornutus* appears in the lower-middle part of the *tenuis* Biozone, rare *Boh. cornutus* was identified in the upper part. *Prist. frequens* passes throught the whole *tenuis* Biozone.

A complete, 19 m thick sequence of graptolite-bearing calcareous shales with subordinate limestone intercalations, exposed along the field tract northwest of Všeradice (Štorch *et al*. 2014), is taken as a reference section of the *tenuis* Biozone. Other sections were reported by Přibyl (1983) from Řeporyje-Mušlovka and Na Požárech quarries, Kosov quarry, and the water-supply gallery in Praha-Podolí.

Neocucullograptus inexpectatus Biozone

This biozone was first recognized in eastern Poland beneath the *Neocucullograptus kozlowskii* Biozone (Urbanek 1970). Přibyl (1983) distinguished the *inexpectatus* Biozone in the Prague Synform but overlain directly by the biozone of *Saetograptus insignitus*, subsequently recognized as a junior synonym of *Pseudomonoclimacis latilobus*. Since then, *Neocucullograptus kozlowskii* was found in several Czech sections between the stratigraphical ranges of *Nd. inexpectatus* and *Pseudomcl. latilobus*. The *inexpectatus* Biozone is currently recognized in a rather restricted interval that corresponds with the lower part of

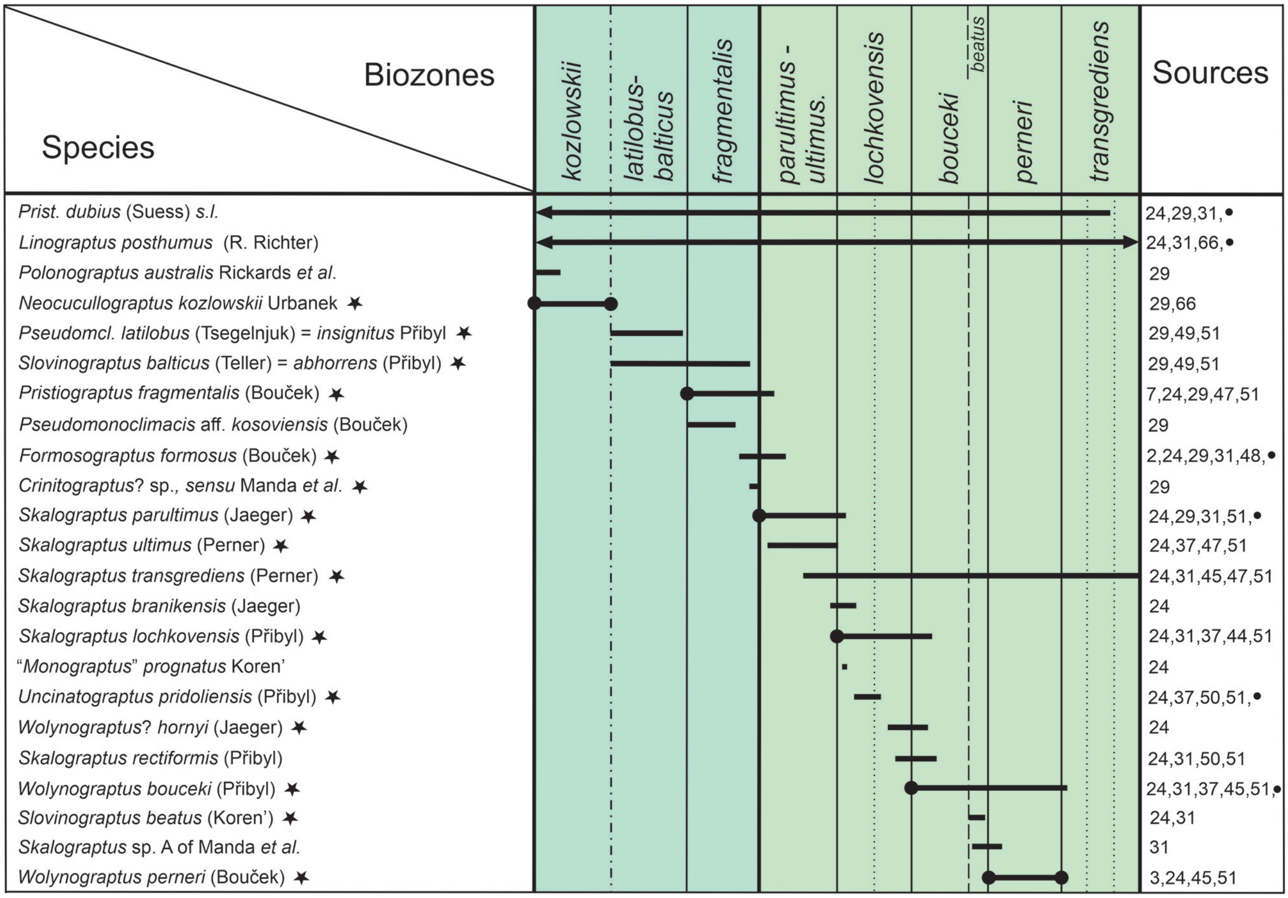


Figure 24. Stratigraphical ranges of Ludfordian and Přídolí graptolites in the Prague Synform, continued from Fig. 21. Dash-and-dot vertical line indicates tentatively delineated zonal boundary. See Figs 5 and 14 for further explanation.

the *inexpectatus* Biozone as recognized by Přibyl (1983).

The revised biozone is defined as an interval between the stratigraphically lowest occurrence of the biozone index *Nc. inexpectatus* (Fig. 23B) and lowest occurrence of its likely descendant (Urbanek 1970, Urbanek & Teller 1997) *Neocucullograptus kozlowskii*. Most of the biozone assemblage consists of long-ranging taxa, such as small specimens of *Pristiograptus dubius* s.l. and *Pseudomcl. dalejensis*, *Boh. tenuis*, *Boh. praecornutus*, *Linograptus posthumus*, and the much larger *Pseudomcl. kosoviensis*. Incoming *Polonograptus chlupaci*, *Polonograptus australis*, *Polonograptus podoliensis*, and *Bohemograptus garratti* appear in the upper part of the *inexpectatus* Biozone and their ranges extend into the overlying *kozlowskii* Biozone.

The *inexpectatus* Biozone is one of the less well-known units of the Czech Silurian biozonal scheme. The section exposed in the 3rd level of Kosov quarry (Štorch 1995a), between a massive bank of brachiopod limestone and the base of the overlying *kozlowskii* Biozone, probably represents only the upper part of the true stratigraphical range of the *inexpectatus* Biozone. It is developed as 1.6 m thick alternating laminated calcareous shales and thin limestone beds. The same level and lithology crops out in Liščí Quarry north of Karlštejn. A complete section of the *inexpectatus* Biozone, 8.7 m thick, was described by Manda *et al.* (2012) from the shale-dominated section exposed in the trench along the field track northwest of Všeradice. Other localities of the *inexpectatus* Biozone, namely various building excavations in Praha-Pankrác and Praha-Podolí and outcrops at Praha-Konvářka and Velký Vrch near Koněprusy, have been studied by Přibyl (1983).

Neocucullograptus kozlowskii Biozone

The *kozlowskii* Biozone, established by Urbanek (1970) in eastern Poland, was recognized in the Prague Basin and distinguished from the underlying *inexpectatus* Biozone by Štorch (1995b). The combined *Neocucullograptus kozlowskii–Polonograptus podoliensis* Biozone of the Silurian time scale (Melchin *et al.* 2020) closely corresponds with the *inexpectatus* and *kozlowskii* biozones of Baltica (East European Platform) and peri-Gondwanan Europe (Loydell 2012). *Polonograptus podoliensis* (Fig. 23L) ranges from about the middle of the *inexpectatus* Biozone through to the top of the *kozlowskii* Biozone in the Prague Synform and has been recorded in association with *Nc. inexpectatus* also in Central Asia (Koren' & Suyarkova 2004). The *Pristiograptus dubius postfrequens* Partial-range Interval Biozone, established by Frýda & Manda (2013) between the *Nc. kozlowskii* and *Pseudomonoclimacis latilobus–Slovinograptus balticus* biozones, is not adopted in the proposed biozonal scheme since the unit was named upon a single graptolite subspecies never recorded in the Prague Synform.

The *kozlowskii* Biozone is defined here as an interval comprising the total stratigraphical range of the biozone fossil *Neocucullograptus kozlowskii* (Fig. 23H). The top also corresponds with a mass graptolite extinction (Fig. 24) known as the *kozlowskii* Event (Urbanek 1993, Štorch 1995a). At that time, all extant ventrally curved graptolites (genera *Neocucullograptus*, *Bohemograptus* and *Polonograptus*) vanished from the fossil record. The graptolite assemblage of the *kozlowskii* Biozone possesses mostly species continuing from the previous *inexpectatus* Biozone. *Polonograptus australis* and *Pol. chlupaci* vanished in the lower part of the biozone. *Pseudomonoclimacis dalejensis*, *Boh. tenuis*, *Boh. praecornutus*, *Boh. garratti* and *Pol. podoliensis* continued through to the mass-extinction at the top. The only survivors, the long ranging *Prist. dubius* s.l., *Pseudomcl. kosoviensis* and *Lin. posthumus* reappeared in the low diversity post-extinction graptolite fauna of the *Pseudomonoclimacis latilobus–Slovinograptus balticus* Biozone.

This biozone is best accessible in the 3rd and 2nd levels of Kosov quarry (Štorch 1995b). Graptolites are uncommon in a 5 m thick succession of laminated calcareous shales alternating with thin-bedded muddy limestones. Another, 3.2 m thick shaly succession of the complete *kozlowskii* Biozone was exposed in the upper part of the trench section running along the field track northwest of Všeradice (Manda *et al.* 2012). The same interval crops out in the cart track from Koněprusy to Velký Vrch, in Praha-Konvářka and was temporarily accessible in the gallery for water supply in Praha-Podolí (Přibyl 1983).

Pseudomonoclimacis latilobus–Slovinograptus balticus Biozone

In the Prague Synform this biozone was originally recognized by Přibyl (1983), named the *Saetograptus insignitus* Biozone, and characterized by the joint first occurrence of the index species and *Monograptus abhorrens*. Urbanek (1997) showed that *Saet. insignitus* is a junior synonym of *Pseudomcl. latilobus*. The associated *Monograptus abhorrens* (Přibyl, 1983) was later assigned to *Slovinograptus balticus* by Štorch *in* Manda *et al*. (2012) and the whole interval is renamed the *latilobus–balticus* Biozone. Přibyl (1983) recognized a *Pristiograptus fecundus* Biozone between his "*insignitus*" and *fragmentalis* biozones based on the graptolite succession recorded in a roadcut at Karlštejn-Budňany and in Mušlovka quarry near Řeporyje. However, this unit and species have not been identified by the present author, nor have they been recognized abroad. It is, therefore, not included in the proposed biozonal scheme.

Manda *et al.* (2012) defined the *latilobus–balticus* Biozone as an interval between the stratigraphically highest occurrence of *Nc. kozlowskii* and highest joint occurrence of *Pseudomcl. latilobus* (Fig. 23F) and *Slov. balticus* (Fig. 23A). The two index taxa are the most prominent elements of this small assemblage (Fig. 24), the latter ranging up to the upper *fragmentalis* Biozone. Other noteworthy occurrences include the long-ranging *Lin. posthumus* and *Prist. dubius* s.l. *Pseudomonoclimacis kosoviensis* make its highest occurrences in the *latilobus-balticus* Biozone.

Significant sea-level fluctuations and consequent gaps in the limestone-dominated sedimentation, with channel structures, gravity deposits and erosional surfaces, left gaps in the late Ludfordian graptolite record of the Prague Synform. Moreover, the post extinction recovery of the graptolite fauna was remarkably slow and correlation of the low-diversity assemblages is a real challenge. The non-graptolitic interval between the top of the *kozlowskii* Biozone and base of the *latilobus–balticus* Biozone ranges from 2.5 m in the Všeradice-trench section to 10 m in Kosov quarry. The most complete *latilobus–balticus* Biozone, with the best developed graptolite fauna occurs in a 2.8 m thick interval of alternating shale and limestone, described by Manda *et al.* (2012) from the trench section along the field track northwest of Všeradice. Other sections with upper Ludfordian graptolites in a 3.0–3.5 m thick *latilobus–balticus* Biozone were documented by Přibyl (1983) in Kosov quarry, Koněprusy-Velký vrch and the water supply gallery in Praha-Podolí.

Pristiograptus fragmentalis Biozone

This biozone was originally defined by Bouček (1936) in the biodetrital and cephalopod limestone facies of the uppermost Kopanina Formation. Přibyl (1983) referred the *fragmentalis* Biozone to the uppermost Ludlow Series, immediately below his *Pseudomonoclimacis*? *ultima* Biozone, now known as the *Skalograptus parultimus–Skalograptus ultimus* Biozone and recognized as the first graptolite biozone of the Přídolí Series. The generally monospecific fauna of the *fragmentalis* Biozone came from several limestone sections with a very limited graptolite record. The graptolite assemblage recorded in the condensed, shale-dominated Všeradice-trench section (Manda *et al*. 2012) exhibits greater diversity. Drill cores from Praha-Pankrác, as well as the Karlštejn-Budňany rock section studied by Kříž *et al*. (1986), revealed the co-occurrence of *Prist. fragmentalis* and *Formosograptus formosus* below the stratigraphically lowest *Skalograptus parultimus*. *Formosograptus formosus* was identified well below the lowest *Sk. parultimus* also in Marble Quarry near Lochkov (Kříž *et al*. 1986). Co-occurrence of the two species is to be expected since *Formosograptus formosus* is a name giving fossil of the globally recognized uppermost biozone of the upper Ludlow Ludfordian Stage (Loydell 2012, Melchin *et al*. 2020). It is assumed that the *fragmentalis* Biozone may be tentatively correlated with the widely adopted *formosus* Biozone (Fig. 7). The joint occurrence of *Prist. fragmentalis* and *F. formosus* reported by Bouček *et al.* (1976) from Serbia seems to confirm this assumption. Better stratigraphical resolution and correlation with the upper Ludfordian of the East European Platform (Poland, Ukraine) is hampered by the absence of age-diagnostic members of the *Wolynograptus acer–Wolynograptus spineus* graptolite lineage (Tsegelnyuk 1976, Urbanek 1997) in the Prague Synform. Since most of graptolite data from the uppermost Ludlow of the Prague Synform are from graptolite-poor biodetrital limestones and data from local graptolitic shale facies are very limited, the *fragmentalis* Biozone has been retained in the proposed biozonal scheme.

The *fragmentalis* Biozone represents an interval delineated by the lowest stratigraphical occurrence of the biozone index species at the base and first appearance of *Skalograptus parultimus* at the top (Fig. 24). Long-ranging species include *Prist. dubius* s.l. and *Lin. posthumus*. The robust *Pseudomonoclimacis* aff. *kosoviensis* is restricted to this interval. *Slovinograptus balticus* continues from the previous biozone to the lower part, poorly preserved specimens tentatively assigned to *Sl. balticus* were found in the upper part of the biozone that sees the incoming of *F. formosus* and the possibly short-ranging, dorsally arcuate *Crinitograptus*? sp. (Fig. 23J). *Pristiograptus fragmentalis* (Fig. 23E) persists into the lowermost part of the overlying biozone. Enhancement of our limited knowledge of the graptolite fauna and biostratigraphy of the upper Ludfordian should be sought in shaly sections.

A condensed, shale-dominated section of the *fragmentalis* Biozone, with a surprisingly diverse graptolite assemblage of 6 species, was exposed by trenching along the field tract northwest of Všeradice (Manda *et al.* 2012). A similar succession of alternating shales and platy limestones crops out above the road near Karlštejn-Budňany Rock (Kříž *et al*. 1986). Biodetrital and cephalopod limestones of the uppermost part of the Kopanina Formation, with a graptolite record limited to robust rhabdosomes of *Prist. fragmentalis*, are known from Lochkov-Orthoceras Quarry, Řeporyje-Mušlovka quarry, and Jinonice-Nová Ves near the former Klukovice railway stop (Přibyl 1983).

Skalograptus parultimus–Skalograptus ultimus Biozone

A *Monograptus ultimus* Biozone was one of the first graptolite biozones established in the upper Silurian of the Prague Synform (Přibyl 1940b). *Monograptus* (now *Skalograptus*) *parultimus*, described by Jaeger (1975), was reported by Přibyl (1983) from the lower part of the *ultimus* Biozone. Kříž *et al*. (1986) found *Sk. ultimus* only above its presumed ancestor *Sk. parultimus* in all sections studied and, thus, recognized separate *parultimus* and *ultimus* biozones in their very detailed study of the graptolite biostratigraphy of the Přídolí Series. Recent revision of some sections has shown that the stratigraphical succession of the two index taxa is not that simple. *Skalograptus parultimus* appears first in all sections but ranges even higher than *Sk. ultimus* in the northern part of the uppermost level of the Kosov quarry and overlaps with the lowermost *Skalograptus lochkovensis* in the Radotín-Hvížďalka section (Manda *et al*. 2023). A combined *parultimus–ultimus* Biozone is preferred in the present biozonal scheme also because of the almost continual variation in thecal and sicular morphology between the two taxa. The *parultimus–ultimus* Biozone has also been preferred by Koren' *et al*. (1996), Loydell (2012) and Melchin *et al*. (2020) in global standard correlation charts.

The *parultimus–ultimus* Biozone represents an interval delineated by the stratigraphically lowest occurrence of *Sk. parultimus* (Fig. 25F) at the base and lowest occurrence of *Sk. lochkovensis* at the top (Fig. 24). The former is the dominant species in the lower part of the combined biozone, but uncommon specimens occur as high as in the lowermost *lochkovensis* Biozone. *Skalograptus ultimus* (Fig. 25A) usually, although not always, predominates in the upper part of the combined biozone but probably does not reach into the *lochkovensis* Biozone. *Formosograptus formosus* (Fig. 25C) and *Prist. fragmentalis* make their highest occurrences in the lower(most) part of the *parultimus-ultimus* Biozone. The lowest occurrences of *Skalograptus transgrediens* appear mid-zone. *Linograptus posthumus* and *Prist. dubius* s.l. are long ranging taxa with intermittent occurrences throughout the biozone.

A complete section through the 6.5 m thick *parultimus-ultimus* Biozone, developed as alternating calcareous shales and laminated limestones, is easily accessible in the uppermost (1st) level of Kosov quarry (Kříž *et al*. 1986). The latter authors described also sections exposed in Marble and Orthoceras quarries near Lochkov, Koledník quarry, Karlštejn-Budňany rock, and Praha-Braník. The lower part of the biozone, in a shale-dominated succession, was studied by Manda *et al.* (2012) in the trench northwest of Všeradice.

Skalograptus lochkovensis Biozone

The *lochkovensis* Biozone, established by Přibyl (1940b) in the lower Přídolí of the Prague Synform, became one of standard upper Silurian biozones recognized worldwide. With regard to the occurrence of *Skalograptus branikensis* in the lower part of the Czech *lochkovensis* Biozone, this unit matches with the *lochkovensis–branikensis* Biozone recognized by Urbanek & Teller (1997) in Poland and, tentatively, with the *branikensis* Biozone of Central Asia (Koren' & Suyarkova 1997) and Arctic Canada (Lenz & Kozłowska-Dawidziuk 2004). The easily correlatable *lochkovensis–branikensis* Biozone appears in the graptolite biozonal scheme of the Silurian Time Scale (Melchin *et al*. 2020). Přibyl (1981, 1983) distinguished a separate *Monograptus pridoliensis* Biozone between the *ultimus* and *lochkovensis* biozones, but Kříž *et al*. (1986) used this unit as a middle subzone in their tripartite subdivision of the *lochkovensis* Biozone. The so-called lower *lochkovensis* Subzone and upper *lochkovensis* Subzone of Kříž *et al.* (1986) are unrecognizable in spot outcrops without broader stratigraphical context and are thus rejected from the present biozonal scheme, whereas the *pridoliensis* Subzone is a useful marker of the lower *lochkovensis* Biozone, especially in sections with limited occurrences of *Sk. lochkovensis*.

This biozone comprises an interval between the stratigraphically lowest occurrences of *Sk. lochkovensis* at the base and the lowest occurrences of *Wolynograptus bouceki*, index fossil of the next biozone, that define the top (Fig. 24). The *pridoliensis* Subzone characterized by common *Uncinatograptus pridoliensis* (Fig. 25H) and delineated by its lowest and highest occurrences,

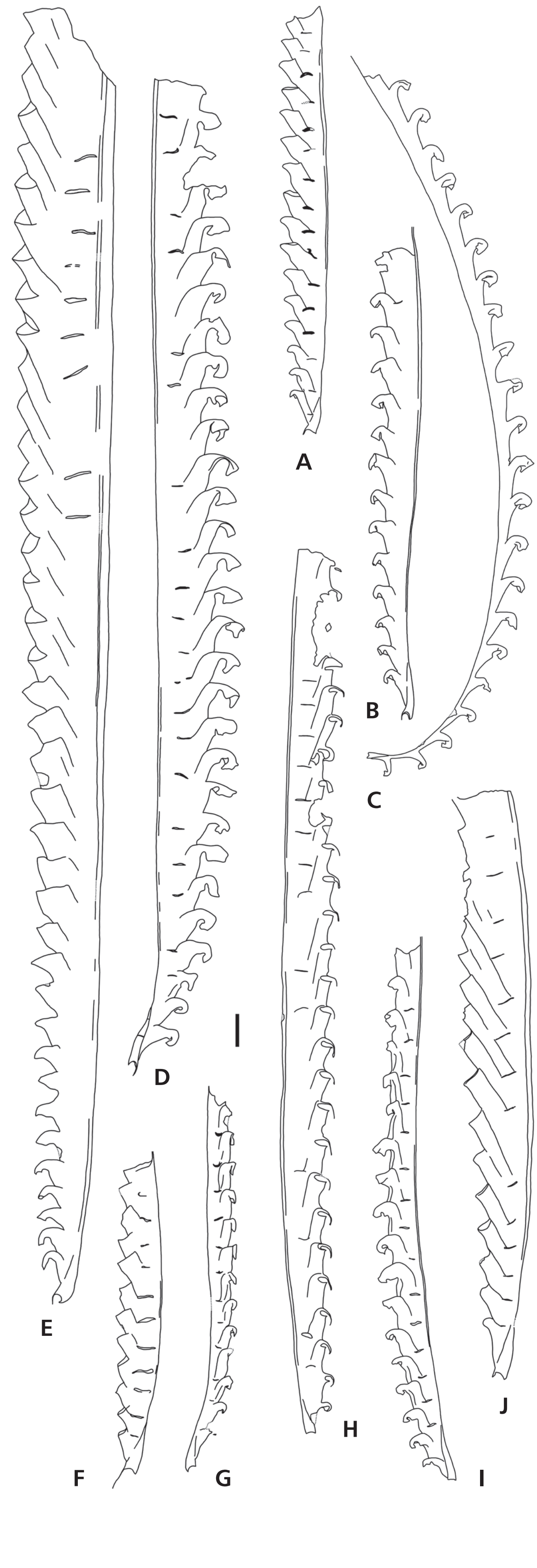


Figure 25. Age-diagnostic graptolites of the Přídolí Series. • A – *Skalograptus ultimus* (Perner), PŠ 4364, *parultimus–ultimus* Biozone. • B – *Wolynograptus*? *hornyi* (Jaeger), HJ059, *lochkovensis* Biozone. • C – *Formosograptus formosus* (Bouček), PŠ 4368, *parultimus–ultimus* Biozone. • D – *Wolynograptus bouceki* (Přibyl), PŠ 4365, *bouceki* Biozone. • E – *Skalograptus lochkovensis* (Přibyl), PŠ 4477, lower *bouceki* Biozone. • F – *Skalograptus parultimus* (Jaeger), PŠ 4418, lower *lochkovensis* Biozone. • G – *Slovinograptus beatus* (Koren'), PŠ 4411, upper *bouceki* Biozone. • H – *Uncinatograptus pridoliensis* (Přibyl), L62904a, *lochkovensis* Biozone. • I – *Wolynograptus perneri* (Bouček), BB 6995, *perneri* Biozone. • J – *Skalograptus transgrediens* (Perner), PŠ 4402, upper *bouceki* Biozone. A–C – Kosov quarry, 1st level; D–G, J – Radotín-Hvížďalka; H – Lochkov-Marble Quarry; J – Praha-Podolí, quarry. All figures × 5, scale bar represents 1 mm.

is recognized in the lower part of the biozone (Fig. 2). *Skalograptus lochkovensis* (Fig. 25E) and *U. pridoliensis* rarely occur together but the lowermost *Sk. lochkovensis* was found below the first *U. pridoliensis* in the Marble Quarry near Lochkov (Kříž *et al*. 1986). The lower part of the *lochkovensis* Biozone sees also the short-lived *Sk. branikensis* along with *Sk. parultimus*, *Sk. ultimus*? and the long-ranging *Prist*. ex. gr. *dubius*, *Sk. transgrediens* and *Lin. posthumus*. *Skalograptus branikensis* is known solely from Praha-Braník and Radotín-Hvížďalka (Kříž *et al*. 1986). *Wolynograptus*? *hornyi* (Fig. 25B) and *Skalograptus rectiformis* appear in the upper part of the *lochkovensis* Biozone.

The *lochkovensis* Biozone was first recognized in Marble Quarry near Lochkov (Přibyl 1940b). The middle and upper part, 4.4 m thick, is rich in graptolites at Radotín-Hvížďalka (Manda *et al*. 2023). Other verified records of the *lochkovensis* Biozone are from Žákův Quarry in Velká Chuchle-Přídolí, Praha-Podolí (former quarry above swimming pool), Praha-Braník, Na Požárech quarry near Řeporyje and Kosov quarry (Přibyl 1940b, Kříž *et al*. 1986). The *pridoliensis* Subzone, at least 5 m thick, is particularly well-represented in platy limestones, with shaly intercalations, exposed in the uppermost level of Kosov quarry (Kříž *et al.* 1986).

Wolynograptus bouceki Biozone

The *bouceki* Biozone is one of the earliest erected and most widely recognized biozones of the upper Silurian graptolite biozonal scheme. It was established by Přibyl (1940b) and further characterized by Přibyl (1983), Kříž *et al*. (1986) and Manda *et al*. (2023). The upper part of the biozone is marked by local occurrences of *Slovinograptus beatus*, which occurs at a closely similar stratigraphical level in the Austrian Carnic Alps (Jaeger *in* Kříž *et al*. 1986), in northwestern China (Ni *et al*. 1998), and most likely also in French Montagne Noire, therein referred as *Monograptus microdon* (see Piçarra *et al*. 1998 for discussion). The *beatus* band, recognized in the upper part of *bouceki* Biozone by Kříž *et al*. (1986), has been upgraded to subzone status in the proposed biozonal scheme (Fig. 2). The *bouceki* Biozone has been adopted in graptolite biozonal schemes of the East European Platform (Teller 1997), Central Asia (Koren' 1983, Koren' & Suyarkova 1997), northwestern China (Ni *et al*. 1998), Arctic Canada (Lenz & Kozłowska-Dawidziuk 2004), Australia (Rickards & Wright 1999), and in the standard charts of Loydell (2012) and Melchin *et al*. (2020).

Manda *et al*. (2023) defined the *bouceki* Biozone as an interval between the stratigraphically lowest occurrence of the biozonal index species and the lowest occurrence of *Wolynograptus perneri* (Fig. 24). *Wolynograptus bouceki* (Fig. 25D) appears in abundance in the lower part of the biozone, in association with the long-ranging *Lin. posthumus*, *Sk. transgrediens*, *Sk. rectiformis*, rare *Prist*. *dubius* s.l., and the highest occurrences of *Sk. lochkovensis*. Kříž *et al*. (1986) reported also *W*.? *hornyi*, continuing from the underlying biozone. Graptolites became generally less common in the upper part of the biozone. There the biozonal index species is accompanied by *Lin. posthumus* and *Sk. transgrediens.* The uppermost part of the *bouceki* Biozone is marked by the tiny *Skalograptus* sp. A. and common occurrences of *Slov. beatus* (Fig. 25G), identified in the Radotín-Hvížďalka and Lochkov-Marble Quarry sections.

A reference section of a more than 9.4 m thick *bouceki* Biozone, developed in typical facies of interbedded calcareous shales and platy limestones, is exposed along the local service road in the working area of Hvížďalka quarry near Radotín (Horný 1962, Kříž *et al*. 1986, Manda *et al*. 2023). Other sections through the *bouceki* Biozone are known from Marble Quarry near Lochkov (Přibyl 1940b), the former quarry above the swimming pool in Praha-Podolí (Přibyl 1943a), Žákův Quarry in Velká Chuchle-Přídolí (Přibyl 1983), and Čertovy schody near the Tmaň-exposure behind VČS headquarters (Kříž *et al.* 1986). The lower part of this interval is well exposed in the uppermost (1st) level of Kosov quarry near Beroun (Kříž *et al*. 1986).

Wolynograptus perneri Biozone

The *perneri* Biozone, established by Přibyl (1940b), was briefly characterized by Přibyl (1983). Outside of the Prague Synform, the *perneri* Biozone was identified in the Montagne Noire (Feist 1978), Poland (Teller 1997), Ukraine (Tsegelnyuk 1976), and Tien Shan (Rinenberg 1985).

The base of the *perneri* Biozone sees the incoming of the biozone index graptolite, which is restricted to this biozone, *i.e.* the top is defined by its stratigraphically highest occurrence (Fig. 24). The biozone index *W. perneri* (Fig. 25I) is particularly abundant on some bedding planes. Rare *W. bouceki* continued from the previous biozone in association with the long-ranging *Sk. transgrediens* and *Lin. posthumus*. In the Hvížďalka section, *Skalograptus* sp. A. persisted into the lower *perneri* Biozone. The presence of "*Formosograptus* sp.n.", reported by Bouček (1932b) and Přibyl (1983), has not been verified by subsequent studies.

Calcareous shales of the 2–3 m thick *perneri* Biozone alternate with platy micritic limestones. The best exposures were recorded by Bouček (1932b) and Přibyl (1940b, 1943a) in the former quarry at Praha-Podolí, Marble Quarry near Lochkov, and Žákův Quarry in Přídolí near

Velká Chuchle. Horný (1962) recognized the *perneri* Biozone in the Radotín-Hvížďalka section.

Skalograptus transgrediens Biozone

The upper Přídolí is marked in the Prague Synform by very low species richness and a low abundance of planktic graptolites despite favourable facies with alternating black shales and platy micritic limestones. The *transgrediens* Biozone was first mentioned by Perner & Kodym (1919) based on apparent misidentification of the index species. A correct *transgrediens* Biozone was recognized by Přibyl (1940b) in the upper Přídolí and since then widely applied in both the Prague Synform (*e.g.* Chlupáč *et al*. 1972, Přibyl 1983, Kříž *et al*. 1986) and world-wide (Loydell 2012, Melchin *et al*. 2020). The lower limit was usually identified only tentatively beyond the best graptolite-bearing sections due to the limited occurrence of *W. perneri* in the otherwise monotonous, low-diversity assemblages of stratigraphically persistent species of little stratigraphical value.

The base of this interval biozone is delineated by the disappearance of *W. perneri*, because the name giving *Sk. transgrediens* (Fig. 25J) appears as low as the lowermost *lochkovensis* Biozone. The top is defined by the incoming basal Devonian marker species, *Uncinatograptus uniformis*. The *transgrediens* Biozone therefore corresponds to an interregnum in the sense of Jaeger (1959), Rickards (1995), and Zalasiewicz *et al*. (2009). The long-ranging *Lin. posthumus* and *Prist. dubius* s.l. are the only other species recorded in this biozone in the Prague Synform.

No complete section of this more than 10 m thick unit has been studied in detail. The best exposures are known from the former quarry at Praha-Podolí (Přibyl 1943a), Budňany Rock in Karlštejn, Marble Quarry near Lochkov and Žákův Quarry in Přídolí near Velká Chuchle. The upper part of the biozone has been documented along with the Silurian–Devonian boundary at Klonk near Suchomasty, Čertovy schody near Tmaň, Karlštejn-Budňany Rock, Radotín-U topolů, and Antipleura Gorge, Praha-Podolí by Chlupáč *et al*. (1972) and Kříž (1992).

Graptolite faunal dynamics and extinction events

Early Silurian graptolite radiation and morphological innovation

The lower Rhuddanian black shales of the *ascensus* and *acuminatus* biozones yield in the Prague Synform moderately diverse assemblages of biserial graptolites dominated by the genera *Neodiplograptus*, *Normalograptus*, *Akidograptus* and *Parakidograptus* in association with the earliest *Glyptograptus*, *Cystograptus*, *Korenograptus* and *Rickardsograptus*. The earliest uniserial monograptids (Rickards & Hutt 1970, Li 1990) are missing in the lower Rhuddanian of the Prague Basin and elsewhere in peri-Gondwanan Europe and also the subsequent early diversification of uniserial monograptids cannot be traced in the Prague Synform due to a stratigraphical gap. The record recommences in the upper part of the *vesiculosus* Biozone with bedding plane assemblages marked by radiating monograptids (*Atavograptus* and *Huttagraptus*), but still dominated by diverse biserials (*Normalograptus*, *Paraclimacograptus*, *Cystograptus*, *Rickardsograptus*, *Korenograptus*, and the lowermost *Metaclimacograptus* in Bohemia) and the uni-biserial *Bulmanograptus* and *Dimorphograptus*. The lowermost *Rhaphidograptus* and ancorate *Pseudorthograptus* appear near the base of the upper Rhuddanian *cyphus* Biozone. Patterns of gross upward change in overall composition of Rhuddanian graptolite faunas observed in the Prague Synform roughly correspond with patterns recorded by Zalasiewicz & Tunnicliff (1994) in central Wales. A marked change demonstrated by proliferation of uni-biserial and uniserial taxa took place at the base of the British *acinaces* Biozone which matches the upper *vesiculosus* Biozone preserved in the Prague Synform.

Biserial and uni-biserial graptolites continue to be important in the upper Rhuddanian, but *Normalograptus* become heavily outnumbered by *Rh. toernquisti*. Ancorate rhabdosomes of *Pseudorthograptus* are accompanied by abundant and robust *Nd. fezzanensis*. Monograptids further diversified, proliferated, and for the first time predominate in the *cyphus* Biozone, being represented by the genera *Atavograptus*, *Huttagraptus*, *Coronograptus*, *Pribylograptus* and *Pernerograptus*.

The mean standing diversity (MSD) exhibits slight decrease in the upper *acuminatus* Biozone and then prominent rising trend (Fig. 26) moderated, in part, by a significant share of short-lived species in the *vesiculosus* and *cyphus* biozones. The number of species per biozone increase from 9 in the *ascensus* Biozone, through temporary decrease in the upper *acuminatus* Biozone, to the maximum Rhuddanian diversity of 39 recorded in the *cyphus* Biozone (Fig. 7). The time-normalized rate of origination (TNOR) shows considerable fluctuation, with a maximum in preserved part of the *vesiculosus* Biozone driven by intense speciation among both biserial taxa and uniserial monograptids. The *acuminatus* and, less so, *cyphus* Biozone is marked by a FADs/LADs ratio below 1 but species richness per biozone and MSD retain a positive trend owing to the increasing number of stratigraphically long-ranging species.

Biserial and uni-biserial graptoloid genera, which continued into the lower Aeronian include the prolific *Rhaphidograptus*, along with *Metaclimacograptus*, *Neodiplograptus*, *Glyptograptus*, and rare *Normalograptus*. *Pseudorthograptus* is replaced by *Petalolithus* in the lower Aeronian *triangulatus* Biozone. *Rhaphidograptus* vanished from the fossil record and the first undoubted retiolitine *Pseudoretiolites* appeared in the *simulans* Biozone. Early Aeronian monograptid diversification gave rise to the earliest *Pristiograptus* and several prominent, stratigraphically important genera characterized by isolated, triangular or parallel-sided tubular metathecae with hooked, and usually transversely extended apertures (*Demirastrites*, *Rastrites*, *Campograptus*), whereas *Pernerograptus*, with its biform thecae, declined. The species richness per biozone slightly decreased in the early Aeronian but both MSD, time-normalized extinction rate (TNER), TNOR and FADs/LADs ratio were steady with minimal fluctuations as shown by Fig. 26.

Mid-Aeronian diversity maximum and late Aeronian *sedgwickii* extinction Event

Maximum mean standing diversity, species richness (Figs 7 and 26) and high morphological disparity were attained in the Prague Basin in the mid-Aeronian in a similar manner as in global diversity analyses conducted by Cooper *et al*. (2014). *Petalolithus* gave origin to *Cephalograptus* (Rickards *et al*. 1977). *Rickardsograptus*, *Metaclimacograptus*, *Pseudoretiolites* and *Rivagraptus* proliferated, whereas single species remained of *Normalograptus* and *Pseudorthograptus*. Monograptids further flourished and diversified in the *folium* and *convolutus* biozones, to produce a much wider variety of colony shape and thecal design. In addition to the abundant *Rastrites*, *Pernerograptus* of the *limatulus* group, *Campograptus* and the last *Demirastrites*, new monograptid genera appeared, such as *Monoclimacis*, *Diversograptus*, the spiraliform *Lituigraptus*, *Torquigraptus* and, with reservation, *Spirograptus* (*S.*? *mirus* Perner). In the Prague Synform, the main MSD spike of 31 is confined to the *folium* Biozone (Figs 7 and 26); maximum species richness has been recorded from the *convolutus* Biozone (43 species). The graptolite assemblage of the *convolutus* Biozone is notable for its high proportion of short-lived species and remarkable number of graptolite last occurrences in the upper part of this interval. Also the time-normalized extinction rate (TNER) rose and FADs/LADs ratio dropped to 0.58 in the *convolutus* Biozone. The species diversity dropped markedly in the upper *convolutus* Biozone, a first sign of the world-wide recorded graptolite crisis.

The late Aeronian interval begins with the globally recognized *sedgwickii* mass-extinction event (Melchin *et al*. 1998), originally named the *convolutus* Event by Štorch (1995a). The high-diversity and low-dominance graptoloid fauna of the *convolutus* Biozone was replaced by a low-diversity and high-dominance fauna (Štorch & Frýda 2012), which is also of low abundance in the lower part of the *sedgwickii* Biozone. *Rivagraptus*, *Neodiplograptus*, *Pseudorthograptus* and *Pernerograptus* vanished from the fossil record. *Petalolithus* was replaced by *Parapetalolithus* in the upper *sedgwickii* Biozone, which hosts also the short-lived *Com. barbatus*. *Normalograptus* and *Cephalograptus* reached high into the *rastrum* Biozone, *Lituigraptus* vanished at the top. Rastritids of the *longispinus* group declined to be subsequently replaced by rastritids of the *linnaei* group. *Campograptus* was replaced by *Stimulograptus* in the lower *sedgwickii* Biozone. *Pristiograptus* proliferated and further diversified. Also dorsally coiled and spiraliform rhabdosomes of the genus *Torquigraptus* underwent major radiation in association with the first undoubted *Spirograptus*. A surprisingly short duration of the combined *sedgwickii* and *rastrum* biozones (0.22 Myr) is deduced from the very short time interval (less than 0.3 Myr) spanned by the combined *sedgwickii* and *halli* biozones in Melchin *et al*. (2020). However, usual relative thickness and lithology of strata corresponding with the two biozones in the sections studied in Bohemia (Štorch & Frýda 2012) and elsewhere (Loydell 1991, Loydell *et al*. 2015) appear to represent a longer period of time. Species richness and, in particular, MSD fell sharply in this interval of high faunal turnover marked by highly elevated TNER and only slightly lower TNOR (Fig. 26).

Ambiguous Telychian diversity high

The early Telychian graptolite record, although limited to subordinate black shale intercalations between predominant pale-coloured mudstones barren of graptolites, has both abundant graptolites and is rich in species. *Parapetalolithus* is still common and relatively diverse in the lowermost Telychian *linnaei* Biozone, but other biserial taxa, including *Metaclimacograptus*, *Glyptograptus* and *Pseudoretiolites*, further declined in this level and did not continue in the subsequent black shale strata referred to the upper *turriculatus* Biozone. The first *Pseudoplegmatograptus* and also *Cochlograptus* made their lowest occurrences in the *crispus* Biozone. Diverse monograptids are primarily represented by the genera *Pristiograptus*, *Monograptus*, *Stimulograptus*, *Streptograptus*, *Torquigraptus*, *Oktavites*, *Spirograptus*, and *Rastrites.* The last two taxa vanished in the *crispus* Biozone, although one specimen probably of *R. distans* is known from the *griestoniensis* Biozone of the pipeline trench section near Velká Ohrada. There are 31 graptolite

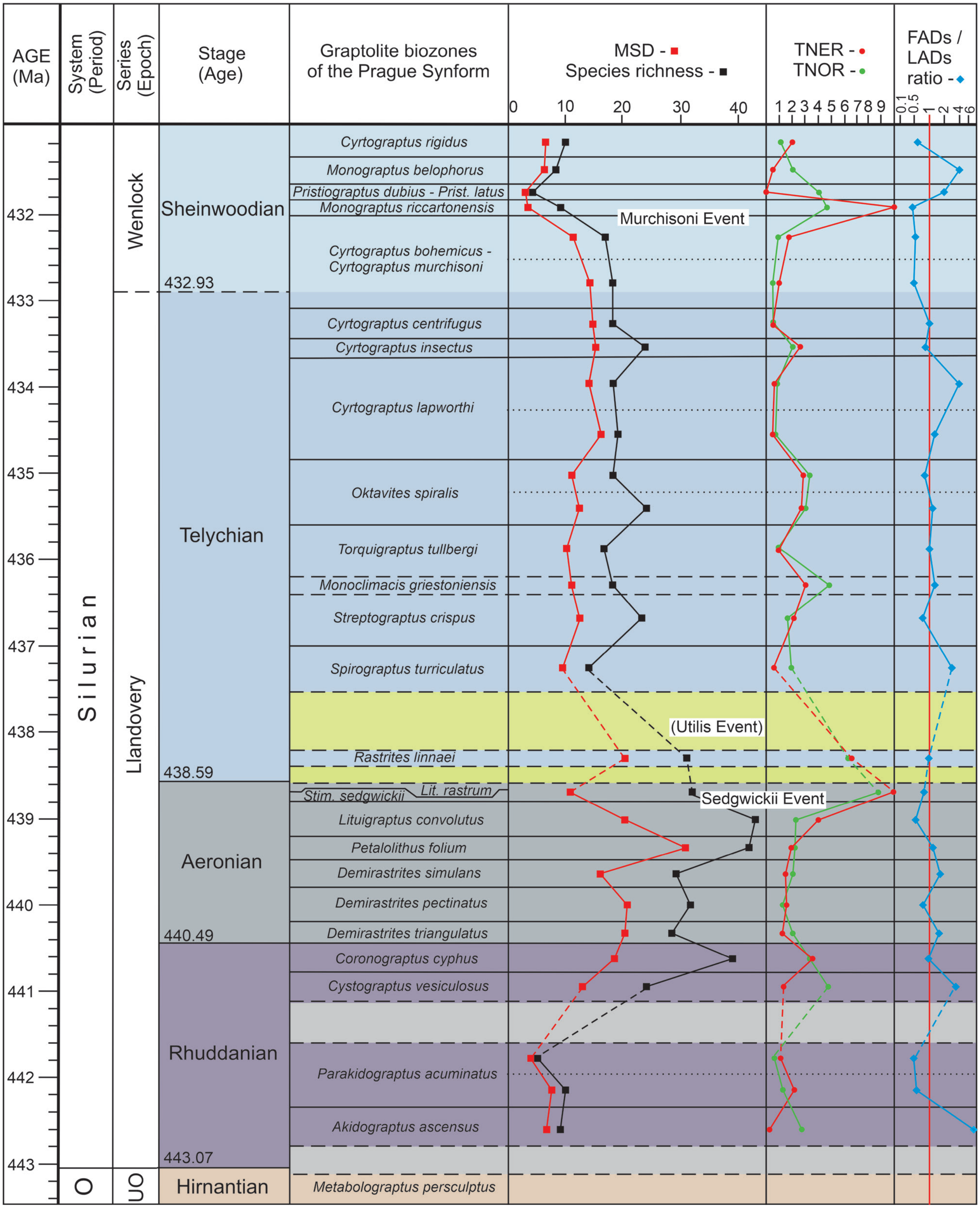


Figure 26. Silurian graptolite biozonal scheme of the Prague Synform plotted with species richness per biozone, mean standing diversity (MSD), time-normalized origination and extinctions rates (TNOR and TNER), FADs/LADs ratio, and globally recognized graptolite extinction events. Dashed horizontal lines mark tentative delineation of zonal boundaries. Dotted horizontal lines indicate subdivision of particularly long biozones into two or three subintervals of equal duration. Basin-wide gaps in the Rhuddanian stratigraphical record are marked by a light grey colour. Major layers of pale-coloured, non-fossiliferous lower Telychian mudstones deposited during a significant time interval are marked by yellow-green colour.

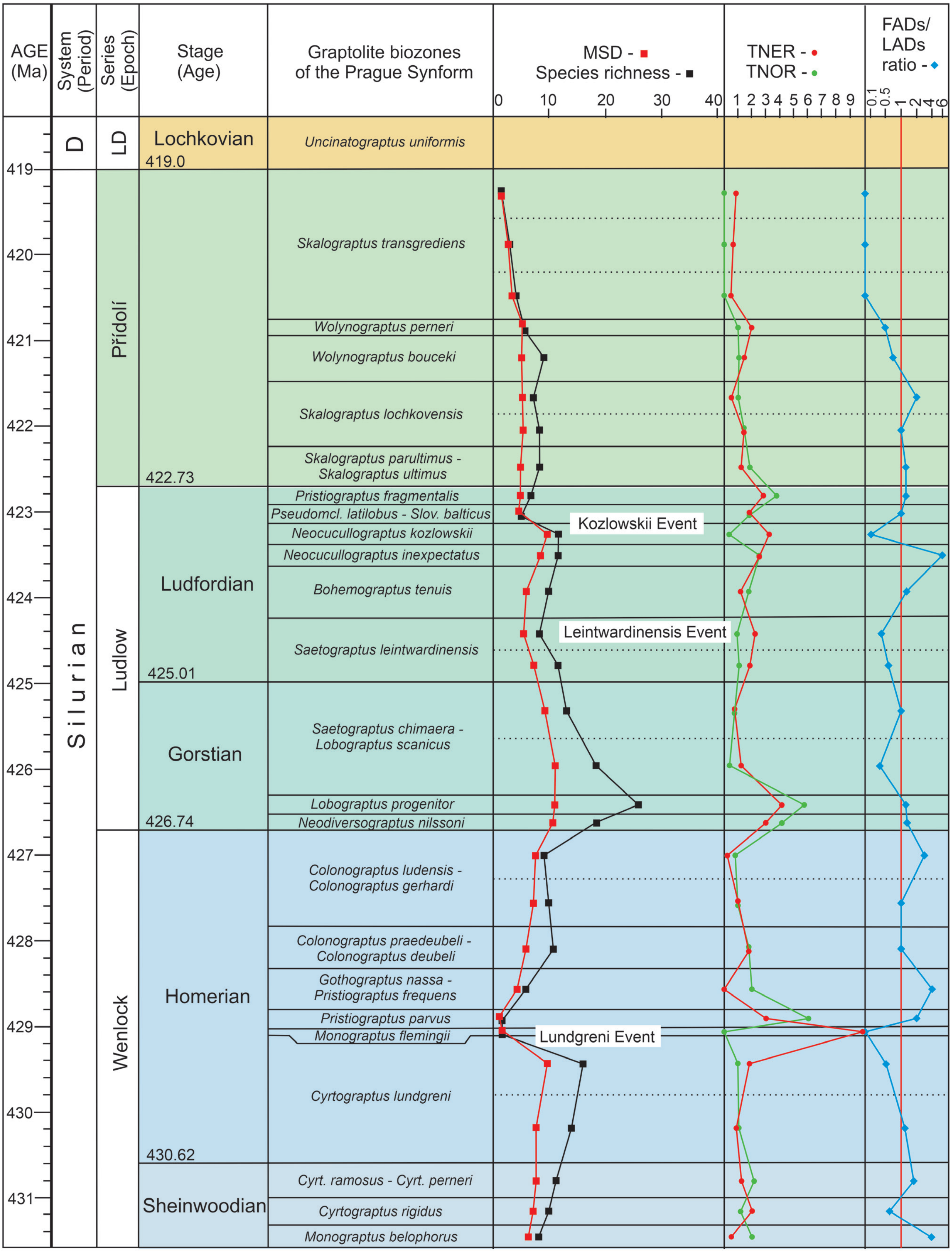


Figure 26. Continued.

species recorded in the short time interval represented by the black shales of the *linnaei* Biozone tentatively correlatable with the upper, but not the uppermost, *guerichi* Biozone of Loydell (1991). The MSD rose to 20.6, lower TNOR and TNER values indicate decreased faunal turnover, and the FADs/LADs ratio is almost neutral (0.96). The intermittent graptolite record in the lower Telychian of the Prague Synform makes high-resolution correlation with more complete records abroad (Loydell 1991, Zalasiewicz 1994, Loydell *et al.* 2015) very difficult. The *utilis* graptolite extinction Event distinguished by Loydell (1994) in the uppermost *guerichi* Biozone is not observed in the Prague Synform because the uppermost *guerichi* and lower and middle *turriculatus* biozones are developed as graptolite-barren mudstones. The effect of this event, however, manifested by the reduced graptolite diversity in the upper *turriculatus* Biozone of the Prague Synform is obvious. Species richness declined to 14 and MSD to 9.5 in the *turriculatus* Biozone. Also, faunal turover recorded in the black-shale facies of the post-*utilis* part of the *turriculatus* Biozone is low, as shown by low TNOR and TNER, though significant recovery of the graptolite fauna after the *utilis* Event can be inferred from the high FADs/LADs score.

The mid-Telychian fauna, although less well-known from section logs in the Prague Synform, is rich and dominated by diverse uniserial monograptids: *Monograptus* and *Monoclimacis* with largely straight rhabdosomes, tightly ventrally coiled *Coch. veles*, mostly ventrally curved species of *Streptograptus*, and spiraliform *Torquigraptus* and *Oktavites*. *Lapworthograptus*, *Cultellograptus*, and common, multi-stiped *Diversograptus* appear in the *spiralis* Biozone. Biserial taxa are represented by the last surviving species of *Parapetalolithus* and abundant retiolitines, mostly *Pseudoplegmatograptus* and *Retiolites*. Rare *Giganteograptus* and *Stomatograptus* appear in the upper *spiralis* Biozone. The mean standing diversity (MSD) remained steady from the lower Telychian *turriculatus* Biozone to the lowermost Sheinwoodian *bohemicus–murchisoni* Biozone despite unequal duration of the respective time intervals. Species richness per biozone fluctuated moderately, with a maximum of 24 species attained in the lower *spiralis* Biozone marked by an elevated proportion of short-lived taxa (if compared with supposed duration of the biozone, Figs 7 and 14). The complex interplay between the generally low time-normalized origination and extinction rates (TNOR and TNER) resulted in a steady evolutionary regime with an increasing proportion of long-ranging species, with the *griestoniensis* and *spiralis* biozones being intervals of elevated faunal turnover (Fig. 26). Both diversity and MSD may actually be higher in the middle Telychian biozones since the present estimates arose from somewhat limited data that do not allow for truly high-resolution correlation with the time-calibrated biozonal scheme of the *Geologic Time Scale 2020* (Melchin *et al.* 2020), which is also based on a relatively limited data set.

Late Telychian diversification, early Sheinwoodian *murchisoni* Event, and late Sheinwoodian recovery

The late Telychian graptolite fauna is marked by proliferation and diversification of *Cyrtograptus* and the newly appeared *Mediograptus* associated with abundant, for the most part long-ranging *Retiolites*, *Monograptus* and *Monoclimacis*. Also *Barrandeograptus* is common, whereas rare *Giganteograptus* disappeared in the latest Telychian. Mean standing diversity remained steady up to the lower *bohemicus–murchisoni* Biozone. Species richness ranges between 17 and 19 with a peak value of 24 in the *insectus* Biozone. This upper Telychian to lowermost Sheinwoodian fauna collapsed in the *firmus* Subzone of the *bohemicus–murchisoni* Biozone. *Retiolites*, *Barrandeograptus* and *Euroclimacis* became extinct in the Prague Basin, *Pseudoplectograptus*, *Cyrtograptus*, *Monoclimacis*, *Mediograptus* and *Pseudoplectograptus* temporarily vanished from the fossil record and also *Monograptus* was nearly eradicated (Štorch 1995b). The much depleted post-extinction fauna of the *riccartonensis* Biozone is represented by proliferating *Prist. dubius*, abundant *M. riccartonensis* and a few rare taxa (*M. solitarius* and *Pseudoplegm. wenlockianus*). Both the *Monograptus priodon* lineage and monoclimacids temporarily disappeared from the fossil record in the middle Sheinwoodian interregnum of the *dubius–latus* Biozone when faunal diversity dropped to 4 species. A sharp decline in both MSD and species richness, associated with a peak TNER recorded in the *riccartonensis* Biozone, is ascribed to the *murchisoni* extinction Event of Melchin *et al.* (1998). FADs/LADs ratio fell to 0.5 in the *riccartonensis* Biozone. The elevated TNOR that accompanied the major TNER spike accounts for the rapid change in the fauna. Mid-Sheinwoodian rediversification sees the incoming of *Med. antennularius*, *M. belophorus*, *Sokolovograptus* and reappearing *Monoclimacis*. Both MSD and species richness rose again in the *belophorus* Biozone. The late Sheinwoodian graptolite fauna is marked by new diversification of *Cyrtograptus* in association with abundant and large rhabdosomes of low-diversity *Pristiograptus*, *Monograptus*, *Monoclimacis* and *Streptograptus*. Species richness per biozone and MSD were increasing towards the lower Homerian maximum, whereas the interplay between origination and extinction rates, along with FADs/LADs ratio, account for slightly varying evolutionary regime (Fig. 26) in the mid and late Sheinwoodian time interval.

Early Homerian diversity high, mid-Homerian *lundgreni* Event and late Homerian recovery

The gradual rediversification of the late Sheinwoodian culminated in the upper part of the lower Homerian *lundgreni* Biozone with MSD 8.7 comprising 11 monograptid species and 5 retiolitines. Phylogenetic radiation can be traced in *Monograptus* and, in particular, in *Cyrtograptus*, which is represented by 8 species in a combined *lundgreni* Biozone. *Monoclimacis* and *Pristiograptus* continued, each represented by a single species, not counting *Pristiograptus lodenicensis* Přibyl, 1943b, which has not been recorded beyond its type, no longer available locality. The short-ranging *Testograptus* is confined to the *testis* Subzone. Mean standing diversity is still relatively low due to the high proportion of short lived species immediately preceding the mid-Homerian graptolite crisis. The early Homerian fauna was almost completely eradicated by the globally recorded mass extinction called the *lundgreni* Event by Koren' (1987) and "Big-crisis" by Jaeger (1991). In the Prague Synform, Manda *et al*. (2019) recognized three successive phases of this mid-Homerian mass extinction. The first phase is marked by a rapid increase in the relative abundance of long-ranging generalists, the appearance of some short-lived species and the disappearance of some other species in the upper *lundgreni* Biozone. This scenario continued with serial extinctions of other specialized and short-lived species in the uppermost *lundgreni* Biozone and resulted in the high-dominance/low-diversity assemblage of the *flemingii* Biozone with two, albeit abundant, surviving species. The ultimate phase resulted in the extermination of *Monograptus* and the apparent Lilliput Effect (Urbanek 1993) on *Pristiograptus*, which left the small *Prist. parvus* as the only local survivor of the *lundgreni* Event. The extinction peaked in the short-lived *flemingii* Biozone with a TNER value of 10 and TNOR falling to zero (Fig. 26).

The early part of the late Homerian witnessed the survival of very few graptoloids, succeeded by a rather slow but prominent recovery (Fig. 26) of this unique clonal macroplankton. The retiolitine *Goth. nassa* joined *Prist. parvus* in the upper *parvus* Biozone, but low-diversity and high-dominance assemblages, indicating stressful environmental conditions, continued. Incipient recovery is indicated by the immigration of normal-sized *Pristiograptus*, and the re-diversification of retiolitines commenced in the overlying *nassa–frequens* Biozone. The low diversity graptolite assemblage of this biozone comprises two species of *Pristiograptus* and the retiolitines *Gothograptu*s, *Semigothograptus*, the earliest *Plectograptus*? and *Spinograptus*. Time-normalized origination and extinctions rates (TNOR and TNER) remain low, but MSD rose through the whole upper Homerian, from 1.5 in the *parvus* Biozone, to 7.6 in the upper part of divided *ludensis–gerhardi* Biozone. The significant morphological novelties of the early colonograptids appeared in moderately diverse graptolite fauna of the *praedeubeli–deubeli* Biozone, with 11 species referred to the monograptid genera *Pristiograptus* and *Colonograptus* and the retiolitine genera *Spinograptus*, *Plectograptus*, *Hoffmanigraptus*, and the stratigraphically highest *Gothograptus* and *Semigothograptus*. This new adaptive radiation of the planktic graptolites gave rise to a seemingly well-balanced, low-dominance assemblage of almost equal diversity in the uppermost Homerian *ludensis–gerhardi* Biozone (Manda *et al*. 2019). Seven species and two genera (*Bohemograptus* and *Neogothograptus*) have their lowest occurrences in the *ludensis–gerhardi* Biozone (Fig. 19). Major proliferation can be observed in *Colonograptus*.

Early Gorstian diversity high and late Gorstian decline

Rediversification of the planktic graptolites through the adaptive radiation that commenced in the late Homerian culminated in the lower Gorstian *nilssoni* and *progenitor* biozones. The MSD reached 11.0 in the *nilssoni* Biozone, 11.5 in the *progenitor* Biozone and 11.7 in the lower *chimaera–scanicus* Biozone. Summary species richness rose to 18 in the *nilssoni* Biozone and 26 in the *progenitor* Biozone (Figs 7 and 26). Retiolitine diversity (8) is only slightly less than that of monograptid species (10). *Neogothograptus*, *Colonograptus*, and *Bohemograptus* diversified and further proliferated; incoming genera include the retiolitine *Valentinagraptus* along with the monograptid *Uncinatograptus* and biform, both unipolar and bipolar *Neodiversograptus*. Spiny *Saetograptus* replaced *Colonograptus* in the lower part of the *progenitor* Biozone, *Neodiversograptus* vanished mid-biozone. Novel monograptid genera include also *Pseudomonoclimacis*, *Heisograptus*, *Crinitograptus* and *Lobograptus*. Monograptid species outnumber retiolitines 15 to 11 in the *progenitor* Biozone. The FADs/LADs ratio is slightly positive and elevated TNOR and also TNER indicate rapid faunal change (Fig. 26). The middle and upper Gorstian *chimaera–scanicus* Biozone is marked by further diversification and proliferation of *Saetograptus* and less so also of *Lobograptus* and *Bohemograptus* which gave rise to rare *Korenea*. However, *Heisograptus* and probably *Crinitograptus* became extinct along with *Plect. macilentus*, the last representative of the retiolitines. Slight but steady decrease in the MSD value commences in the upper *chimaera–scanicus* Biozone. The overall species richness declined significantly beginning with the lower part of the *chimaera–scanicus* Biozone. Also time-normalized origination and extinction rates and the FADs/LADs score declined in this long biozone. Decline in graptolite diversity continued in the lower Ludfordian as minimum MSD (5.7) and species richness (8) were recorded in the upper half of the *leintwardinensis* Biozone. *Saetograptus* is still common and most diverse (4 species). It is associated with *Pristiograptus*, *Pseudomonoclimacis*, *Bohemograptus*, *Cucullograptus* and last *Lobograptus*.

Modest early Ludfordian *leintwardinensis* Event and subsequent rediversification

The *leintwardinensis* extinction Event, distinguished by Koren' (1987), was identified by Štorch *et al*. (2014) at the end of *leintwardinensis* Biozone, at that time newly recognized in the Prague Synform. The extincton is confined to the formerly abundant and diversified genus *Saetograptus* shortly followed by *Cucullograptus*, but graptolites, in general, become much less common in the Prague Basin, even in relatively deep, shale-dominated offshore facies, by comparison with the rich early Silurian and Gorstian faunas. Štorch *et al*. (2014) regarded the *leintwardinensis* Event as an extended turnover of moderate diversity fauna rather than a true mass-extinction event. A weak effect of the so called *leintwardinensis* Event showed up also in analyses of Melchin *et al*. (1998) and Cooper *et al*. (2014). It is possible that some environmental changes or evolutionary events in other planktic groups accelerated biotic competition in the water column and graptolites were outcompeted by other pelagic macrofauna including myodocopid ostracods, phyllocarid crustaceans and thin-walled pelagic cephalopods to name organisms common in the associated fossil record (Štorch *et al*. 2014). In the Prague Synform the MSD decreased to 5.7 and species richness dropped to 8 species in the upper part of the *leintwardinensis* Biozone (Figs 7 and 26). The whole *leintwardinensis* Biozone is marked by elevated TNER and the FADs/LADs score well below 1. Species richness decreased to a minimum of 6 species in the lowermost *tenuis* Biozone (Fig. 22). The graptolite fauna of the middle and upper part of the *tenuis* Biozone interregnum comprises five long-ranging species of the genera *Pristiograptus*, *Pseudomonoclimacis* and *Bohemograptus*. Štorch *et al*. (2014) recorded also *Egregiograptus* and the short-lived *Boh. cornutus* in the upper part of this biozone. Subsequent rediversification resulted in the moderately diverse graptoloid fauna of the *inexpectatus* and *kozlowskii* biozones, which consists of 12 species per biozone, assigned to the genera *Pristiograptus*, *Pseudomonoclimacis*, *Bohemograptus*, *Polonograptus*, *Neocucullograptus* and *Linograptus*. The TNOR rose in the *inexpectatus* Biozone but further potential diversification of the graptolite fauna was interrupted in the upper *kozlowskii* Biozone by profound environmental disturbances and faunal mass-extinction (the *kozlowskii* Event) associated with sea-level drawdown and a relatively long-lasting and prominent positive $\delta^{13}C$ isotope excursion, presumably a reflection of the major environmental changes taking place (Lehnert *et al*. 2007, Frýda & Manda 2013).

Mid-Ludfordian *kozlowskii* Event and failed late Ludfordian recovery

The mid-Ludfordian *kozlowskii* mass-extinction Event, distinguished by Urbanek (1993) and Melchin *et al*. (1998), is marked in the Prague Synform by a sudden, almost simultaneous disappearance of all of the extant, dominant graptolites with ventrally curved rhabdosomes (the genera *Bohemograptus*, *Polonograptus* and *Neocucullograptus*) and minute *Pseudomcl. dalejensis* (Štorch 1995a, 1996; Manda *et al*. 2012). Three long-ranging generalist survivors belong to *Pristiograptus*, *Pseudomonoclimacis* and *Linograptus*. A sharp decline in the origination rate and peak in the extinction rate are further underlined by the very low FADs/LADs score as shown in Fig. 26. The upper Ludfordian succession sees a new extension of limestone or mixed limestone–shale sedimentation with erosional unconformities, gaps in sedimentation and local intraformational conglomerates (Manda *et al*. 2012). Graptolites became uncommon even in relatively offshore, shaly facies. Mean standing diversity fell to 4.6 in the *latilobus–balticus* Biozone and remained almost equally low up to the lower Přídolí *parultimus–ultimus* Biozone (Figs 7 and 26). Species richness rose a little, from 5 to 7 species per biozone in the course of late Ludfordian. A faunal assemblage comprising *Slovinograptus* in association with *Pseudomonoclimacis* and long-ranging *Pristiograptus* and *Linograptus* developed in the *latilobus–balticus* Biozone. However, some prominent late Ludfordian graptolite lineages known from the East European Platform and central Asia, such as that of *Wolynograptus acer–W. protospineus–W. spineus* (Tsegelnyuk 1976; Urbanek 1995, 1997), are missing in the Prague Synform and the appearance of the lowest *Formosograptus* is delayed into the upper(-most) *fragmentalis* Biozone.

Decline of Přídolí graptoloids

Origin of novel, but morphologically restricted fauna of the Přídolí Series coincided with a period of rising sea-level recorded, for instance, by Kříž (1991, 1998a) and Johnson (2006, 2010). The novel fauna of the *parultimus–ultimus* Biozone, comprises 8 species of the genera *Skalograptus*, *Pristiograptus*, *Formosograptus* and *Linograptus*. The middle Přídolí *bouceki* and *perneri* biozones are marked in the Prague Synform by abundant *Wolynograptus*, associated with *Pristiograptus*, *Skalograptus* and *Linograptus*. The MSD remains at rather uniform values (4.9–5.4) through the lower and middle Přídolí *parultimus–ultimus*, *lochkovensis*, *bouceki* and *perneri* biozones (Figs 7 and 26). Relatively well-balanced FADs/LADs ratio of the first three biozones fell to 0.5 in the last-named biozone (Fig. 26). The graptolite fauna of the upper Přídolí *transgrediens* Biozone is further reduced to the biozone index species, occasionally accompanied by the multicladial *Linograptus*. The middle Přídolí depletion of the graptolite fauna tentatively correlates with last occurrences of *W. perneri* that is markedly earlier than at the top of the *transgrediens* Biozone as indicated by Urbanek (1993). Minor increase of global graptolite diversity recorded by Cooper *et al*. (2014) in the Silurian–Devonian boundary interval is missing in the Prague Synform despite its black shale facies generally favoured by graptolites. More precise evaluation and timing of the late Přídolí graptolite evolutionary crisis will need further attention world-wide.

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References

Aïfa, T., Pruner, P., Chadima, M. & Štorch, P. 2007. Structural evolution of the Prague Synform (Czech Republic) during Silurian times: an AMS, rock magnetism, and palaeomagnetic study of the Svatý Jan pod Skalou dikes, 249–265. *In* Linnemann, U., Nance, R.D., Kraft, P. & Zulauf, G. (eds) *The Evolution of the Rheic Ocean: From Avalonian–Cadomian Active Margin to Alleghenian–Variscan Collision. Special Papers Geological Society of America 423*. DOI 10.1130/2007.2423(11)

Barca, S. & Jaeger, H. 1990. New geological and biostratigraphical data on the Silurian in SE-Sardinia. Close affinity with Thuringia. *Bolletino della Societá Geologica Italiana 108*, 101–117.

Barrande, J. 1846. *Notice préliminaire sur le système silurien du centre de la Bohême*. 44 pp. Leipzig. DOI 10.5962/bhl.title.9142

Barrande, J. 1850. *Graptolites de Bohême*. 74 pp. 4pls, Prague.

Barrande, J. 1852. *Système silurien du centre de la Bohême. Vol. I. Recherches paléontologiques I. Trilobites*. 935 pp. 51 pls, Prague & Paris. DOI 10.5962/bhl.title.14776

Barrande, J. 1861. *Défense des colonies. I. Groupe probatoire. La Colonie Haidinger, la Colonie Krejči, la Coulée Krejči.* 34 pp. Prague.

Barrande, J. 1862. *Défense des colonies. II. Incompabilité entre le systéme des plis et des la réalité des faites matériels.* 62 pp. Prague.

Barrande, J. 1865. *Défense des colonies. III. Étude générale sur nos étages G, H avec application spéciale aux environs de Hlubočepy, prés Prague*. 367 pp. Prague. DOI 10.1017/S0016756800167603

Barrande, J. 1870. *Défense des colonies. IV. Description de la Colonie d'Archiac; caractères genéraux des colonies dans les bassin Silurien de la Bohême.* 136 pp. Prague.

Barrande, J. 1881. *Défense des colonies. V. Apparition et réapparition en Angleterre et en Ecosse des espèces coloniales siluriennes de la Bohême.* 77 pp. Prague.

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. 1931a. Předběžná zpráva o některých nových druzích graptolitů z českého gotlandienu. *Věstník Státního geologického ústavu 7(3)*, 1–21.

Bouček, B. 1931b. Dva příspěvky k poznání paleontologie a stratigrafie graptolitových zón českého gotlandienu. *Věstník Státního geologického ústavu 7(2)*, 174–181.

Bouček, B. 1932a. Zpráva o nálezu zony *Cyrtograptus rigidus* Tullb. a jiných v českém gotlandienu. *Věstník Státního geologického ústavu 8(1)*, 85–98.

Bouček, B. 1932b. Předběžná zpráva o některých nových druzích graptolitů z českého gotlandienu (část II.). *Věstník Státního geologického ústavu 8(3)*, 150–155.

Bouček, B. 1933. Monographie der silurischen Graptolithen aus der Familie Cyrtograptidae. *Práce geologicko-paleontologického ústavu Karlovy university v Praze 1933(1)*, 1–84.

Bouček, B. 1934. Bemerkungen zur Stratigraphie des böhmischen Gotlandien und seinen Faziesverhältnissen. *Zentralblatt für Geologie und Paläontologie, Abt. B, 11*, 477–494.

Bouček, B. 1936. Graptolitová fauna českého spodního ludlowu. *Rozpravy České akademie věd a umění, Třída 2, 46(16)*, 1–26.

Bouček, B. 1937. Stratigrafie siluru v dalejském údolí u Prahy a v jeho nejbližším okolí. *Rozpravy České akademie věd a umění, Třída 2*, *46(27)*, 1–20.

Bouček, B. 1941. O novém odkryvu siluru u Lodenic. *Zprávy Geologického ústavu pro Čechy a Moravu 17(4)*, 165–172.

Bouček, B. 1944. O některých ostnitých diplograptidech českého a saského siluru. *Rozpravy České Akademie věd a umění, Třída 2, 53(2)*, 1–6.

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

Bouček, B. 1960. Einige Bemerkungen zur Entwicklung der Graptolithenfaunen in Mitteldeutschland und Böhmen. *Geologie 9*, 556–564.

Bouček, B. & Münch, A. 1944. Die Retioliten des mitteleuropaischen Llandovery und unteren Wenlock. *Rozpravy České Akademie věd a umění, Třída 2, 53(41)*, 1–54.

Bouček, B. & Münch, A. 1952. Retioliti středoevropského svrchního wenlocku a ludlowu. *Sborník Ústředního ústavu geologického, Oddíl paleontologický 19*, 1–54.

Bouček, B. & Přibyl, A. 1942a. O rodu *Petalolithus* Suess z českého siluru. *Rozpravy České akademie věd a umění, Třída 2, 51(11)*, 1–22.

Bouček, B. & Přibyl, A. 1942b. O Petalolithech ze skupiny *P. folium* (His.) a o rodu *Cephalograptus* Hopk. *Rozpravy České Akademie věd a umění, Třída 2, 51(26)*, 1–22.

Bouček, B. & Přibyl, A. 1943. O českých monograptech z podrodu *Streptograptus* Yin. *Rozpravy České Akademie věd a umění, Třída 2, 52(1)*, 1–23.

Bouček, B. & Přibyl, A. 1952a. Nové poznatky o cyrtograptidech z českého siluru a jejich stratigrafickém významu. *Rozpravy České Akademie věd a umění, Třída 2, 62(9)*, 1–24.

Bouček, B. & Přibyl, A. 1952b. O některých tenkých druzích rodu *Monograptus* Geinitz, zvláště z podrodů *Globosograptus* a *Mediograptus*. *Rozpravy České Akademie věd a umění, Třída 2, 61(13)*, 1–31.

Bouček, B. & Přibyl, A. 1953. O rodu *Diversograptus* Manck z českého siluru. *Sborník Ústředního ústavu geologického, Oddíl paleontologický 20*, 485–576. DOI 10.1115/1.4010752

Bouček, B., Mihajlovič, M. & Veselinovič, M. 1976. Graptolites of Upper Silurian and Lower Devonian of Zvonačka Banja (Eastern Yugoslavia). *Glas 2296 de l'Académie serbe des sciences et des arts, Classe des sciences mathematiques et naturelles 39*, 79–114.

Chlupáč, I. 1998. Devonian, 101–133. *In* Havlíček, V., Kříž, J., Kukal, Z. & Štorch, P. (eds) *Palaeozoic of the Barrandian (Cambrian to Devonian)*. Český geologický ústav, Praha.

Chlupáč, I. & Štorch, P. (eds) 1997. Zásady české stratigrafické klasifikace (3. vydání). *Bulletin of the Czech Geological Survey 72(2)*, 193–204.

Chlupáč, I., Jaeger, H. & Zikmundová, J. 1972. The Siluro-Devonian boundary in the Barrandian. *Bulletin of Canadian Petroleum Geology 20*, 104–174.

Chlupáč, I., Havlíček, V., Kříž, J., Kukal, Z. & Štorch, P. 1998. *Palaeozoic of the Barrandian (Cambrian to Devonian)*. 183 pp. Czech Geological Survey, Prague.

Cocks, L.R.M. & Torsvik, T.H. 2002. Earth geography from 500 to 400 million years ago: a faunal and paleomagnetic review. *Journal of the Geological Society 159*, 631–644. DOI 10.1144/0016-764901-118

Cocks, L.R.M. & Torsvik, T.H. 2006: European geography in a global context from the Vendian to the end of Palaeozoic. *In* Gee, D.G. & Stephenson, R.A. (eds) *European Lithosphere Dynamics*. *Geological Society London, Memoir 32*, 83–95. DOI 10.1144/GSL.MEM.2006.032.01.05

Cooper, R.A., Sadler, P.M., Munnecke, A. & Crampton, J.S. 2014. Graptoloid evolutionary rates track Ordovician–Silurian global climate change. *Geological Magazine 151*, 349–364. DOI 10.1017/S0016756813000198

Cramer, B.D., Brett, C.E., Melchin, M.J., Männik, P., Kleffner, M.A., McLaughlin, P.I. *et al*. 2011. Revised chronostratigraphic correlation of the Silurian System of North America with global and regional chronostratigraphic units and $\delta^{13}C_{carb}$ chemostratigraphy. *Lethaia*, *44*, 185–202. DOI 10.1111/j.1502-3931.2010.00234.x

Dufka, P., Kříž, J. & Štorch, P. 1995. Silurian graptolites and chitinozoans from the Uranium Industry boreholes drilled in 1968–1971 (Prague basin, Bohemia). *Bulletin of the Czech Geological Survey 70*, 5–13.

Ebbestad, J.O.R., Frýda, J., Wagner, P.J., Horný, R.J., Isakar, M., Stewart, S., Percival, I.G., Bertero, V., Rohr, D.M., Peel, J.S., Blodgett, R.B. & Högström, A.E.S. 2013. Biogeography of Ordovician and Silurian gastropods, monoplacophorans and mimospirids, 199–220. *In* Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic biogeography and palaeogeography*. *Geological Society London, Memoir 38*. DOI 10.1144/M38.15

Elles, G.L. 1900. The zonal classification of the Wenlock Series of the Welsh Borderland. *Quarterly Journal of the Geological Society of London 56*, 370–414. DOI 10.1144/GSL.JGS.1900.056.01-04.25

Elles, G.L. & Wood, E.M.R. 1911. A monograph of British graptolites, Part 8. *Monograph of the Palaeontographical Society 64(316)*, 359–414. DOI 10.1080/02693445.1911.12035554

Eriksson, M.E., Hints, O., Paxton, H. & Tonarová, P. 2013. Ordovician and Silurian polychaete diversity and biogeography, 265–272. *In* Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic biogeography and palaeogeography*. *European Lithosphere Dynamics*. *Geological Society London, Memoir 38*. DOI 10.1144/M38.18

Feist, R. 1978. Das Altpaläozoikum Südfrankreichs. *Österreichische Akademie der Wissenschaften, Schriftenreihe der erdwissenschaftlichen Komissionen 3*, 191–200. DOI 10.1007/978-3-7091-4468-8_15

Foote, M. 1994. Temporal variation in extinction risk and temporal scaling of extinction metrics. *Paleobiology 20*, 424–444. DOI 10.1017/S0094837300012914

Foote, M. 2000. Origination and extinction components of taxonomic diversity: General problems. *Paleobiology supplement 26*, 74–102. DOI 10.1017/S0094837300026890

Foote, M., Cooper, R.A., Crampton, J.S. & Sadler, P.M. 2018. Diversity-dependent evolutionary rates in early Palaeozoic zooplankton. *Proceedings of the Royal Society B, 285*, 1–8. DOI 10.1098/rspb.2018.0122

Frýda, J. & Frýdová, B. 2014. First evidence for the Homerian (late Wenlock, Silurian) positive carbon isotope excursion from peri-Gondwana: new data from the Barrandian (Perunica). *Bulletin of Geosciences 89*, 617–634. DOI 10.3140/bull.geosci.1493

Frýda, J. & Manda, Š. 2013. A long lasting steady period of isotopically heavy carbon in the late Silurian ocean: evolution of the $\delta^{13}C$ record and its significance for an integrated $\delta^{13}C$, graptolite and conodont stratigraphy. *Bulletin of Geosciences 88*, 463–482. DOI 10.3140/bull.geosci.1436

Fu, L.P., Zhang, Z.F. & Geng, L.G. 2000. The Most Complete Sequence of Telychian Graptolite Zones in the World. *Acta Geologica Sinica (English Edition) 74(2)*, 126–131. DOI 10.1111/j.1755-6724.2000.tb00439.x

Goldman, D., Maletz, J., Melchin, M.J. & Fan, J.X. 2013. Chapter 26 Graptolite palaeobiogeography. *Geological Society London, Memoir 38*, 415–428. DOI 10.1144/M38.26

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(1)*, 71–92. DOI 10.1017/S0016756897007802

Gutiérrez-Marco, J.C., Lenz, A.C., Robardet, M. & Piçarra, J.M. 1996. Wenlock-Ludlow graptolite biostratigraphy and extinction: a reassessment from the southwestern Iberian Peninsula (Spain and Portugal). *Canadian Journal of Earth Sciences 33*, 656–663. DOI 10.1139/e96-049

Hammer, Ø. & Harper, D.A.T. 2006. *Paleontological data analysis*. 351 pp. Blackwell Publishing. DOI 10.1002/9780470750711

Havlíček, V. 1981. Development of a linear sedimentary depression exemplified by the Prague Basin (Ordovician-Middle Devonian, Barrandian area – Central Bohemia). *Sborník geologických věd, Geologie 35*, 7–48.

Havlíček, V. & Kříž, J. 1973. Svrchní llandover a spodní devon u Hýskova (Barrandien). *Věstník Ústředního ústavu geologického 48*, 103–107.

Havlíček, V. & Marek, L. 1973. Bohemian Ordovician and its international correlation. *Časopis pro mineralogii a geologii 18*, 225–232.

Havlíček, V. & Štorch, P. 1990. Silurian brachiopods and benthic communities in the Prague Basin (Czechoslovakia). *Rozpravy Ústředního ústavu geologického 48*, 1–275.

Havlíček, V., Vaněk, J. & Fatka, O. 1994. Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic communities). *Sborník geologických věd, Geologie 46*, 23–56.

Holland, C.H. & Bassett, M.G. 1989. A Global Standard for the Silurian System. *National Museum of Wales Geological Series 10*, 1–325.

Holland, C.H. & Palmer, D.C. 1974. *Bohemograptus*, the youngest graptoloid known from the British Silurian sequence. *Special Papers in Palaeontology 13*, 215–236.

Horný, R. 1955. Studie o vrstvách budňanských v západní části Barrandienu. *Sborník Ústředního ústavu geologického, Oddíl geologický 21*, 315–447.

Horný, R. 1956. Zona *Akidograptus ascensus* v jižním křídle barrandienského siluru. *Věstník Ústředního ústavu geologického 31*, 62–69.

Horný, R. 1960. Stratigraphy and tectonics of the western closures of the Silurian–Devonian synclinorium in the Barrandian area. *Sborník Ústředního ústavu geologického 26*, 495–524.

Horný, R. 1962. Das mittelböhmische Silur. *Geologie 11(8)*, 873–916.

Horný, R., Prantl, F. & Vaněk, J. 1958. K otázce hranice mezi wenlockem a ludlowem v Barrandienu. *Sborník Ústředního ústavu geologického, Oddíl paleontologický 24*, 217–278.

Hutt, J. 1974. The Llandovery graptolites of the English Lake District, Part 1. *Palaeontographical Society Monographs 128(540)*, 1–56. DOI 10.1080/25761900.2022.12131726

Jaeger, H. 1959. Graptolithen und Stratigraphie des jüngsten Thüringer Silurs. *Abhandlungen der deutsch Akademie der Wissenschaften zu Berlin (Gem. Geol. Biol.) 1959(2)*, 1–197.

Jaeger, H. 1975. Die Graptolithenführung in Silur/Devon des Cellon-Profils (Karnische Alpen). *Carinthia II 165/185*, 111–126.

Jaeger, H. 1991. Neue Standard-Graptolithenzonenfolge nach der "Grossen Krise" an der Wenlock/Ludlow-Grenze (Silur). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 182*, 303–354. DOI 10.1127/njgpa/182/1991/303

Johnson, M.E. 2006. Relationship of Silurian sea-level fluctuations to oceanic episodes and events. *GFF 128*, 123–129. DOI 10.1080/11035890601282123

Johnson, M.E. 2010. Tracking Silurian eustasy: alignment of empirical evidence or pursuit of deductive reasoning? *Palaeogeography, Palaeoclimatology, Palaeoecology 296*, 276–284. DOI 10.1016/j.palaeo.2009.11.024

Jones, H., Zalasiewicz, J. & Rickards, R.B. 2002. Clingfilm preservation of spiraliform graptolites: Evidence of organically sealed Silurian seafloors. *Geology 30(4)*, 343–346. DOI 10.1130/0091-7613(2002)030<0343:CPOSGE>2.0.CO;2

Jones, O.T. & Pugh, W.J. 1916. The geology of the district around Machynlleth and the Llyfnant Valley. *Quarterly Journal oft he Geological Society of London 71*, 343–385. DOI 10.1144/GSL.JGS.1915.071.01-04.16

Kettner, R. & Bouček, B. 1936. *Tableaux synoptiques des formations du Barrandien*. Travaux de l'Institute géologique et paléontologique de l'Université Charles à Praha.

Kettner, R. & Kodym, O. 1919. Nová stratigrafie Barrandienu. *Časopis Musea Království českého 93*, 47–55.

Koren', T.N. 1983. New late Silurian monograptids from Kazakhstan. *Palaeontology 26*, 407–434.

Koren', T.N. 1986. Graptolites, 86–138. *In* Nikitin, I.F. & Bandaletov, S.M. (eds) *Balkhashski segment. Tokrauski gorizont verkhnego Silura*. Izd. Nauka Kazakhskoi SSR, Alma-Ata. [in Russian]

Koren', T.N. 1987. Graptolite dynamics in Silurian and Devonian time. *Bulletin of the Geological Society of Denmark 35*, 149–159. DOI 10.37570/bgsd-1986-35-16

Koren', T.N. 1991. The *lundgreni* Extinction Event in Central Asia and its bearing on graptolite biochronology within the Homerian. *Proceedings of the Estonian Academy of Sciences, Geology 40*, 74–78. DOI 10.3176/geol.1991.2.06

Koren', T.N. 1993. Osnovnye rubezhi v evolutsii ludlovskikh graptolitov. *Stratigrafia, Geologicheskaya korelatsia 1*, 44–52. [in Russian]

Koren', T.N. & Suyarkova, A.A. 1997. Late Ludlow and Pridoli monograptids from the Turkestan-Alai mountains, South Tien Shan. *Palaeontographica, Abt. A*, *247*, 59–90. DOI 10.1127/pala/247/1997/59

Koren', T.N. & Suyarkova, A.A. 2004. The Ludlow (Late Silurian) neocucullograptid fauna from the Southern Tien Shan, Kyrghizstan. *Alcheringa 28*, 333–387. DOI 10.1080/03115510408619287

Koren', T.N. & Suyarkova, A.A. 2007. Silurian graptolite biostratigraphy of the Kaliningrad District, Northwest Russia. *Acta Palaeontologica Sinica 46(suppl.)*, 232–236.

Koren', T.N., Lenz, A.C., Loydell, D.K., Melchin, M.J., Štorch, P. & Teller, L. 1996. Generalized graptolite zonal sequence defining Silurian time intervals for global palaeogeographic studies. *Lethaia 29*, 59–60. DOI 10.1111/j.1502-3931.1996.tb01837.x

Koren', T.N., Modzalevskaya, T.L. & Suyarkova, A.A. 2009. Regionalnaya stratigraficheskaya skhema silura Vostochno-Evropeiskoy Platformy. *Regionalnaya geologia i metallogenia 39*, 24–32. [in Russian]

Kozłowska, A. 2021. *Hoffmanigraptus* n. gen., a new retiolitine (Graptolithina), an early member of the *Plectograptus* lineage from the Silurian of Baltica, Poland. *Comptes Rendus Palevol 20(45)*, 931–939. DOI 10.5852/cr-palevol2021v20a46

Kozłowska-Dawidziuk, A., Lenz, A.C. & Štorch, P. 2001. Upper Wenlock and Lower Ludlow (Silurian) graptolites; Všeradice section, Barrandian area, Czech Republic. *Journal of Paleontology 75*, 147–164. DOI 10.1666/0022-3360(2001)075<0147:UWALLS>2.0.CO;2

Kříž, J. 1961. Průzkum zaniklé paleontologické lokality Joachima Barranda, označované jím jako "Butowitz". *Časopis pro mineralogii a geologii 6(2)*, 173–178.

Kříž, J. 1975. Revision of the Lower Silurian stratigraphy in central Bohemia. *Věstník Ústředního Ústavu geologického 50*, 275–283.

Kříž, J. 1989. The Přídolí Series in the Prague Basin (Barrandian area, Bohemia), 90–100. *In* Holland, C.H. & Bassett, M.G. (eds) *A global standard for the Silurian System*. *National Museum of Wales, Geological Series 9*.

Kříž, J. 1991. The Silurian of the Prague Basin (Bohemia) – tectonic, eustatic and volcanic controls on facies and faunal development, 179–203. *In* Bassett, M.G., Lane, P.D. & Edwards, D. (eds) *The Murchison Symposium: Proceedings of an international conference on the Silurian System*. *Special Papers in Palaeontology 44*.

Kříž, J. 1992. Silurian Field Excursions: Prague Basin (Barrandian), Bohemia. *National Museum Wales, Geological Series 13*, 1–111.

Kříž, J. 1998a. Silurian, 79–101. *In* Chlupáč, I., Havlíček, V., Kříž, J., Kukal, Z. & Štorch, P. (eds) *Paleozoic of the Barrandian (Cambrian to Devonian)*. Český geologický ústav, Praha.

Kříž, J. 1998b. Recurrent Silurian–Lowest Devonian Cephalopod Limestones of Gondwanan Europe and Perunica. *New York State Museum Bulletin 491*, 183–198.

Kříž J., Jaeger, H., Paris, F. & Schönlaub, H.P. 1986. Přídolí – the fourth subdivision of the Silurian. *Jahrbuch der Geologischen Bundesanstalt 129(2)*, 291–360.

Kříž, J., Dufka, P., Jaeger, H. & Schönlaub, H.P. 1993. The Wenlock/Ludlow Boundary in the Prague Basin (Bohemia). *Jahrbuch der Geologischen Bundesanstalt, Wien 136*, 809–839.

Kröger, B. 2013. Cambrian–Ordovician cephalopod palaeogeography and diversity, 429–448. *In* Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic biogeography and palaeogeography*. *Geological Society London, Memoir 38*. DOI 10.1144/M38.27

Krs, M. & Pruner, P. 1995. Palaeomagnetism and palaeogeography of the Variscan formations of the Bohemian Massif, comparison with other European regions. *Journal of Geosciences 40*, 3–46. DOI 10.1007/BF02295824

Krs, M. & Pruner, P. 1999. To the paleomagnetic investigations of paleogeography of the Barrandian Terrane, Bohemian Massif. *Acta Universitatis Carolinae, Geologica 43*, 519–522.

Krs, M., Pruner, P. & Man, O. 2001. Tectonic and palaeogeographic interpretation of the paleomagnetism of Variscan and pre-Variscan formations of the Bohemian Massif, with special reference to the Barrandian Terrane. *Tectonophysics 332*, 93–114. DOI 10.1016/S0040-1951(00)00251-1

Lapworth, C. 1878. The Moffat Series. *Quarterly Journal of the Geological Society of London 34*, 240–346. DOI 10.1144/GSL.JGS.1878.034.01-04.23

Lapworth, C. 1879–1880. The geological distribution of the Rhabdophora. *Annals and Magazine of Natural History, London 3* (1879), 245–257, 449–455; *4* (1879), 333–341, 423–431; *5* (1880), 45–62, 273–285, 358–369; *6* (1880), 16–29, 185–207.

Lapworth, H. 1900. The Silurian sequence of Rhayader. *Quarterly Journal of the Geological Society of London 56*, 67–137. DOI 10.1144/GSL.JGS.1900.056.01-04.09

Lehnert, O., Frýda, J., Buggisch, W., Munnecke, A., Nützel, A., Kříž, J. & Manda, Š. 2007. $\delta^{13}C$ records across the late Silurian Lau Event: new data from middle palaeo-latitudes of northern peri-Gondwana (Prague Basin, Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology 245*, 227–244. DOI 10.1016/j.palaeo.2006.02.022

Lenz, A.C. 1982. Llandoverian graptolites of the Northern Canadian Cordillera: *Petalograptus*, *Cephalograptus*, *Rhaphidograptus*, *Dimorphograptus*, Retiolitidae, and Monograptidae. *Life Sciences Contributions, Royal Ontario Museum 130*, 1–154. DOI 10.5962/bhl.title.60100

Lenz, A.C. 1995. Upper Homerian (Wenlock, Silurian) graptolites and graptolite biostratigraphy, Arctic Archipelago, Canada. *Canadian Journal of Earth Sciences 32*, 1378–1392. DOI 10.1139/e95-111

Lenz, A.C. & Kozłowska-Dawidziuk, A. 2002. Upper Homerian (upper Wenlock, Silurian) graptolites from Arctic Canada. *Journal of Paleontology 76*, 321–346. DOI 10.1666/0022-3360(2002)076<0321:UHUWSG>2.0.CO;2

Lenz, A.C. & Kozłowska-Dawidziuk, A. 2004. *Ludlow and Pridoli (Upper Silurian) graptolites from the Arctic Islands, Canada*. 141 pp. NRC Research Press, Ottawa, Canada. DOI 10.1139/9780660193267

Lenz, A.C. & Melchin, M.J. 1991. Wenlock (Silurian) graptolites, Cape Phillips Formation, Canadian Arctic Islands. *Transactions of the Royal Society of Edinburgh*, *Earth Sciences 82*, 211–237. DOI 10.1017/S0263593300005320

Lenz, A.C., Senior, S., Kozłowska, A. & Melchin, M.J. 2012. Graptolites from the mid Wenlock (Silurian), middle and upper Sheinwoodian, Arctic Canada. *Palaeontographica Canadiana 32*, 1–93.

Lenz, A.C., Bates, D.E.B., Kozłowska, A. & Maletz, J. 2018. Part V, Second Revision. Chapter 26: Family Retiolitidae: Introduction, morphology, and systematic descriptions. *Treatise Online 114*, 1–37. DOI 10.17161/to.v0i0.8249

Lenz, A.C., Noble, P.J., Masiak, M., Poulson, S.R. & Kozłowska, A. 2006. The *lundgreni* Extinction Event: integration of paleontological and geochemical data from Arctic Canada. *GFF 128*, 153–158. DOI 10.1080/11035890601282153

Li, J.J. 1990. Discovery of monograptids in basal part of Lower Silurian from S. Anhui with special reference to their origin. *Acta Palaeontologica Sinica 29*, 204–215. [in Chinese with English summary]

Libertín, M., Kvaček, J., Bek, J., Žárský, V. & Štorch, P. 2018. Sporophytes of early polysporangiate land plants from the early Silurian may have been photosynthetically autonomous. *Nature Plants 4*, 269–271. DOI 10.1038/s41477-018-0140-y

Linnemann, U., Romer, R.L., Gehmlich, M. & Drost, K. 2004. Paläogeographic und Provenance des Saxothuringikums unter besonderer Beachtung der Geochronologie von prävariszischen Zirkonen und der Nd-Isotopie von Sedimenten, 121–132. *In* Linnemann, U. (ed.) *Das Saxothuringikum: Abriss der präkambrischen und paläozoischen Geologie von Sachsen and Thüringen*. *Geologica Saxonica 48/49*.

Loydell, D.K. 1991. The biostratigraphy and formational relationships of the upper Aeronian and lower Telychian (Llandovery, Silurian) formations of western mid-Wales. *Geological Journal 26*, 209–244. DOI 10.1002/gj.3350260304

Loydell, D.K. 1992. Upper Aeronian and lower Telychian graptolites from western mid-Wales, Part 1. *Palaeontographical Society Monograph 146(589)*, 1–55. DOI 10.1080/25761900.2022.12131772

Loydell, D.K. 1994. Early Telychian changes in graptoloid diversity and sea level. *Geological Journal 29*, 355–368. DOI 10.1002/gj.3350290404

Loydell, D.K. 2012. Graptolite biozone correlation charts. *Geological Magazine 149*, 124–132. DOI 10.1017/S0016756811000513

Loydell, D.K. & Cave, R. 1996. The Llandovery-Wenlock boundary and related stratigraphy in eastern mid-Wales with special reference to the Banwy River section. *Newsletters on Stratigraphy 34*, 39–64. DOI 10.1127/nos/34/1996/39

Loydell, D.K., Štorch, P. & Melchin, M.J. 1993. Taxonomy, evolution, and biostratigraphical importance of the Llandovery graptolite *Spirograptus*. *Palaeontology 36*, 909–926.

Loydell, D.K., Štorch, P. & Bates, D.E.B. 1997. Revision of the Silurian graptolite genus *Retiolites*. *Palaeontology 40(3)*, 747–762.

Loydell, D.K., Männik, P. & Nestor, V. 2003. Integrated biostratigraphy of the lower Silurian of the Aizpute-41 core, Latvia. *Geological Magazine 140*, 205–229. DOI 10.1017/S0016756802007264

Loydell, D.K., Sarmiento, G.N., Štorch, P. & Gutiérrez-Marco, J.C. 2009. Graptolite and conodont biostratigraphy of the upper Telychian – lower Sheinwoodian (Llandovery – Wenlock) of the Jabalón River section, Corral de Calatrava, Spain. *Geological Magazine 146(2)*, 187–198. DOI 10.1017/S0016756808005840

Loydell, D.K., Nestor, V. & Männik, P. 2010. Integrated biostratigraphy of the lower Silurian of the Kolka-54 core, Latvia. *Geological Magazine 147*, 205–229. DOI 10.1017/S0016756809990574

Loydell, D.K., Frýda, J. & Gutiérrez-Marco, J.C. 2015. The Aeronian/Telychian (Llandovery, Silurian) boundary, with particular reference to sections around the El Pintado reservoir, Seville Province, Spain. *Bulletin of Geosciences 90(4)*, 743–794. DOI 10.3140/bull.geosci.1564

Loydell, D.K., Walasek, N., Schovsbo, N.H. & Nielsen, A.T. 2017. Graptolite biostratigraphy of the lower Silurian of the Sommerodde-1 core, Bornholm, Denmark. *Bulletin of the Geological Society of Denmark 65*, 135–160. DOI 10.37570/bgsd-2017-65-09

Maletz, J. 2017. Part V, Second Revision, Chapter 27: Superfamily Monograptoidea and Family Dimorphograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online 87*, 1–9. DOI 10.17161/to.v0i0.6534

Maletz, J. 2019a. Part V, Second Revision, Chapter 24: Infraorder Neograptina and Family Normalograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online 116*, 1–15. DOI 10.17161/to.v0i0.9768

Maletz, J. 2019b. Part V, Second Revision, Chapter 25: Superfamily Retiolitoidea and Family Neodiplograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online 117*, 1–8. DOI 10.17161/to.v0i0.9769

Maletz, J. & Loydell, D.K. 2021. Part V, Second Revision, Chapter 28: Family Monograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online 156*, 1–43. DOI 10.17161/to.vi.15934

Manda, Š., Štorch, P., Slavík, L., Frýda, J., Kříž, J. & Tasáryová, Z. 2012. The graptolite, conodont and sedimentary record through the late Ludlow kozlowskii Event (Silurian) in the shale-dominated succession of Bohemia. *Geological Magazine 149(3)*, 507–531. DOI 10.1017/S0016756811000847

Manda, Š., Štorch, P., Frýda, J., Slavík, L. & Tasáryová, Z. 2019. The mid-Homerian (Silurian) biotic crisis in offshore settings of the Prague Synform, Czech Republic: integration of the graptolite fossil record with conodonts, shelly fauna and carbon isotope data. *Palaeogeography, Palaeoclimatology, Palaeoecology 528*, 14–34. DOI 10.1016/j.palaeo.2019.04.026

Manda, Š., Slavík, L., Štorch, P., Tasáryová, Z. & Čáp, P. 2023. Division of Přídolí Series in Central Bohemia: graptolite and conodont biostratigraphy, faunal changes, and geochemical record. *Newsletters on Stratigraphy 56(1)*, 89–123. DOI 10.1127/nos/2022/0695

Marek, L. 1951. Nález druhu *Akidograptus acuminatus* (Nicholson) v českém siluru. *Věstník Ústředního ústavu geologického 24*, 382–384.

Marek, L. & Havlíček, V. 1967. The articulate brachiopods of the Kosov Formation (Upper Ashgillian). *Věstník Ústředního ústavu geologického 42*, 275–284.

Marr, J.E. 1880. On the predevonian rocks of Bohemia. *Quarterly Journal of the Geological Society of London 36*, 591–619. DOI 10.1144/GSL.JGS.1880.036.01-04.44

Marr, J.E. 1892. On the Wenlock and Ludlow strata of the Lake District. *Geological Magazine, Decade III, 9*, 534–541. DOI 10.1017/S0016756800196189

Marr, J.E. & Nicholson, H.A. 1888. The Stockdale Shales. *Quarterly Journal of the Geological Society of London 44*, 654–732. DOI 10.1144/GSL.JGS.1888.044.01-04.42

Meidla, T., Tinn, O., Salas, M.J., Williams, M., Siveter, D., Vandenbroucke, T.R.A. & Sabbe, K. 2013. Biogeographical patterns of Ordovician ostracods, 337–354. *In* Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic biogeography and palaeogeography*. *Geological Society London, Memoir 38*. DOI 10.1144/M38.21

Melchin, M.J. 1989. Llandovery graptolite biostratigraphy and paleobiogeography, Cape Phillips Formation, Canadian Arctic Islands. *Canadian Journal of Earth Sciences 26*, 1726–1746. DOI 10.1139/e89-147

Melchin, M.J., Koren', T.N. & Štorch, P. 1998. Global diversity and survivorship patterns of Silurian graptoloids, 165–182. *In* Landing, E. & Johnson, M.E. (eds) *Silurian cycles: linkages of dynamic processes in the atmosphere and oceans. New York State Museum Bulletin 491*.

Melchin, M.J., Sadler, P.M. & Cramer, B.D. 2012. The Silurian Period, 525–558. *In* Gradstein, F. M., Ogg, J.G. & Smith, A.G. (eds) *Geologic Time Scale 2012*. Elsevier, Amsterdam. DOI 10.1016/B978-0-444-59425-9.00021-4

Melchin, M.J., Lenz, A.C. & Kozłowska, A. 2017a. Retiolitine graptolites from the Aeronian and lower Telychian (Llandovery, Silurian) of Arctic Canada. *Journal of Paleontology 91(1)*, 116–145. DOI 10.1017/jpa.2016.107

Melchin, M.J., Sheets, D., Mitchell, C.A. & Fan, J.X. 2017b. A new approach to quantifying stratigraphical resolution: application to global stratotypes. *Lethaia 50*, 407–423. DOI 10.1111/let.12193

Melchin, M.J., Sadler, P.M. & Cramer, B.D. 2020. The Silurian Period, 695–732. *In* Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (eds) *Geologic Time Scale 2020*. Elsevier, Amsterdam. DOI 10.1016/B978-0-12-824360-2.00021-8

Melchin, M.J., Davies, J.R., Weirdt, J. de, Russell, C., Vandenbroucke, T.R.A. & Zalasiewicz, J.A. 2018. *Integrated stratigraphic study of the Rhuddanian-Aeronian (Llandovery, Silurian) boundary succession at Rheidol Gorge, Wales: a preliminary report*. 16 pp. British Geological Survey Open Report OR/18/139.

Melichar, R. 2004. Tectonics of the Prague Synform: a hundred years of scientific discussion. *Krystalinikum 30*, 167–187.

Molyneux, S.G., Delabroye, A., Wicander, R. & Servais, T. 2013: Biogeography of early to mid Palaeozoic (Cambrian–Devonian) marine phytoplankton, 365–397. *In* Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic biogeography and palaeogeography*. *Geological Society London, Memoir 38*. DOI 10.1144/M38.23

Mu, E.Z., Lin, Y.K. & Ni, Y.N. 2002. *Fossil graptolites of China*. 1205 pp. Nanjing University Press, Nanjing. [in Chinese]

Ni, Y.N., Lenz, A.C. & Chen X. 1998. Pridoli graptolites from northern Xinjiang, Northwest China. *Canadian Journal of Earth Sciences 35*, 1123–1133. DOI 10.1139/e98-059

Obut, A.M., Sobolevskaya, R.F. & Merkureva, A.P. 1968. *Graptolity Llandoveri v Kernakh Burovykh Skvazhin Norilskogo Rayona*, 162 pp. Akademiya Nauk USSR, Sibirskoje Otdelenie, Institut Geologii i Geofiziki, Moscow. [in Russian]

Palmer, D. 1971. The Ludlow graptolites *Neodiversograptus nilssoni* and *Cucullograptus* (*Lobograptus*) *progenitor*. *Lethaia 4*, 357–384. DOI 10.1111/j.1502-3931.1971.tb01860.x

Patočka, F., Pruner, P. & Štorch, P. 2003. Palaeomagnetism and geochemistry of Early Palaeozoic rocks of the Barrandian (Teplá–Barrandian Unit, Bohemian Massif): palaeotectonic implications. *Physics and Chemistry of the Earth 28*, 735–749. DOI 10.1016/S1474-7065(03)00126-8

Pedersen, T.B.P. 1922. Rastritesskiferen pa Bornholm. *Meddelelser fra Dansk geologisk Forening 6(11)*, 3–29.

Perner, J. 1897. *Études sur les Graptolites de Bohême. Part 3. section a.* 25 pp. Raimond Gerhard, Prague.

Perner, J. & Kodym, O. 1919. O rozčlenění svrchního siluru v Čechách. *Časopis Musea Království českého 93*, 6–24.

Perner, J. & Kodym, O. 1922. On the zonal division and correlation of the Silurian of Bohemia. *American Journal of Science 4*, 53–72. DOI 10.2475/ajs.s5-4.19.53

Piçarra, J. M., Gutiérrez-Marco, J. C., Lenz, A. C. & Robardet, M. 1998. Přídolí graptolites from the Iberian peninsula: a review of previous data and new records. *Canadian Journal of Earth Sciences 35*, 65–75. DOI 10.1139/e97-082

Piras, S. 2006a. *Valentinagraptus* a new genus of plectograptid graptoloid from the lower Ludlow (Silurian) of Barrandian, Bohemia. *Geological Journal 41*, 581–590. DOI 10.1002/gj.1059

Piras, S. 2006b. *Ludlow (Silurian) graptolites and biostratigraphy of the western part of the Prague Basin (Barrandian area, Bohemia)*. 103 pp. 5 pls, unpublished Ph.D. thesis, Universita degli Studi di Modena e Reggio Emilia, Italy.

Porębska, E., Kozłowska-Dawidziuk, A. & Masiak, M. 2004. The *lundgreni* Event in the Silurian of the East European Platform, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology 213*, 271–294. DOI 10.1016/j.palaeo.2004.07.013

Prantl, F. & Přibyl, A. 1940. Příspěvek k poznání siluru v okolí Stodůlek. *Věstník Královské české společnosti nauk. Třída matematicko-přírodovědná, Ročník 1940*, 1–13.

Prantl, F. & Přibyl, A. 1944. Příspěvek k poznání geologických poměrů u Tachlovic. *Rozpravy České Akademie věd a umění, Třída 2, 54(3)*, 1–12.

Prantl, F. & Přibyl, A. 1948. Revision of the Bohemian Silurian Eurypterida. *Rozpravy Státního Geologického ústavu Československé republiky 10*, 1–116.

Přibyl, A. 1937. O stratigrafických poměrech vrstev Eα u Hl. Třebáně. *Věstník Státního geologického Ústavu 13*, 274–278.

Přibyl, A. 1938. Stratigrafie graptolitových zon na Vyskočilce u Malé Chuchle. *Věda přírodní 1938*, 1–2.

Přibyl, A. 1940a. Stratigrafické rozčlenění graptolitových zon z tzv. „Barrandeových kolonií“. *Věstník Královské české společnosti nauk. Třída matematicko-přírodovědná, Ročník 1940*, 1–12.

Přibyl, A. 1940b. Graptolitová fauna českého středního Ludlow (svrchní eβ). *Věstník Státního geologického Ústavu 16*, 63–73.

Přibyl, A. 1940c. O českých zástupcích monograptidů ze skupiny *Pristiograptus nudus*. *Rozpravy České Akademie věd a umění, Třída II, 50(16)*, 1–14.

Přibyl, A. 1940d. Revise českých graptolitů rodu *Monoclimacis* Frech. *Rozpravy České Akademie věd a umění, Třída 2, 50(23)*, 1–19.

Přibyl, A. 1941a. *Pernerograptus* n.g. a jeho zástupci z českého a cizího siluru. *Věstník Královské České společnosti nauk. Třída matematicko-přírodovědecká, Ročník 1941*, 1–18.

Přibyl, A. 1941b. O českých a cizích zástupcích rodu *Rastrites* Barrande, 1850. *Rozpravy České Akademie věd a umění, Třída 2, 51(6)*, 1–21.

Přibyl, A. 1941c. O několika nových druzích graptolitů z českého siluru. *Rozpravy České Akademie věd a umění, Třída 2, 51(7)*, 1–9.

Přibyl, A. 1942a. Příspěvek k poznání monograptidů ze skupiny druhu *Monograptus flexilis*. *Rozpravy České Akademie věd a umění, Třída 2, 52(15)*, 1–24.

Přibyl, A. 1942b. Revize Pristiograptů z podrodu *Colonograptus* nov. subg. a *Saetograptus* nov. subg. *Rozpravy České Akademie věd a umění, Třída 2, 52(15)*, 1–24.

Přibyl, A. 1943a. O stratigrafických poměrech siluru a devonu v podolské cementárně v Praze. *Rozpravy České Akademie věd a umění, Třída 2, 53*, 1–20.

Přibyl, A. 1943b. O několika nových graptolitech z českého a německého siluru. *Věstník Královské České společnosti nauk. Třída matematicko-přírodovědecká, Ročník 1943*, 1–26.

Přibyl, A. 1943c. Revize rodu *Pristiograptus* ze skupiny *P. dubius* a *P. vulgaris* z českého a cizího siluru. *Rozpravy České akademie věd a umění, Třída 2, 53(4)*, 1–48.

Přibyl, A. 1945. O středoevropských monograptech z rodu *Spirograptus* Gürich. *Rozpravy České Akademie věd a umění, Třída 2, 54(19)*, 1–46.

Přibyl, A. 1946. Přehled vývoje graptolitů z čeledě Monograptidae, Lapworth 1873 a poznámky k druhu *Demirastrites denticulatus* (Törnquist). *Věstník Královské České společnosti nauk. Třída matematicko-přírodovědecká, Ročník 1944*, 1–24.

Přibyl, A. 1948. Bibliographic index of Bohemian Silurian graptolites. *Knihovna Státního Geologického Ústavu České Republiky 22*, 1–96.

Přibyl, A. 1981. New graptolites of the family Monograptidae from the Upper Silurian. *Věstník Ústředního ústavu geologického 56*, 371–375.

Přibyl, A. 1983. Graptolite biozones of the Kopanina and Přídolí formations in the Upper Silurian of central Bohemia. *Časopis pro mineralogii a geologii 28*, 149–167.

Přibyl, A. & Münch, A. 1942. Revize středoevropských zástupců rodu *Demirastrites* Eisel. *Rozpravy České akademie věd a umění, Třída 2, 51(31)*, 1–29.

Přibyl, A. & Štorch, P. 1983. *Monograptus* (*Stimulograptus*) subgen. n. (Graptolites) from the lower Silurian of Bohemia. *Věstník Ústředního ústavu geologického 58*, 221–225.

Přibyl, A. & Štorch, P. 1985. *Prochnygraptus* gen. n. (Graptolithina, Monograptidae) from the middle and upper Llandovery of Europe. *Věstník Ústředního ústavu geologického 60*, 159–164.

Radzevičius, S. 2006. Late Wenlock biostratigraphy and the *Pristiograptus virbalensis* group (Graptolithina) in Lithuania and the Holy Cross Mountains. *Geological Quarterly 50*, 333–444.

Radzevičius, S. & Paškevičius, J. 2005. *Pristiograptus* (Graptoloidea) from the Upper Wenlock of the Baltic Countries. *Stratigraphy and Geological Correlation 13(2)*, 159–169.

Radzevičius, S., Stankevič, R, Budginas, R., Cichon-Pupienis, A., Venckutė-Aleksienė, A., Meidla, T., Ainsaar, L. & Spiridonov, A. 2023. Integrated stratigraphy of the Ludlow (Silurian) of the Baubliai-2 core (western Lithuania) and the record of $\delta^{18}O$ and $\delta^{13}C$ climatically driven co-variability. *Newsletters on Stratigraphy 56(1)*, 75–88. DOI 10.1127/nos/2022/0712

Raumer, J. von & Stampfli, G.M. 2008. The birth of the Rheic Ocean – Early Palaeozoic subsidence patterns and subsequent tectonic plate scenarios. *Tectonophysics 461*, 9–20. DOI 10.1016/j.tecto.2008.04.012

Rickards, R.B. 1965. New Silurian graptolites from the Howgill Fells (northern England). *Palaeontology 8(2)*, 247–271, pls 29–31.

Rickards, R.B. 1976. The sequence of Silurian graptolite zones in the British Isles. *Geological Journal 11*, 153–188. DOI 10.1002/gj.3350110205

Rickards, R.B. 1995. Utility and precision of Silurian graptolite biozones. *Lethaia 28*, 129–137. DOI 10.1111/j.1502-3931.1995.tb01602.x

Rickards, R.B. & Hutt, J.E. 1970. The earliest monograptid. *Proceedings of the Geological Society of London 1663*, 115–119.

Rickards, R.B. & Wright, A.J. 1999. Systematics, biostratigraphy and evolution of the late Ludlow and Přídolí graptolites of the Yass District, New South Wales, Australia. *Records of the Australian Museum 51(3)*, 187–214. DOI 10.3853/j.0067-1975.51.1999.1306

Rickards, R.B., Hutt, J.E. & Berry, W.B.N. 1977. Evolution of the Silurian and Devonian graptoloids. *Bulletin of the British Museum (Natural History), Geology 28*, 1–120. DOI 10.5962/p.313890

Rinenberg, R.E. 1985. The graptolite-based stratigraphy of the Silurian deposits from South Tien-Shan. *Bulletin Moskovskogo Obschestva ispytatelei prirody. Otdelenie geologii 60*, 73–79. [in Russian]

Robardet, M. 2003. The Armorica microplate: fact or fiction? Critical review of the concept and contradictory palaeobiogeographical data. *Palaeogeography, Palaeoclimatology, Palaeoecology 195*, 25–148. DOI 10.1016/S0031-0182(03)00305-5

Sadler, P.M., Cooper, R.A. & Melchin, M.J. 2011. Sequencing the graptolite clade: building a global diversity curve from local range-charts, regional composites and global time-lines. *Proceedings of the Yorkshire Geological Society 58(4)*, 329–343. DOI 10.1144/pygs.58.4.296

Salvador, A. (ed.) 1994. *International Stratigraphic Guide (second edition)*. 214 pp. IUGS and Geological Society of America, Boulder, Colorado.

Schauer, M. 1968. Zur Taxionomie und Stratigraphie der Gattung *Cyrtograptus* (Graptolithina). *Freiberger Forschungshefte Reihe C 221*, 33–41.

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

Snelling, A. & Zalasiewicz, J. 2011. The evolutionary lineage of *Petalolithus* to *Cephalograptus*: evidence from Coalpit Bay, Northern Ireland. *Proceedings of the Yorkshire Geological Society 58(4)*, 345–350. DOI 10.1144/pygs.58.4.305

Stampfli, G.M., Raumer, J. von & Borel, G.D. 2002. Paleozoic evolution of pre-Variscan terranes: from Gondwana to the Variscan collision, 263–280. *In* Martínez Catalán, J.R., Hatcher, R.D. Jr., Arenas, R. & Díaz García, F. (eds) *Variscan–Appalachian Dynamics: The Building of the Late Paleozoic Basement. Special Papers of the Geological Society of America 364*. DOI 10.1130/0-8137-2364-7.263

Štorch, P. 1980. *Demirastrites pribyli* Bouček, 1953 (Graptolithina) and the *Demirastrites pribyli* Biozone in the lower Silurian of Bohemia. *Věstník Ústředního ústavu geologického 55*, 305–309.

Štorch, P. 1982. Ordovician-Silurian boundary in the northernmost part of the Prague Basin (Barrandian, Bohemia). *Věstník Ústředního ústavu geologického 57*, 231–236.

Štorch, P. 1983a. The genus *Diplograptus* (Graptolithina) from the lower Silurian of Bohemia. *Věstník Ústředního ústavu geologického 58*, 159–170.

Štorch, P. 1983b. Subfamily Akidograptinae (Graptolithina) from the lowermost Silurian of Bohemia. *Věstník Ústředního ústavu geologického 58*, 295–299.

Štorch, P. 1985. *Orthograptus* s.l. and *Cystograptus* (Graptolithina) from the Bohemian lower Silurian. *Věstník Ústředního ústavu geologického 60*, 87–99.

Štorch, P. 1986. Ordovician-Silurian boundary in the Prague Basin (Barrandian area, Bohemia). *Sborník geologických Věd, Geologie 41*, 69–103.

Štorch, P. 1988. Earliest Monograptidae (Graptolithina) in the lower Llandovery sequence of the Prague Basin. *Sborník geologických Věd, Paleontologie 29*, 9–48.

Štorch, P. 1991. Faciální vývoj, stratigrafie a korelace svrchního ordoviku a spodního siluru pražské pánve (Barrandien). 232 pp. 22 pls, unpublished Ph.D. thesis, Charles University, Prague, Czech Republic.

Štorch, P. 1992. Some new and little known graptolites from the Lower Silurian of Bohemia (Prague Basin, Barrandian Area). *Časopis pro mineralogii a geologii 37*, 193–201.

Štorch, P. 1994a. Graptolite biostratigraphy of the Lower Silurian (Llandovery and Wenlock) of Bohemia. *Geological Journal 29*, 137–165. DOI 10.1002/gj.3350290204

Štorch, P. 1994b. Llandovery-Wenlock boundary beds in the graptolite-rich sequence of the Barrandian area (Bohemia). *Journal of the Czech Geological Society 39*, 163–182.

Štorch, P. 1995a. Upper Silurian (upper Ludlow) graptolites of the *N. inexpectatus* and *N. kozlowskii* biozones from Kosov Quarry near Beroun (Barrandian area, Bohemia). *Bulletin of the Czech Geological Survey 70(4)*, 65–89.

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

Štorch, P. 1996. The basal Silurian *Akidograptus ascensus–Parakidograptus acuminatus* Biozone in peri-Gondwanan Europe: graptolite assemblages, stratigraphical ranges and palaeobiogeography. *Bulletin of the Czech Geological Survey 71*, 171–178.

Štorch, P. 1998. Graptolites of the *Pribylograptus leptotheca* and *Lituigraptus convolutus* biozones of Tmaň (Silurian, Czech Republic). *Journal of the Czech Geological Society 43*, 209–272.

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 Barrandian area of the Czech Republic. *Geological Journal 41*, 163–192. DOI 10.1002/gj.1038

Štorch, P. 2015. Graptolites from Rhuddanian-Aeronian boundary interval (Silurian) in the Prague Synform, Czech Republic. *Bulletin of Geosciences 90(4)*, 841–891. DOI 10.3140/bull.geosci.1568

Štorch, P. & Frýda, J. 2012. The late Aeronian graptolite sedgwickii Event, associated positive carbon isotope excursion and facies changes in the Prague Synform (Barrandian area, Bohemia). *Geological Magazine 149(6)*, 1089–1106. DOI 10.1017/S001675681200026X

Štorch, P. & Kraft, P. 2009. Graptolite assemblages and stratigraphy of the lower Silurian Mrákotín Formation, Hlinsko Zone, NE interior of the Bohemian Massif (Czech Republic). *Bulletin of Geosciences 84(1)*, 51–74. DOI 10.3140/bull.geosci.1077

Štorch, P. & Loydell, D.K. 1992. Graptolites of the *Rastrites linnaei* Group from the European Llandovery (Lower Silurian). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 184*, 63–86.

Štorch, P. & Loydell, D.K. 1996. The Hirnantian *graptolites Normalograptus persculptus* and "*Glyptograptus bohemicus*": stratigraphical consequences of their synonymy. *Palaeontology 39(4)*, 869–881.

Štorch, P. & Manda, Š. 2019. Little known Homerian (lower Silurian) graptolites from Kosov quarry near Beroun, Czech Republic. *Fossil Imprint 75(1)*, 44–58. DOI 10.2478/if-2019-0003

Štorch, P. & Melchin, M.J. 2018. Lower Aeronian triangulate monograptids of the genus *Demirastrites* Eisel, 1912: biostratigraphy, palaeobiogeography, anagenetic changes and speciation. *Bulletin of Geosciences 93(4)*, 513–537. DOI 10.3140/bull.geosci.1731

Štorch, P. & Piras, S. 2009. Silurian graptolites of Sardinia: assemblages and biostratigraphy, 77–93. *In* Corradini, C., Ferretti, A. & Štorch, P. (eds) *Silurian of Sardinia*. *Rendiconti della Societa Paleontologica Italiana 3(1).*

Štorch, P., Serpagli, E. & Barca, S. 2002. Silurian graptolites of the *spiralis* and *lapworthi* biozones (upper Telychian, Llandovery) in the Sulcis area, SW Sardinia. *Bolletino della Societa Paleontologica Italiana 41(2–3)*, 184–195.

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.

Štorch, P., Manda, Š. & Loydell, D.K. 2014. The Early Ludfordian *leintwardinensis* graptolite Event and the Gorstian-Ludfordian boundary in Bohemia (Silurian, Czech Republic). *Palaeontology 57(5)*, 1003–1043. DOI 10.1111/pala.12099

Štorch, P., Manda, Š., Slavík, L. & Tasáryová, Z. 2016. Wenlock-Ludlow boundary interval revisited: New insights from the off-shore facies of the Prague Synform, Czech Republic. *Canadian Journal of Earth Sciences 53*, 666–673. DOI 10.1139/cjes-2015-0161

Štorch, P., Manda, Š., Tasáryová, Z., Frýda, J., Chadimová, L. & Melchin, M.J. 2018. A proposed new global stratotype for Aeronian Stage of the Silurian System: Hlásná Třebaň section, Czech Republic. *Lethaia 51(3)*, 357–388. DOI 10.1111/let.12250

Štorch, P., Roqué Bernal, J. & Gutiérrez-Marco, J.C. 2019. A graptolite-rich Ordovician–Silurian boundary section in the south-central Pyrenees, Spain. *Geological Magazine 156(6)*, 1069–1091. DOI 10.1017/S001675681800047X

Suchý, V., Sýkorová, I., Stejskal, M., Šafanda, J., Machovič, V. & Novotný, M. 2002. Dispersed organic matter from Silurian shales of the Barrandian basin, Czech Republic: optical properties, chemical composition and thermal maturity. *International Journal of Coal Geology 53*, 1–25. DOI 10.1016/S0166-5162(02)00137-4

Sun, Z.Y., Štorch, P., Fan, J.X., Melchin, M.J. & Suyarkova, A.A. 2022. Lower Aeronian graptolites of the genera *Rastrites* and *Stavrites*: Systematics, biostratigraphy and palaeobiogeography. *Papers in Palaeontology*, e1429. DOI 10.1002/spp2.1429

Suyarkova, A.A. 2017. Biostratigrafiya nizhnesilurijskikh otlozhenii Kaliningradskoy oblasti po graptolitam. *Trudy VSEGEI, New series 358*, 1–126. [in Russian]

Tait, J., Bachtadse, V. & Soffel, H.C. 1994. Silurian palaeogeography of Armorica – new palaeomagnetic data from Central Bohemia. *Journal of Geophysical Research: Solid Earth 99*, 2897–2907. DOI 10.1029/93JB02642

Tait, J., Bachtadse, V. & Soffel, H.C. 1995. Upper Ordovician palaeogeography of the Bohemian Massif – implications for Armorica. *Geophysical Journal International 122*, 211–218. DOI 10.1111/j.1365-246X.1995.tb03548.x

Tasáryová, Z., Schnabl, P., Čížková, K., Pruner, P., Janoušek, V., Rapprich, V., Štorch, P., Manda, Š., Frýda, J. & Trubač, J. 2014. Gorstian palaeoposition and geotectonic setting of Suchomasty Volcanic Centre (Silurian, Prague Basin, Teplá-Barrandian Unit, Bohemian Massif). *GFF 136*, 262–265. DOI 10.1080/11035897.2013.879735

Teller, L. 1969. The Silurian biostratigraphy of Poland based on graptolites. *Acta geologica Polonica 19*, 1–393.

Teller, L. 1997. Graptolites and stratigraphy of the Přídolí Series in the East European Platform. *Palaeontologia Polonica 56*, 59–70.

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

Toghill, P. 1968b. The stratigraphical relationships of the earliest Monograptidae and the Dimorphograptidae. *Geological Magazine 105*, 46–51. DOI 10.1017/S0016756800046471

Törnquist, S.L. 1879. Några iakttagelser öfver Dalarnes graptolitskiffar. *Geologiska Föreningens i Stockholms Förhandlingar 5*, 446–457. DOI 10.1080/11035897909446283

Törnquist, S.L. 1897. On the Diplograptidae and Heteroprionidae of the Scanian Rastrites Beds. *Lunds Universitets Arsskrifter 33(11)*, 3–29.

Törnquist, S.L. 1899. Researches into the Monograptidae of the Scanian Rastrites Beds. *Lunds Universitets Arsskrifter 35*, 1–25.

Torsvik, T.H. & Cocks, L.R.M. 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. *In* Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic biogeography and palaeogeography*. *Geological Society London, Memoir 38*, 5–24. DOI 10.1144/M38.2

Torsvik, H.T. & Cocks, L.R.M. 2017. *Earth history and palaeogeography*. 317 pp. Cambridge University Press, Cambridge. DOI 10.1017/9781316225523

Tsegelnyuk, P.D. 1976. Late Silurian and early Devonian monograptids from the South-Western margin of the East European Platform, 91–133. *In* Shulga, P.L. (ed.) *Palaeontology and stratigraphy of the Upper Precambrian and Lower Paleozoic of the SW part of the East European Platform*. Naukova Dumka, Kiev.

Tullberg, S.A. 1883. Skånes graptoliter (2), Graptolitfaunorna i Cardiolaskiffern och Cyrtograptusskiffrarne. *Sveriges geologiska Undersökning*. *Afh., (C) 55*, 1–43.

Turek, V. 1990. Comments to upper Wenlock zonal subdivisions in the Silurian of Central Bohemia. *Časopis pro mineralogii a geologii 35*, 337–353.

Ulst, R. 1974. The early sequence of pristiograptids in conterminous deposits of Wenlock and Ludlow of the Middle Pribaltic, 90–105. *In* Obut, A.M. (ed.) *Graptolites of the USSR*. Nauka, Novosibirsk.

Urbanek, A. 1966. On the morphology and evolution of the Cucullograptinae (Monograptidae, Graptolithina). *Acta Palaeontologica Polonica 11*, 291–544.

Urbanek, A. 1970. Neocucullograptinae n. subfam. (Graptolithina) – their morphology and stratigraphic bearing. *Acta Palaeontologica Polonica 15*, 163–388.

Urbanek, A. 1993. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. *Historical Biology 7*, 29–50. DOI 10.1080/10292389309380442

Urbanek, A. 1995. Phyletic evolution of the latest Ludlow spinose monograptids. *Acta Palaeontologica Polonica 40*, 1–17.

Urbanek, A. 1997. Late Ludfordian and early Přídolí monograptids from the Polish Lowland. *Palaeontologia Polonica 56*, 87–231.

Urbanek, A. & Teller, L. 1997. Graptolites and stratigraphy of the Wenlock and Ludlow Series in the East European Platform. *Palaeontologia Polonica 56*, 87–231.

Van Valen, L.M. 1984. A resetting of Phanerozoic community evolution. *Nature 307*, 50–52. DOI 10.1038/307050a0

Waern, B. 1948. The Silurian Strata of the Kullatorp Core. *Bulletin of the Geological Institute of Upsala 32*, 433–474.

Wood, E.M.R. 1900. The Lower Ludlow Formation and its graptolite fauna. *Quarterly Journal of the Geological Society of London 56*, 415–492. DOI 10.1144/GSL.JGS.1900.056.01-04.26

Wood, E.M.R. 1906. The Tarannon Series of Tarannon. *Quarterly Journal of the Geological Society of London 62*, 644–701. DOI 10.1144/GSL.JGS.1906.062.01-04.31

Williams, M., Zalasiewicz, J., Boukhamsin, H. & Cesari, C. 2016. Early Silurian (Llandovery) graptolite assemblages of Saudi Arabia: biozonation, palaeoenvironmental significance and biogeography. *Geological Quarterly 60(1)*, 3–25. DOI 10.7306/gq.1270

Zalasiewicz, J. 1994. Middle to late Telychian (Silurian: Llandovery) graptolite assemblages of central Wales. *Palaeontology 37*, 375–396.

Zalasiewicz, J. & Tunnicliff, S. 1994. Uppermost Ordovician to lower Silurian graptolite biostratigraphy of the Wye Valley, central Wales. *Palaeontology 37*, 695–720.

Zalasiewicz, J.A. & Williams, M. 1999. Graptolite biozonation of the Wenlock (Silurian) rocks of the Builth Wells district, central Wales. *Geological Magazine 136*, 263–283. DOI 10.1017/S0016756899002599

Zalasiewicz, J., Loydell, D.K. & Štorch, P. 1995. A taxonomic revision of three mid-Telychian monoclimacids. *Journal of Paleontology 69*, 961–967. DOI 10.1017/S0022336000035605

Zalasiewicz, J.A., Taylor, L., Rushton, W.A., Loydell, D.K., Rickards, R.B. & Williams, M. 2009. Graptolites in British stratigraphy. *Geological Magazine 146*, 23–57. DOI 10.1017/S0016756809990434

Zhang, Y.D., Wang, Y., Zhan, R.B., Fan, J.X., Zhou, Z.Q. & Fang, X. 2014. *Ordovician and Silurian Stratigraphy and Palaeontology of Yunnan, Southwest China*. 138 pp. Science Press, Beijing.

Appendix. Locality names, current status and GPS coordinates. Abbreviations: cover. – covered and inaccessible; access. – accessible; part access. – accessible in part.

No.	Locality	Status	References	GPS coordinates	
1	Praha-Běchovice	cover.	(Marek 1951, Bouček 1953)	50° 5′ 24.0″ N	14° 36′ 17.8″ E
2a	Praha-Řepy housing estate	cover.	(Štorch 1982)	50° 4′ 0.7″ N	14° 18′ 31.9″ E
2b	Praha-Zličín housing estate	cover.	Unpublished locality, *belophorus* Biozone	50° 3′ 51.3″ N	14° 17′ 59.6″ E
3	Běleč	trench	(Štorch 1986, 1994a)	49° 54′ 56.4″ N	14° 10′ 47.0″ E
4	Vočkov near Karlštejn	access.	(Štorch 1986)	49° 55′ 34.1″ N	14° 10′ 53.6″ E
5	Karlík	access.	(Štorch 1986, 1994a)	49° 56′ 30.0″ N	14° 16′ 8.6″ E
6	Loděnice-water tank	cover.	(Štorch 1986)	49° 59′ 23.2″ N	14° 9′ 42.3″ E
7	Loděnice-Sedlec	access.	(Štorch 1986)	49° 58′ 50.0″ N	14° 08′ 41.3″ E
8	Zadní-Třebaň railway cut	access.	(Štorch 1986, 1994a)	49° 55′ 10.5″ N	14° 11′ 5.8″ E
9a	Hlásná Třebaň-section	access.	(Bouček 1953; Štorch 1986, 1994a; Štorch *et al*. 2018)	49° 55′ 22.9″ N	14° 12′ 43.0″ E
9b	Hlásná Třebaň-rock	part access.	(Bouček 1953, Štorch 1991)	49° 55′ 27.6″ N	14° 12′ 41.7″ E
10a	Velká Ohrada pipeline trench	cover.	(Štorch 2006)	50° 2′ 19.6″ N	14° 18′ 57.5″ E
10b	Velká Ohrada building excavations	cover.	(Štorch 1994b)	50° 2′ 14.4″ N	14° 20′ 9.3″ E
11	Černošice-Barrande's Colony Solopisky	access.	(Bouček 1953; Štorch 1986, 1994a)	49° 57′ 27.1″ N	14° 18′ 23.0″ E
12a	Černošice-Solopisky test-pit	test-pit	(Horný 1956)	49° 57′ 30.1″ N	14° 18′ 10.1″ E
12b	Solopisky-road cut south of the village	access.	Přibyl (1945)	49° 57′ 32.3″ N	14° 17′ 53.5″ E
13	Radotín-tunnel	gallery	(Štorch *et al*. 2009, Štorch & Frýda 2012)	49° 59′ 49.0″ N	14° 22′ 23.3″ E
14	Velká Chuchle-Barrande's Colony Haidinger	access.	(Přibyl 1940a, Štorch 1986)	50° 0′ 12.1″ N	14° 22′ 52.7″ E

Appendix. Continued.

No.	Locality	Status	References	GPS coordinates	
15	Beroun-Jarov	trench	Unpublished locality, *ascensus – convolutus* biozones	49° 56′ 42.8″ N	14° 3′ 33.5″ E
16	Praha-Nové Butovice housing estate	cover.	(Štorch 2006)	50° 2′ 51.1″ N	14° 20′ 37.5″ E
17a	Želkovice-trench	trench	(Horný 1956)	49° 52′ 40.9″ N	14° 2′ 49.1″ E
17b	Želkovice-behind farm	part access.	(Bouček 1953, Štorch 1994a)	49° 52′ 33.5″ N	14° 2′ 20.1″ E
18	Všeradice-field	access.	(Štorch 2015)	49° 52′ 36.3″ N	14° 6′ 12.9″ E
19	Tmaň-Sv. Jiří, field	access.	(Štorch 1998)	49° 54′ 24.7″ N	14° 2′ 50.7″ E
20	Zdice-Barrande's Colony Lapworth	access.	(Bouček 1930, 1953; Štorch 1994a)	49° 54′ 22.3″ N	13° 59′ 56.0″ E
21	Hýskov-V Jakubince	trench	(Štorch 2001)	50° 0′ 13.8″ N	14° 4′ 20.1″ E
22a	Zadní Třebaň-railway station	access.	Unpublished locality, *sedgwickii* Biozone	49° 55′ 5.2″ N	14° 11′ 53.9″ E
22b	Zadní Třebaň, slope high above railway	access.	Unpublished locality, *rastrum Biozone*	49° 55′ 2.2″ N	14° 11′ 50.3″ E
23	Litohlavy, railway cut	access.	(Kříž 1992, Štorch 1994a)	49° 56′ 0.5″ N	14° 2′ 38.8″ E
24a	Malá Chuchle-tunnel entrance	access.	(Štorch 1986, 2006)	50° 1′ 36.2″ N	14° 23′ 33.4″ E
24b	Malá Chuchle-Vyskočilka	access.	(Bouček 1953, Štorch 1994a)	50° 1′ 46.9″ N	14° 23′ 47.9″ E
24c	Malá Chuchle-former railway station	cover.	(Bouček & Přibyl 1952a, Bouček 1953)	50° 1′ 23.3″ N	14° 23′ 29.1″ E
25a	Beroun-Lištice, pipeline trench	cover.	(Kříž *et al*. 1993)	49° 57′ 35.5″ N	14° 5′ 46.4″ E
25b	Beroun-Lištice, behind sewage disposal plant	access.	(Kříž 1992)	49° 57′ 29.1″ N	14° 5′ 47.8″ E
26	Malá Ohrada, pipeline trench	cover.	Unpublished locality, *crispus – rigidus* biozones	50° 2′ 26.4″ N	14° 20′ 4.3″ E
27	Praha-Motol, road cut	part access.	(Štorch 1994a)	50° 4′ 1.3″ N	14° 19′ 44.4″ E
28a	Kosov quarry-5th level	access.	(Turek 1990)	49° 56′ 24.8″ N	14° 3′ 8.3″ E
28b	Kosov quarry-4th level	access.	(Manda *et al*. 2019)	49° 56′ 22.4″ N	14° 3′ 11.0″ E
28c	Kosov quarry-3rd level	access.	(Štorch 1995a)	49° 56′ 12.8″ N	14° 3′ 22.9″ E
28d	Kosov quarry-northern part of 1st level	access.	(Kříž *et al*. 1986)	49° 56′ 25.2″ N	14° 3′ 27.6″ E
28e	Kosov quarry-northern part, behind canteen	access.	(Přibyl 1983, Kříž 1992)	49° 56′ 27.1″ N	14° 3′ 20.5″ E
29	Nesvačily-trench	trench	(Štorch *et al*. 2016)	49° 53′ 13.2″ N	14° 6′ 55.1″ E
30	Všeradice-trench along field track northwest of village	trench	(Kříž 1992, Kozlowska-Dawidziuk *et al*. 2001, Manda *et al*. 2012, Štorch *et al*. 2014)	49° 52′ 36.4″ N	14° 5′ 49.6″ E
31	Bykoš-trench east of village	trench	Unpublished locality, *ludensis-gerhardi – progenitor* biozones	49° 53′ 0.2″ N	14° 5′ 6.6″ E
32	Na Požárech quarry near Řeporyje	access.	(Kříž *et al*. 1986)	50° 1′ 43.9″ N	14° 19′ 27.9″ E
33	Rovina near Lety, building excavation	cover.	Unpublished locality, *perneri-ramosus* Biozone	49° 55′ 25.0″ N	14° 13′ 29.4″ E
34	Koněprusy-road cut southeast of village	access.	(Kříž *et al*. 1993)	49° 55′ 9.7″ N	14° 4′ 23.8″ E
35	Radotín-Hvížďalka	access.	(Kříž *et al*. 1986, Manda *et al*. 2023)	49° 59′ 46.5″ N	14° 20′ 1.1″ E
36a	Mušlovka quarry near Řeporyje	access.	(Bouček 1937, Kříž 1992)	50° 1′ 53.2″ N	14° 19′ 58.7″ E
36b	Mušlovka, hillslope west of the quarry	access.	(Bouček 1937, Kříž 1992)	50° 1′ 53.7″ N	14° 19′ 56.7″ E
36c	Řeporyje-Trunečkův Mill	lost	(Bouček 1937)	unknown	
36d	Řeporyje, cart track to Velká Ohrada	lost	(Bouček 1937)	unknown	
37	Čertovy schody near Tmaň, VCS headquarters	access.	(Horný 1962, Kříž *et al*. 1986)	49° 54′ 37.1″ N	14° 3′ 17.8″ E
38	Klonk near Suchomasty	access.	(Chlupáč *et al*. 1972)	49° 54′ 1.6″ N	14° 3′ 45.6″ E

Appendix. Continued.

No.	Locality	Status	References	GPS coordinates	
39a	Jinonice-Nová Ves, well excavation	lost	(Bouček 1953)	unknown	
39b	Jinonice-Nová Ves, former Klukovice railway station	lost	(Přibyl 1983)	unknown	
40	Koněprusy-Havlíčkův Mill	lost	(Přibyl 1945)	unknown	
41	Radotín-U topolů	access.	(Chlupáč *et al*. 1972)	49° 59′ 50.8″ N	14° 20′ 1.8″ E
42a	Praha-Hodkovičky, former quarry near bridge	cover.	(Bouček 1953)	50° 1′ 34.4″ N	14° 24′ 18.4″ E
42b	Praha-Braník, severage gallery west of brewery	lost	Unpublished locality, *spiralis* Biozone	unknown	
43	Praha-Pankrác, well excavation	lost	(Bouček 1953)	unknown	
44a	Praha-Podolí, water supply gallery	lost	(Přibyl 1983)	unknown	
44b	Praha-Podolí, former quarry above swimming pool	part access.	(Přibyl 1943a)	50° 3′ 2.6″ N	14° 25′ 8.0″ E
45	Praha-Braník, Braník Rocks	access.	(Kříž *et al*. 1986)	50° 2′ 21.″ N	14° 24′ 46.2″ E
46	Žákův Quarry, Velká Chuchle-Přídolí	access.	(Přibyl 1983, Kříž *et al*. 1986)	50° 0′ 58.1″ N	14° 22′ 36.5″ E
47	Praha-Stodůlky, former Šafránek's brick pit	cover.	(Prantl & Přibyl 1940)	50° 2′ 25.5″ N	14° 19′ 40.1″ N
48	Tachlovice-borehole	cover.	(Prantl & Přibyl 1944)	50° 0′ 38.5″ N	14° 14′ 40.7″ E
49	Loděnice-Černidla	access.	(Bouček 1941, *belophorus*, *rigidus* and *lundgreni* biozones	49° 58′ 53.2″ N	14° 9′ 25.0″ E
50a	Svatý Jan-U elektrárny	access.	Unpublished locality, *belophorus* Biozone	49° 58′ 25.5″ N	14° 7′ 45.0″ E
50b	Svatý Jan-Sedlec rock	access.	Unpublished locality, *belophorus* Biozone	49° 58′ 24.8″ N	14° 8′ 15.3″ E
51	Karlík valley near Mořinka	lost	Unpublished locality, *rastrum* Biozone	unknown	
52	Liščí Quarry near Karlštejn	access.	Unpublished locality, *inexpectatus* Biozone	49° 57′ 17.7″ N	14° 10′ 21.3″ E
53	Karlštejn, rocky slope above road to Hlasna Třebaň	access.	Unpublished locality, *lapworthi* Biozone	49° 55′ 46.5″ N	14° 11′ 20.5″ E
54	Karlštejn- Budňany Rock and road cut	access.	(Přibyl 1983, Kříž *et al*. 1986)	49° 56′ 5.0″ N	14° 10′ 46.9″ E
55	Karlštejn, cart track from Budňany to Hlásná Třebaň	access.	(Bouček 1931a)	49° 55′ 52.5″ N	14° 11′ 40.6″ E
56	Koledník quarry near Beroun	access.	(Kříž *et al*. 1986)	49° 56′ 28.5″ N	14° 4′ 12.3″ E
57	Velký Vrch, cart track from Koněprusy	access.	(Přibyl 1981, 1983)	49° 55′ 16.8″ N	14° 4′ 39.0″ E
58	Bykoš, roadcut southeast of the village	access.	(Přibyl 1983)	49° 52′ 41.6″ N	14° 4′ 25.3″ E
59	Slavíky-forrest track above the road west of the village	lost	(Bouček 1932a)	unknown	
60	Malkov, hillslope west of the village	lost	(Bouček 1932a)	unknown	
61	Lejškov near Suchomasty	lost	(Bouček 1933)	unknown	
62	Housina hillcrest, road from Bykoš to Neumětely	access.	(Bouček 1953)	49° 52′ 18.4″ N	14° 3′ 13.3″ E
63	Praha-Konvářka	part access.	(Přibyl 1983)	50° 3′ 10.2″ N	14° 24′ 9.8″ E
64a	Lochkov-Marble Quarry	access.	(Přibyl 1940b, 1983; Kříž *et al*. 1986)	50° 0′ 2.6″ N	14° 20′ 28.8″ E
64b	Lochkov-Ortoceras Quarry	access.	(Přibyl 1940b, 1983; Kříž *et al*. 1986)	49° 59′ 54.9″ N	14° 20′ 29.9″ E
65	Radotín-road to Lahovská	cover.	(Bouček 1953)	49° 59′ 21.0″ N	14° 21′ 10.9″ E
66	Praha-Butovice, Na Břekvici	trench	Kříž (1961)	50° 2′ 44.2″ N	14° 21′ 47.4″ E
67	Modřany-Barrande's Colony Vinice	part access.	Přibyl (1940a)	50° 0′ 43.6″ N	14° 24′ 9.8″ E