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The early Ludfordian leintwardinensis graptolite Event and the Gorstian–Ludfordian boundary in Bohemia (Silurian, Czech Republic)

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Abstract

The late Gorstian to early Ludfordian hemipelagic succession of the south-eastern part of the Prague Synform preserves a rich fossil record dominated by 28 species of planktic graptoloids associated with pelagic myodocopid ostracods, pelagic and nektobenthic orthocerid cephalopods, epibyssate bivalves, nektonic phyllocarids, rare dendroid graptolites, brachiopods, crinoids, trilobites, sponges and macroalgae. Faunal dynamics have been studied with particular reference to graptolites. The early Ludfordian *leintwardinensis* graptolite extinction Event manifests itself as a stepwise turnover of a moderate diversity graptolite fauna rather than an abrupt destruction of a flourishing biota. The simultaneous extinction of the spinose saetograptids *Saetograptus clavulus*, *Saetograptus leintwardinensis* and the rare *S. sp. B.* at the top of the *S. leintwardinensis* Zone was preceded by a short-term acme of *S. clavulus*. *Cucullograptus cf. aversus* and *C. rostratus* vanished from the fossil record in the lower part of the *Bohemograptus tenuis* Biozone. No mass proliferation of *Bohemograptus* has been observed in the postextinction interval. Limited indigenous speciation gave rise to *Pseudomonoclimacis kosoviensis* and *Pseudomonoclimacis cf. dalejensis*. *Egregiograptus* (the only novel element of cryptic origin) made its earliest occurrence in association with the latest cucullograptids. A postextinction graptolite assemblage of moderate diversity, composed for the most part of long-ranging taxa, persisted through the middle and upper *tenuis* Biozone until new rediversification in the *Neocucullograptus inexpectatus* Biozone. Unlike the graptoloids, the planktic, epiplanktic, nektonic and nektobenthic shelly fauna did not suffer significant extinction in the early Ludfordian. The Gorstian–Ludfordian boundary is placed at the lowest occurrence of *S. leintwardinensis* in spite of the very modest graptolite record available from the Ludfordian GSSP where no graptolites occur below the basal bed of the Lower Leintwardine Formation. Elsewhere, the Gorstian–Ludfordian boundary has been placed at the base of the *Saetograptus linearis* Biozone which has been considered roughly correlative with the *leintwardinensis* Biozone. Indeed, our morphometric study places the worldwide biozonal index species *S. linearis* in synonymy with *S. leintwardinensis* and thus considerably enhances the biostratigraphical utility of the latter index species. *Pseudomonoclimacis antiqua* sp. nov. is described.

Among Silurian invertebrates, the evolutionary pattern of graptolites is one of the best understood due to their generally complete fossil record in offshore sedimentary strata and extensive research since the mid-nineteenth century. The rapid evolution and planktic mode of life of graptolites makes them an almost ideal group for biostratigraphical correlation. The 'standard' biozonal scheme of Silurian graptolites is more refined and stable than those based upon other groups used in early Palaeozoic biostratigraphy. As Lapworth (1878) demonstrated that they are a useful tool for correlation, graptolite biozonation has been repeatedly upgraded. However, bio- and ecological aspects of the graptolite biodiversity pattern were mostly overlooked until Koren's (1987) study on graptolite faunal dynamics. Then, Jaeger (1991) analysed the 'Great Crisis', a major extinction among late Wenlock graptolites, and his approach to graptolite evolutionary dynamics has been widely accepted and further developed. Four extinction events affecting late Silurian graptolite faunas were recognized by Koren' (1993) and Urbanek (1993). In the entire Silurian succession of the Barrandian Prague Synform, eight graptolite extinction events were identified by Štorch (1995b). Ten globally recognized Silurian graptolite crises of various magnitudes were discussed by Melchin *et al.* (1998). Subsequent research has revealed temporal coincidence (or not) with extinctions in conodonts or other animal groups, and with falls in sea level and particularly with distinct changes in the ocean carbon cycle (i.e. positive carbon isotope excursions in sedimentary sequences) associated with most of these graptolite mass extinctions (Lenz *et al.* 2006; Loydell 2007; Manda *et al.* 2012; Štorch and Frýda 2012; Cooper *et al.* 2013).

Loydell (1994, 1998) and Melchin *et al.* (1998) stated that graptolite extinction events coincided with temporary eustatic sea-level falls and enhanced bottom-water oxygenation of graptolite-bearing offshore successions. However, the *leintwardinensis* extinction Event, defined by the sudden demise of the previously flourishing and cosmopolitan saetograptids, accompanied by the ultimate extinction of the last plectograptines and subsequent extinction of cucullograptids (Urbanek 1993), appears to coincide with the beginning of deepening. It is unusual also because the graptolite extinction was accompanied by neither perturbations in the oceanic carbon cycle nor extinction of conodonts. Jeppsson and Aldridge (2000) suggested a coincidence of the *leintwardinensis* Event with the Linde conodont extinction Event, but this coincidence is poorly supported. Only the local extinction of some invertebrates has been documented in Bohemian sections (Manda and Kříž 2006). The appearance, rapid diversification and extinction of morphologically distinct graptolite groups possessing specific evolutionary novelties, such as the dorso-lateral spines on the otherwise simple cylindrical thecae of saetograptids and the complex lateral apertural lobes of cucullograptid thecae, are quite common in the evolutionary history of graptolites, but usually such extinctions coincided with global environmental changes. It is striking that the *leintwardinensis* Event has been described only from Poland (Urbanek 1993), Tien Shan (Koren' 1993) and the Anglo-Welsh Basin (Watkins and Berry 1977) despite the fact that saetograptids are usually common in the fossil record and exhibit a cosmopolitan distribution. Detailed regional studies based upon sections from different

palaeoplates and sedimentary settings and with a relevant fossil record are needed to answer the question as to whether the *leintwardinesis* Event simply represents background stepwise extinction, a previously underestimated crisis or a limited, highly selective extinction. The present study is based upon data acquired from the section with so far the most complete, largely pelagic upper Gorstian and lower Ludfordian offshore faunal record in the Gondwanan part of Europe. The graptolite biostratigraphy and faunal dynamics rely on the systematic revision of 28 taxa. Many saetograptids have been described from Bohemian sections by Barrande (1850), Perner (1899), Bouček (1936) and Přibyl (1942), although these were for the most part based on specimens collected from particular intervals or certain beds in graptolite-poor carbonate-dominated successions. Poor original material, complex synonymies and vague biostratigraphy called for a systematic revision. Apart from a mostly complete saetograptid history, the Všeradice section revealed also the presence and extinction of the last true operculate monograptids (the cucullograptids).

Attention has been also paid to the Gorstian–Ludfordian boundary, which is tentatively correlated with the lowest occurrence of the biozonal index graptolite *Saetograptus leintwardinensis* (Lapworth), in spite of the very modest graptolite record available from the Ludfordian GSSP at Sunnyhill Quarry, south-west of Ludlow, England, where no graptolites occur below the lowest *S. leintwardinensis* in the basal bed of the Lower Leintwardine Formation (Cherns 1988). Elsewhere, the Gorstian–Ludfordian boundary has been placed at the base of the *Saetograptus linearis* Biozone which has been considered roughly correlative with the *leintwardinensis* Biozone. We took advantage of the continuous graptolite record in the Všeradice section, with abundant saetograptid rhabdosomes, and focused on the suspected synonymy of the two biozonal index species.

Geological setting

In the Prague Synform, the upper Silurian succession usually comprises carbonate rocks with rare and/or poorly preserved graptolites (Bouček 1936; Kříž 1992). The relatively deeper water, generally oxygen-depleted hemipelagic shale facies, potentially rich in diverse graptolites, is restricted to the south-western closure of the south-eastern and north-western flanks of the Prague Synform (Kříž 1991). There are only a few, poorly exposed sections in the shale-dominated area, usually insufficient for detailed investigations. The single exception is the section along the field track near Všeradice village (Fig. 1). This area is regarded as the deepest preserved part of the basin infill (Kříž 1991). The Všeradice section is located on a gentle, south-facing slope along a field track running north–north-west from the Bykoš–Všeradice road, north-west from Všeradice village. Discontinuous exposures and subcrops may be traced along the field track over a length of about 200 m. The section begins in the middle Wenlock and terminates in the lowest part of Přídolí Series and exhibits a shale-dominated, relatively offshore facies. Sedimentation here was least

influenced by syn-sedimentary basaltic volcanic activity, which left a significant record in most of the other Silurian sections of the Prague Synform (Kříž 1992).

Figure 1. Location of the area studied within the Czech Republic. A, Silurian outcrop of the Prague Synform. B, location of the Všeradice section on a topographical map. GPS coordinates of the section: 49°52'36.4"N, 14°05'49.6"E.

The first note on this important section was published by Horný (1960). Much later, Kříž (1992) presented a more detailed, but still incomplete log. His section started from marly shales high in the Homerian *Cyrtograptus lundgreni* Biozone and terminated in the upper Ludfordian with the longest of several interruptions in the *Saetograptus chimaera* Biozone. In the lower and middle Ludfordian part of the section, Kříž (1992) referred to the '*S. linearis*' Zone and '*Bohemograptus bohemicus tenuis* Interzone' and listed a few graptolites (*Saetograptus fritschii linearis*, *Bohemograptus bohemicus* and *B. bohemicus tenuis*) and bivalves. The boundaries between the Gorstian and Ludfordian and between the *linearis* and *tenuis* biozones were not detected. Kříž *et al.* (1993) and later Kozłowska-Dawidziuk *et al.* (2001) examined the uppermost Wenlock (upper Homerian) part of the section with particular emphasis on the *lundgreni* Event and postextinction recovery. Piras (2006a, b) studied the lower Gorstian beds comprising the *Neodiversograptus nilssoni* and *Lobograptus progenitor* biozones.

In early 2009, excavations were conducted to expose the reportedly graptolite-rich, shale-dominated section through the middle Ludlow. Our data came from up to 2.5-m-deep trenches, VC and VD, excavated on the south-west side of the field track (Fig. 1). An almost 40-m-thick succession of late Gorstian and early Ludfordian age was made accessible for detailed study (Figs 2, 3). Budil *et al.* (2010) studied the phyllocarid fauna from the same exposure. Manda *et al.* (2012) dealt with the late Ludfordian and earliest Přídolí strata exposed by trenches VA and VB in the upward continuation of the section described in this article.

Figure 2. Stratigraphy and lithology of the Vřerádice section across the Gorstian–Ludfordian boundary interval and *leintwardinensis* graptolite extinction Event; including graptolite fossil record and sample intervals referred to in the text.

Figure 3. Stratigraphy, lithology and nongraptolite fossil record of the Vřeradice section. See Figure 2 for lithology explanation and complete bed numbers. *Abbreviations.* EPI, epibenthic; EPIZ, epizoa; Microc., microconchids, NEK, nektonic; nektob., nekto-benthic; VB, vagrant benthic.

Material and methods

The shale-dominated late Gorstian and early Ludfordian succession was collected for graptolites and associated fauna in a similar manner as the mid- and late Ludfordian interval studied by Manda *et al.* (2012) and late Homerian interval studied by Kozłowska-Dawidziuk *et al.* (2001). Isolated limestone beds and tuffitic intercalations enabled division of the c. 40-m-thick succession illustrated by Figures 2 and 3 into 60 arbitrary units of different stratigraphical thickness (beds 17–77 in descending order). Many shaly units were further subdivided into up to five subunits (sampling intervals) designated by supplementary letters (a–e). Each of these sampling intervals was studied bed by bed down the section, and all of its fossil samples were placed in the same sample bag(s). The majority of these shaly sampling intervals were about 30 cm thick. Many intervals were rich in graptolites; some others were poor. Every graptolite that was at least tentatively determinable was collected from a rock volume of 0.03–0.05 m³. Graptolites are housed in

the collection of Petr Štorch in the Czech Geological Survey (prefix PŠ). Type specimens from collections of the National Museum, Prague, have numbers prefixed L, and specimens from the Lapworth Museum, University of Birmingham, have numbers prefixed BU. Nongraptolite macrofauna is deposited in the collection of Štěpán Manda in the Czech Geological Survey (unnumbered specimens in locality collection, prefix SM Všeradice section).

Sedimentary succession

The part of the Všeradice section studied exhibits a shale-dominated succession with relatively thin and subordinate limestone and tuffite beds (Figs 2, 3). Two shale facies are distinguished. The first, and prevailing, facies comprises grey and brown-grey, finely laminated shale; the second is formed by calcareous, dark grey or even black, coarsely laminated shale. These two types of shale differ also in their fossil content. The dark grey shale yielded more common bivalves and cephalopods, while graptolites and ostracods are more abundant in the grey shale. The dark grey shales occur especially in the upper *scanicus–chimaera* Biozone and in the middle part of the *tenuis* Biozone. Slump structures were observed in the shale of the lowermost Ludfordian part of the section. Bioturbation is missing except in two beds in the lower *S. leintwardinensis* Biozone (= *S. linearis* Zone of previous Czech authors).

The shales contain common elliptical, muddy limestone nodules rich in pyrite. These nodules, exceptionally attaining 40 cm in diameter, occur occasionally throughout the whole succession but also form discrete horizons (e.g. units 42 and 52) in the shale or at the contact of shale and tuffite (units 45 and 57). Rare remains of bivalves, cephalopods and graptolites occur in some nodules.

Muddy, diagenetic limestones are developed in the form of thin, laterally restricted beds with a maximum thickness of 30 cm, in places showing coarse lamination. The shale-limestone contacts are sharp or gradual in these diagenetically Ca-enriched beds. The mudstone of unit 29 also contains common shale intraclasts. The limestones yielded poorly preserved graptolites along with less common ostracods, disarticulated bivalves and fragments of cephalopod shells.

Tuffites are represented by thin, usually upward fining beds with a maximum thickness of 20 cm. Their colour varies from yellow to yellow-brown. An exceptional deposit is the tuffite bed of unit 63 containing common fragments of brachiopods and crinoids. A tuffitic matrix also surrounds the limestone nodules (ball structure) of coarse wacke-packstone with abundant unsorted fragments of cephalopods and disarticulated bivalves (*Cardiola docens*) accompanied by graptolite fragments.

Interpretation of the sedimentary environment

Off-shore hemipelagic deposits predominate in the Silurian succession exposed in the Všeradice section, whereas shallow water carbonate platform deposits occur several kilometres to the north (Kříž 1992). Pelagic graptolites, ostracods and cephalopods prevail in the fossil record in the upper Gorstian and lower Ludfordian part of the section. The benthic fauna is dominated by epibyssate bivalves that colonized empty cephalopod shells. Soft bottom, almost anoxic, conditions prevailed. Minor, small-scale bioturbation of *Chondrites* type is restricted to two thin beds only. Sponge spicules are common on some bedding planes of brown-grey laminated shale. Cephalopod shells are commonly oriented with the axis oblique to the bedding plane, in places with entangled graptolite rhabdosomes, so-called graptolite comets (Turek 1983). This, together with the character of the benthic fauna and complete and poorly oriented cephalopod shells, indicates only occasional weak subsurface currents that enhanced bottom ventilation. Most of the limestone beds and nodules are of diagenetic origin because the same fauna occurs in shale and limestone, transitions between the two lithotypes are commonly gradual, and also the lamination is more or less preserved in the limestone. Tuffitic beds indicate the occasional deposition of volcanic ash, probably derived from Silurian basalt volcanoes situated north of this section (Kříž 1991). A particular depositional event is represented by bed no. 63, which consists of coarse pyroclastic material embedding balls of mud, both with bioclasts transported downslope from the carbonate platform. The pyroclastic flow deposit was derived from a volcanic eruption, and this represents one of the youngest biostratigraphically well-dated signatures of syndimentary volcanic activity in the Prague Synform. Younger strata contain only thin beds of fine-grained tuffites. This bed probably resulted from a dense pyroclastic flow accompanying a submarine effusion. Two discrete, small-scale slump beds have been identified. In summary, the log presented on Figures 2 and 3 records relatively continuous and steady hemi-pelagic sedimentation without any apparent break or condensed horizon. In the *leintwardinensis* Biozone, the more common benthic fauna comprising bivalves, rare trilobites, monoplacophorans and crinoids along with nekto-benthic cephalopods may indicate a weak shallowing corresponding with the early Ludfordian lowstand recorded in several shallow water sections in the Prague Synform (Manda and Kříž 2006).

Nongraptolite fauna

Despite the uniform lithology of the shales, their fossil content varies considerably bed-by-bed or even between individual laminae. The pelagic myodocopid ostracods *Richteria migrans* (Barrande) and *Parabolbozoe bohémica* (Barrande) appear in the lower Ludfordian and soon become a common component of the fauna; as with the graptolites, their abundance fluctuated markedly. Kříž (1999) established two assemblages, with '*Entomis*' *migrans* and '*Bolbozoe*' *bohémica*. In places, the two species co-occur. However, Kříž (1999) suggested that the two ostracod assemblages inhabited different depth zones and considered '*Entomis*' to be more shallow. In the Všeradice section, the *Parabolbozoe* Assemblage prevails. Benthic ostracods are very rare, occurring in two beds only and in both represented by a single

specimen. The phyllocarid *Ceratiocaris papilio* Salter is common in the early Ludfordian strata (Budil *et al.* 2010). *Ceratiocaris* sp. appears in the upper *Bohemograptus tenuis* Biozone. The pelagic cephalopods *Parakionoceras originale* (Barrande), *Michelinoceras* sp., *Kopaninoceras* sp., and *Arionoceras* sp. were found in most shale beds. They are usually rare, but a few laminae with densely packed flattened shells were found in the lower Ludfordian (samples 46a, 46b). *Parakionoceras* occurs especially in dark grey shales of the *tenuis* Biozone. Nektobenthic cephalopods, represented by *Lycoceras* sp., *Pseudocycloceras* sp. and *Cyrtocycloceras* cf. *nitidum* (Barrande), are rare and occur in a few beds only.

Bivalves dominate the sparse evidence for benthic communities in the shales. They were found in many shale beds, but their abundance is rather low. All shells are disarticulated and more-or-less flattened. Most common is the epibyssate *C. docens* Barrande. Finds of other cardioids are rare and restricted to a few beds. The small epibyssate bivalve *Spanila* appears in the upper *tenuis* Biozone. In addition, a single shell of the univalved mollusc *Drahomira kriziana* Horný was found. Brachiopods are virtually absent: a single specimen of a juvenile strophomenid and one indeterminate lingulate were found. Broadly funnel-shaped dendroids (*Palaeodictyota* sp.) were common in sample 24b. Crinoids were found in grey shales of the *leintwardinensis* Biozone. Several holdfasts of two morphotypes (circular and pentagonal) were found attached to cephalopod shells in a few beds. Two calyces of *Endimerocrinus* sp. nov., determined by R. Prokop, came from samples 58 and 62b. Spirorbiform tubes of *Microconchus* sp. infesting the cephalopod shells are common in some beds.

The limestone mud-balls of bed 63 contain common fragments of cephalopod and bivalve shells (*C. docens*, *Arionoceras* sp., *Kopaninoceras* sp., Geisonoceratidae indet.) as well as crinoid debris, indeterminate rhynchonellid and strophomenid brachiopods and trilobites in the matrix (a transported fauna of shallow water origin). Crinoids and brachiopods in the matrix were derived from very shallow water environments, whereas the cephalopods and bivalves in the mud-balls came from deeper water environments below wave base.

Graptolite fauna

Graptolite rhabdosomes are moderately diverse and abundant in the late Gorstian and early Ludfordian laminated hemipelagic shales of the Všeradice section. Twenty-eight graptolite taxa have been identified from the upper *scanicus–chimaera* Biozone through to the top of the *tenuis* Biozone. Species richness declined from seven or eight species per sample near the base of the section to three or four species per sample in the uppermost part of the *scanicus–chimaera* Biozone.

A cumulative richness of 13 species occurs in the 9.1-m-thick succession assigned to the upper part of the *scanicus–chimaera* Biozone. In addition to the numerically prevailing saetograptids, *Bohemograptus bohemicus* (Barrande) and *Pristiograptus frequens* (Jaekel) are also common in this interval, being accompanied by *Pristiograptus tumescens* (Wood) in the uppermost part of the biozone. The lowest occurrence of *S. leintwardinensis* (Lapworth) is tentatively correlated with the base of the Ludfordian Stage in spite of the very modest graptolite record available from the Ludfordian GSSP at Sunnyhill Quarry where the only graptolite species occurs. The biozonal index *S. leintwardinensis* is reported from the basal bed of the Lower Leintwardine Formation, just above the formal base of the Ludfordian (Cherns 1988, fig. 5). In peri-Gondwanan Europe, Arctic Canada and Central Asia, the Gorstian–Ludfordian boundary has been placed at the base of the *S. linearis* Biozone (Loydell 2012), which has been always considered roughly correlative with the *leintwardinensis* Biozone.

A new increase in graptolite abundance and diversity takes place in the lower part of the *leintwardinensis* Biozone. Eight species per sample are found a little above the base of the biozone, and, after a temporary decline in the middle part, nine species are found in the uppermost sample of this biozone. In total, 19 species were recorded in the 11.6-m-thick succession of the *leintwardinensis* Biozone within which two successive faunal associations can be recognized. The lower association is dominated by *P. tumescens* accompanied by common *S. leintwardinensis*, *P. frequens*, bohemograptids, the latest *Lobograptus scanicus* (Tullberg) s.l., *S. fritschi* (Perner) and a few other, subordinate taxa. The upper association is numerically dominated by two saetograptids, *S. leintwardinensis* and *Saetograptus clavulus* (Perner), associated with *Cucullograptus hemiaversus* Urbanek?, *B. tenuis* (Bouček) replaced *B. bohemicus*, whereas *S. fritschi* gave way to *S. clavulus*. A single *Lobograptus* aff. *cirrifer* Urbanek was identified in the middle of the biozone; *Neodiversograptus* sp., *Cucullograptus* cf. *aversus* and *Pseudomonoclimacis dalejensis* (Bouček) appeared near the top.

A sudden decline in graptolite abundance and diversity followed at the base of the *tenuis* Biozone. This drop coincides with the sudden extinction of the previously proliferating saetograptids. Four species per sample is a typical number in the lower part of the *tenuis* Biozone until moderate rediversification, represented by the lowest occurrences of *Pseudomonoclimacis kosoviensis* (Bouček), *Pseudomonoclimacis* cf. *dalejensis* (Bouček) and *Egregiograptus* cf. *rinellae* Koren' and Sujarkova, commenced in the middle part of the biozone. Despite this recovery, with a single exception of eight species in a sample, species richness remained at three to five per sample in the middle and upper parts of the *tenuis* Biozone. The assemblage is composed for the most part of long-ranging taxa: *P. frequens*, *B. tenuis*, *Bohemograptus praecornutus*?, *P. kosoviensis*, *P. dalejensis* and, in the middle

part, also *E. cf. rinellae*. No species markedly predominate among the uncommon graptolite rhabdosomes. Twelve species have been identified from this c. 19-m-thick interval.

Graptolite biozones and correlation

The three graptolite biozones recognized in the upper Gorstian and lower Ludfordian succession of the Všeradice section are defined as interval zones embracing an interval between two biohorizons (in the sense of the *International Stratigraphic Guide*, edited by Salvador 1994).

Lobograptus scanicus – *S. chimaera* Biozone

The lowermost part of the present section (Fig. 2) hosts a graptolite association indicating a combined *scanicus*–*chimaera* Biozone. The assemblage is characterized by common *S. chimaera* (Barrande) accompanied intermittently by *L. scanicus* (Tullberg) *s.l.* and the long-ranging *P. frequens* (Jaekel), *Pseudomonoclimacis antiqua* sp. nov., *B. bohemicus* (Barrande) and several other taxa. The stratigraphically highest occurrences of the plectograptid *Holoretolites* sp. came from this level. Common *P. tumescens* (Wood) is confined to the broad boundary interval with the overlying *leintwardinensis* Biozone. Přibyl (1983) reported *P. tumescens* as a marker species for the transitional beds between the *scanicus* and *linearis* biozones. The upper limit of the *scanicus*–*chimaera* Biozone is defined by the lowest occurrence of *S. leintwardinensis*, the nominal species of the succeeding biozone.

The combined *scanicus*–*chimaera* Biozone is used in the Barrandian area due to the relatively sparse occurrence of *L. scanicus s.l.* that are sufficiently well preserved to be distinguishable from *Lobograptus parascanicus* (Kühne) and *Lobograptus amphirostris* Urbanek. Urbanek (1966) emphasized the relatively short range of the morphologically distinct *L. scanicus* and consequently did not use this species as a biozonal index taxon in the biostratigraphical subdivision of the subsurface Silurian rocks of Poland. *S. chimaera* is readily distinguishable from other saetograptids and exhibits a much longer stratigraphical range embracing both the *L. parascanicus* and *Lobograptus invertus* biozones of Urbanek and Teller (1997) as could be inferred also from the occurrence of *P. tumescens* in our upper *scanicus*–*chimaera* and lower *leintwardinensis* biozones. A ‘*Saetograptus incipiens* or *P. tumescens* Biozone’ was reported from about this level in Great Britain (Zalasiewicz *et al.* 2009). Precise correlation between the lobograptid–cucullograptid-based biozonation (Urbanek 1966) and that based on saetograptids (Urbanek and Teller 1997, table 2; Zalasiewicz *et al.* 2009) remains doubtful. A proposed correlation of the upper Gorstian to lower Ludfordian graptolite biozones of this article, the lobograptid–cucullograptid biozonation of Urbanek and Teller (1997) and other principal graptolite biozonations worldwide is depicted in Figure 4.

SERIES	STAGE	PRAGUE SYNFORM PERI-GONDWANAN EUROPE	POLAND EAST EUROPEAN PLATFORM	KALININGRAD AREA EAST EUROPEAN PLATFORM	BRITISH ISLES AVALONIA	ARTIC CANADA LAURENTIA	TIEN SHAN CENTRAL ASIA MICROPLATES
LUDLOW	LOWER LUDFORDIAN	<i>kozłowskii</i>	<i>kozłowskii</i>	no data	no graptolites	<i>tenuis</i> - <i>praecornutus</i>	<i>podoliensis</i>
		<i>inexpectatus</i>	<i>inexpectatus</i>				<i>tenuis</i>
		<i>tenuis</i>	<i>auriculatus</i> <i>cornutus</i> <i>praecornutus</i> <i>rostratus</i>		<i>tenuis</i>		
			<i>leintwardinensis</i>		<i>aversus</i>		<i>leintwardinensis</i> (- <i>linearis</i>)
	GORSTIAN	<i>scanicus-chimaera</i>	<i>hemiaversus</i>	<i>scanicus-chimaera</i>	<i>scanicus</i>	<i>scanicus</i>	<i>scanicus</i> - <i>chimaera</i>
			<i>invertus</i> <i>parascanicus</i>				
		<i>progenitor</i>	<i>progenitor</i>	<i>progenitor</i>	<i>nilssoni</i>	<i>progenitor</i>	<i>progenitor</i> - <i>colonus</i>
		<i>nilssoni</i>	<i>nilssoni</i>				

Figure 4. Correlation of principal Gorstian and lower Ludfordian graptolite biozonations. Key references used in construction of the chart, in addition to Loydell (2012): Urbanek and Teller (1997), Koren' and Sujarkova (2004, 2007), Lenz and Kozłowska-Dawidziuk (2004), Zalasiewicz *et al.* (2009), Manda *et al.* (2012) and this study. Dashed biozonal boundaries are only tentatively correlatable with those defined in the Prague Synform.

Saetograptus leintwardinensis Biozone

The *S. leintwardinensis* Biozone is defined as an interval between the lowest and highest occurrence of the eponymous graptolite until now recorded as *S. linearis* (Bouček) in Bohemia and many other regions. The common index species is accompanied by *P. frequens*, *B. tenuis* (Bouček) and *P. antiqua*. *S. fritschi* (Perner), *S. incipiens* (Wood)?, *B. bohemicus* and common *P. tumescens* complete the assemblage in the lower part of the 11.6-m-thick succession of the *leintwardinensis* Biozone, whilst abundant *S. clavulus* (Perner) and *C. hemiaversus* Urbanek? characterize the upper part of the biozone. The terminal proliferation of *S. clavulus* and the lowest occurrence of *P. dalejensis* (Bouček), *Cucullograptus* cf. *aversus* (Eisenack) and *Neodiversograptus* sp. in the topmost part of the biozone immediately precede the *leintwardinensis* Event.

Bohemograptus tenuis Biozone

Manda *et al.* (2012) defined the *B. tenuis* Biozone as an interval between the highest occurrences of saetograptids, the demise of *S. leintwardinensis* in conjunction with that of *S. clavulus* and the lowest occurrence of *Neocucullograptus inexpectatus* (Bouček). The long-ranging *B. tenuis*, accompanied

by *P. dalejensis*, is common in this interval although no particular proliferation has been recorded. The lowest 4 m of the c. 19-m-thick succession of the *tenuis* Biozone is marked by cucullograptids and rare *Neodiversograptus* sp.; *Cucullograptus rostratus* Urbanek is restricted to this level. Fairly common *E. cf. rinellae* Koren' and Sujarkova characterizes the middle part of the biozone, being accompanied by the lowest occurrences of the robust *P. kosoviensis* (Bouček). The upper part of the *tenuis* Biozone contains *B. praecornutus* Urbanek? and rare *Bohemograptus cornutus* Urbanek, which herald the moderate graptolite diversification in the succeeding *N. inexpectatus* Biozone recorded by Štorch (1995a) and Manda *et al.* (2012).

An interval between the highest occurrences of saetograptids and the lowest occurrence of *N. inexpectatus* is probably coeval with the *B. praecornutus*, *B. cornutus* and *Neolobograptus auriculatus* biozones recognized by Urbanek and Teller (1997) in the subsurface Silurian of Poland. In our section, however, *C. rostratus* disappeared from the fossil record well above the last saetograptids, whereas the latter authors recognized a specific *rostratus* Subzone equating with the upper *leintwardinensis* Biozone. However, the Mielnik reference section (Urbanek 1966) and our data suggest that the *rostratus* Subzone is correlatable instead with the lowermost *B. tenuis* Biozone (Fig. 4) and that the range of *C. rostratus* postdates the saetograptid extinction. Koren' and Sujarkova (2004) recognized a *B. tenuis* Interzone sandwiched between the *S. linearis* and *Polonograptus podoliensis* biozones in Tien Shan, Kyrgyzstan, as *B. praecornutus* and *B. cornutus* which have their own biozones in the Polish succession made their lowest occurrences as early as in the *scanicus-chimaera* and *linearis* biozones in Tien Shan. In Bohemia, *B. praecornutus* ranges from the uppermost *tenuis* Biozone through to the *kozlowskii* Biozone (Štorch 1995a, Manda *et al.* 2012) although similar morphological trends, such as the development towards robust, slightly everted thecae with gentle apertural elevations, can be observed in the *Bohemograptus* stem lineage as early as in the lowermost *leintwardinensis* Biozone. The only Bohemian *B. cornutus* comes from the upper *tenuis* Biozone of the present section. We retain an undivided *tenuis* Biozone to designate the postsaetograptid extinction interval in the Barrandian area until more data are available for higher-resolution subdivision. Holland and Palmer (1974) used the *B. tenuis* Biozone to designate strata with a monospecific bohemograptid fauna overlying the *S. leintwardinensis* Biozone in the Welsh Borderland (see *Bohemograptus* proliferation Zone in Zalasiewicz *et al.* 2009).

***Leintwardinensis* Event – discussion**

Earlier studies on the diversity and dynamics of Ludlow graptolite faunas of the Prague Synform published by Přibyl (1983) and Štorch (1995b) reviewed, for the most part, data gathered from a number of taxonomic papers and a number of scattered localities and outcrops. No reasonably complete section running through the late Gorstian and early Ludfordian hemipelagic succession was sampled in detail.

Inevitably, graptolite diversity was significantly underestimated with c. 7 species reported from both the *leintwardinensis* and *tenuis* biozones. More complete data, based upon the considerably more diverse graptolite faunas of the Polish part of the East European Platform and Arctic Canada, have been presented by Urbanek (1966) and Lenz (1988, 1990) respectively.

Urbanek (1970) recognized an early Ludfordian graptolite extinction event in the Mielnik deep boring on the East European Platform. This crisis, manifested by the extinction of the last plectograptid retiolitids, the spinose monograptids of the genus *Saetograptus* and the last operculate monograptids of the genus *Cucullograptus*, was further investigated by Urbanek (1993) and Koren' (1993). The Všeradice section exhibits features both differing from and agreeing with the model presented by Urbanek (1993). The sudden demise of the saetograptids, succeeded by the extinction of cucullograptid species, and completed with the disappearance of the last *C. rostratus*, is regarded as the principal signature of the so-called *leintwardinensis* Event. This corresponds with Urbanek's (1993) Figure 2. However, no particular proliferation, or monospecific assemblages of *Bohemograptus* were recorded in the postextinction interval in Bohemian sections, although *B. tenuis* is common and accompanied by *B. praecornutus*? and rare *B. cornutus*. *Eggregiograptus* may be regarded as an opportunistic immigrant of cryptic origin. It should be noted that most taxa that appeared in the Barrandian succession just before and during the *leintwardinensis* Event, such as *P. dalejensis*, *B. cornutus*, *C. rostratus*, *Eggregiograptus* and possibly also *B. praecornutus* and *Cucullograptus aversus*, made their lowest occurrences much earlier in the *leintwardinensis/linearis* or even *scanicus/chimaera* biozones in the East European Platform (Urbanek 1966, 1993) and Tien Shan (Koren' and Sujarkova 2004). In the Prague Basin, some of these taxa appear to have been opportunistic immigrants probably benefiting from a changing environment and/or filling empty niches.

Melchin *et al.* (1998, p. 175) assumed that the magnitude of the *leintwardinensis* Event, although calculated from limited published data, fell within the range of background extinction rates. This appears true if only the biodiversity curve and origination/extinction rates are considered. The extinction crisis, however, includes many aspects that cannot be clearly expressed in the form of a biodiversity curve, that is, the nature, abundance and palaeogeographical distribution of species. It is important to note that the *leintwardinensis* Event saw the extinction of an abundant and cosmopolitan graptolite genus (*Saetograptus*) and several other taxa also appeared/disappeared from the fossil record close to this stratigraphical level. After the *leintwardinensis* Event, graptolites became markedly less abundant in the sedimentary succession of the Prague Synform. Graptolite lineages with a successful morphological novelty, such as the lateral apertural spines of *Saetograptus*, usually did not vanish during background extinction, but during a global crisis. This provides a good reason to examine the *leintwardinensis* Event in more detail.

There is a general consensus in tracking early Ludfordian eustatic oscillations. Johnson (1996, 2006, 2009) and Haq and Schutter (2008) concluded that the late *leintwardinensis* Zone coincides with a low-stand interval and the *tenuis* (*bohemicus*) Zone with a rising sea level or high stand. Eustatic curves differ a little, particularly in the way that they are plotted against biozones. Johnson (2006, 2009) grouped several biozones together, so it is difficult to be precise about timing. The general picture, however, is in full agreement with the relatively shallow, limestone-dominated facies of the Prague Synform, where shallow water skeletal limestones of the *leintwardinensis* (former *linearis*) Biozone are topped with muddy limestones or platy limestones intercalated with shales (see Manda and Kříž 2006). As noted above, the same eustatic pattern is documented in the offshore Všeradice section. Consequently and unusually, the extinction of saetograptids and cucullograptids, and the lesser abundance of graptolites must have coincided with rising sea level.

Jeppsson (1990, 1998) and Jeppsson and Aldridge (2000) described a conodont extinction (the Linde Event) and suggested that this extinction coincided with the *leintwardinensis* Event of Urbanek (1993). However, the definition of the Linde Event and its correlation with graptolite zones is dubious, as Jeppsson and Aldridge (2000, p. 1141) stated that 'no section has yet been identified that displays the onset of the event'. The *Ancoradella ploeckensis* conodont Biozone terminates in the Požáry section at the base of the limestone bank with *Metacalymene baylei* (Slavík *et al.* 2010) in the middle part of the *leintwardinensis* Biozone. As the Linde Event falls in the uppermost part of the latter conodont zone, it may be concluded that the Linde Event preceded the *leintwardinensis* Event. The synchronicity of conodont and graptolite extinctions is commonly questionable. Loydell (2007) showed that the conodont extinctions that marked the early Silurian Ireviken and Mulde events accompanied high sea level and clearly preceded the subsequent graptolite extinctions. In a similar manner, Manda *et al.* (2012) encountered the conodont extinction associated with the Lau Event slightly below the graptolite extinction of the *kozłowskii* Event. It appears clear that these two groups, with their different modes of life, strategies and niches, responded in a different manner to environmental changes.

It is difficult to evaluate the effect of the *leintwardinensis* Event on other macrofauna due to the low biostratigraphical resolution of published data. The task is difficult even in the Prague Synform, which is one of the best-known areas. The cephalopods may serve to demonstrate this point. They were abundant and diverse, including many lineages with different life strategies (Manda and Frýda 2010). More than 80 species of cephalopods are known from the *leintwardinensis* (= *linearis*) Biozone, whilst 40 species are reported from the overlying *tenuis* Biozone. The majority of taxa that did not survive into the *tenuis* Zone are nautiloids (see e.g. Engesner 1996 for systematic position of nautiloids, straight-shelled orthoceratoids and pseudorthocerids within the Cephalopoda).

Nautiloids, in contrast to the straight-shelled forms, are characterized by a long embryonic development in eggs and a generally demersal habit of early-hatched specimens. Consequently, they are less tolerant to changes in environment and are usually strongly affected during global crises (Manda and Frýda 2010). The vast majority of nautiloids known from the *leintwardinensis* Biozone represent immigrants of Baltic origin and their descendants. The immigration of nautiloids from the tropical zone into the Prague Basin (*sensu* Kříž 1991), located in the southern temperate zone, usually coincided with low stands during which migration pathways were opened (Histon 2012) and large submarine highs suitable for nautiloids appeared in the basin. During the deepening, these local populations usually became extinct and only a small proportion of the immigrant species survived. Similar distribution patterns can be found in many other groups with an evolutionary centre in the tropical zone, such as the onychochiloid gastropods or calymenid trilobites known from the *leintwardinensis* Biozone, but unknown in the *tenuis* Biozone. Consequently, the extinction of several groups of macrofauna in the Prague Basin may be explained by eustatic oscillation and associated changes in the current system and shallow water domains and in fact may represent recurrent pulsation of dispersion areas during which various lineages survived in the tropical zone and extinction terminated only local populations and endemic species inhabiting marginal parts of the dispersion areas (e.g. Manda 2008).

In evaluating the graptolite extinction, it is important to note that the *leintwardinensis* Event did not affect the pelagic straight-shelled cephalopods, which are, together with the graptolites, the prevailing pelagic fossils in the Silurian. This is not an exception as other graptolite crises exhibit a similar pattern (Manda and Frýda 2010). In the Všeradice section, nevertheless, the abundance and shell size of pelagic orthocerids substantially decreased in the postextinction interval. Myodocopid ostracods (Perrier *et al.* 2011), important components of the pelagic fauna, did not change during the early Ludfordian. The nektonic phyllocarid *Ceratiocaris papillio* disappeared during the *leintwardinensis* Event, but its descendants reappear higher up the section (Budil *et al.* 2010).

As noted above, the Všeradice section records an offshore environment with rather stable conditions. The graptolite record can be traced from the upper Wenlock through to the lower Přídolí in a single continuous section, including the well-developed middle Homerian *lundgreni* Event and middle Ludfordian *kozłowskii* Event. Hence, the two well-defined and worldwide recognized graptolite crises can be compared with the supposed *leintwardinensis* Event within the same section and equivalent depositional settings. All three crises are marked by a sudden drop in graptolite diversity and a postextinction interval characterized by either long-ranging generalists or their offshoots evolved through iterative speciation. The *lundgreni* Event brought graptolites near to extinction (Jaeger 1991; Urbanek 1993; among others), whilst the *kozłowskii* Event was selective in its elimination of all of the ventrally curved taxa

(Manda *et al.* 2012). The *leintwardinensis* Event was the least destructive but still wiped out proliferating and widespread taxa. Further comparison of the three graptolite crises revealed the following:

1. Saetograptids maintained species diversity and further proliferated in abundance before their sudden demise at the top of the *leintwardinensis* Zone. A similar pattern of species abundance is known from the *lundgreni* Event (demise of abundant *Monograptus* and early plectograptids), but is less evident in the *kozlowskii* Event due to the relatively low abundance of late Ludfordian graptolites in general.
2. The postextinction interval of the *kozlowskii* crisis is almost devoid of graptolites, whilst the postextinction interval of the *leintwardinensis* Event hosts several albeit uncommon surviving taxa. A marked proliferation of *Bohemograptus* (see Urbanek 1993 for references) after the *leintwardinensis* Event has not been observed in the Všeradice section.
3. The postextinction interval of the *lundgreni* Event (i.e. *P. parvus* – *G. nassa* Biozone) exhibits the proliferation of two surviving taxa (*Pristiograptus* and *Gothograptus*) as well as distinct dwarfism (lilliput effect of Urbanek 1993), which developed in pristiograptid populations across Gondwana and Baltica. The small rhabdosomes of *P. dalejensis* (Bouček), an important component of the postextinction assemblage after the *leintwardinensis* Event, can also be regarded as a dwarf offshoot, this time from the *Pseudomonoclimacis* stem lineage.
4. The *leintwardinensis* and *kozlowskii* extinctions opened niches for the subsequent immigration of exotic taxa of cryptic origin (*Egregiograptus* after the former and *Slovinograptus* after the latter). After the *lundgreni* Event, immigration of exotic elements of cryptic origin was not that rapid, beginning in the *Colonograptus praedeubeli* – *Colonograptus deubeli* Zone.

In the light of our detailed study of the Všeradice section and with respect to other relevant sections within the Prague Synform, the early Ludfordian *leintwardinensis* Event manifests itself as a moderate extinction with different impacts on different groups of the macrofauna. It may be readily distinguished from background extinction. The graptolite extinction comprised the sudden disappearance of the cosmopolitan *Saetograptus*, demise of the last plectograptines and extinction of *Cucullograptus*. The extinction is followed by a postextinction interval with low-diversity faunas and subsequent immigration of some taxa of cryptic origin. With the exception of the *transgrediens* Event, it is the only graptolite extinction connected with deepening, something usually coupled with graptolite proliferation (Melchin *et al.* 1998). The roughly coeval extinction in pelagic cephalopods is in need of further investigation in carbonate-dominated sections with better preserved shells. Weak effects on other fauna are possible, but more data are needed. The Linde conodont extinction Event most probably preceded the *leintwardinensis* Event, although sections with combined graptolite and conodont records enabling high-resolution correlation between these two principal biostratigraphical tools are unknown. The

environmental background to the *leintwardinensis* Event remains obscure. Offshore shaly sedimentation remained unchanged in the Všeradice section. Most of the Silurian global extinction events are coupled with carbon isotope excursions, a feature until now unknown from the lower Ludfordian. Cramer *et al.* (2011) illustrated a very slight carbon isotope excursion in the early Ludfordian, but based on very limited data. The data obtained by Lehnert *et al.* (2007) from limestone-dominated sections of the Prague Synform do not exhibit significant and consistent changes in $\delta^{13}\text{C}_{\text{carb}}$ values across this interval. However, data are rather limited and further studies are needed due to the potential gaps in limestone sedimentation.

Systematic palaeontology

This published work and the nomenclatural act it contains have been registered in

Zoobank:<http://www.zoobank.org/References/970FAFA2-CA29-4865-8570-798F07927B08>.

Genus HOLORETIOLITES Eisenack, 1951

Type species

Holoretiolites mancki (Münch, 1931); from erratic boulders from Uckemark, Templin, Germany (lower Ludlow).

Diagnosis

After Kozłowska-Dawidziuk (1995, p. 307).

Holoretiolites sp. Figure 5B–C

Remarks

Several fragmentary rhabdosomes assignable to *Holoretiolites* came from samples 70a and 68 (upper part of the *scanicus–chimaera* Biozone) in the middle part of the VD trench. This is the stratigraphically highest record of plectograptines in the Prague Synform. The distally narrowing rhabdosomes possess zig-zag parietal lists and a poorly developed reticular meshwork. Width of ancora umbrella is 0.7–0.9 mm; appendix and distal part of the rhabdosome have not been preserved. Among described species of *Holoretiolites*, the present specimens are most similar to *H. mancki* (Münch, 1931) and *Holoretiolites erraticus* Eisenack, 1951.

Figure 5. A, D, *Pseudomonoclimacis kosoviensis* (Bouček, 1931); A, PŠ3116, sample 26b, *tenuis* Biozone; D, PŠ3058, sample 40c, lower *tenuis* Biozone. B–C, *Holoretiolites* sp., PŠ3198(1, 2), sample 68, upper *scanicus–chimaera* Biozone. E–F, M, *Pseudomonoclimacis dalejensis* (Bouček, 1936); E, PŠ3059, sample 34b, *tenuis* Biozone; F, L30887, ?*tenuis* Biozone, paratype figured by Bouček (1936, text-fig. 2f); M, PŠ3049, sample 38b, lower *tenuis* Biozone. G, O, *Pseudomonoclimacis antiqua* sp. nov.; G, PŠ3153, sample 52b, upper *leintwardinensis* Biozone; O, PŠ3102, sample 70b, *scanicus–chimaera* Biozone. H, P–R, *Pristiograptus tumescens* (Wood, 1900); H, PŠ3187, *scanicus–chimaera* Biozone, sample 70b; P, PŠ3184, sample 58a; Q, PŠ3146, sample 58b; R, PŠ3208, sample 62a, lower *leintwardinensis* Biozone. I–J, *Colonograptus roemeri* (Barrande, 1850); I, PŠ3208, sample 62a; J, PŠ3143, sample 60b, lower *leintwardinensis* Biozone. K, *P. cf. dalejensis* (Bouček, 1936), PŠ3056, sample 40c, *tenuis* Biozone. L, N, *Pristiograptus frequens* (Jaekel, 1889); L, PŠ3179, sample 54a, *leintwardinensis* Biozone; N, PŠ3200, sample 62b, lowermost *leintwardinensis* Biozone. All specimens from the Všeradice section, except for L30887 (F) from Mušlovka quarry near Řeporyje. All scale bars represent 1 mm.

Genus PRISTIOGRAPTUS Jaekel, 1889

Type species

Pristiograptus frequens Jaekel, 1899; from erratic boulders from North Germany (lower Ludlow, *L. scanicus* Biozone).

Diagnosis

After Urbanek (1958, p. 12).

Pristiograptus frequens (Jaekel, 1889) *sensu* Jaeger, 1991 Figures 5L, N, 6A–C, E

1889

Pristiograptus frequens Jaekel, pp. 669–671, pl. 28, figs 1, 2.

1936

Pristiograptus dubius (Suess) *ludlowensis* n. mut.; Bouček, pp. 6–7, pl. 1, figs 8–10.

non 1943

Pristiograptus frequens Jaekel; Přibyl, pp. 22–23, pl. 3, fig. 13; text-fig. 3a.

1943

Pristiograptus dubius ludlowensis (Bouček); Přibyl, pp. 5–6.

1943

Pristiograptus vicinus (Perner); Přibyl, pp. 15–16 (*partim*), text-fig. 1, fig. 2; text-fig. 2n (*non* o, p).

?1955

Monograptus dubius (Suess); Kühne, p. 360, fig. 2a–d, g–h.

1991

Monograptus dubius frequens (Jaekel); Jaeger, p. 314, text-fig. 25, figs 9, 11, 15.

2012

Pristiograptus dubius frequens Jaekel; Urbanek *et al.*, pp. 600, 602–603; figs 5 m, 11a–c, f–h.

Figure 6. A–C, E, *Pristiograptus frequens* (Jaekel, 1889); A, PŠ3179, sample 54a, *leintwardinensis* Biozone; B, PŠ3250, sample 78, *scanicus–chimaera* Biozone; C, PŠ3200, sample 62b, lower *leintwardinensis* Biozone; E, PŠ3097, sample 20b, lower *inexpectatus* Biozone. D, K–M, *Pristiograptus tumescens* (Wood, 1900); D, PŠ3187, sample 70b, upper *scanicus–chimaera* Biozone; K, PŠ3146, sample 58b, lower *leintwardinensis* Biozone; L, PŠ3208, sample 62a, lower *leintwardinensis* Biozone; M, PŠ3184, sample 58a, lower *leintwardinensis* Biozone. F, H, J, *Pseudomonoclimacis dalejensis* (Bouček, 1936); F, PŠ3055, sample 36, *tenuis* Biozone; H, L30887, ?*tenuis* Biozone, paratype figured by Bouček (1936, text-fig. 2f); J, PŠ3049, sample 38b, lower *tenuis* Biozone. G, I, *Pseudomonoclimacis* cf. *dalejensis* (Bouček, 1936); G, PŠ3056; I, PŠ3057, sample 40c, lower *tenuis* Biozone. N, *Saetograptus* sp. A. PŠ3178b, sample 54a, *leintwardinensis* Biozone. O, *Pseudomonoclimacis* sp. PŠ3251, sample 50, upper *leintwardinensis* Biozone. P, *Pseudomonoclimacis kosoviensis* (Bouček, 1931), PŠ3116, sample 26b, upper *tenuis* Biozone. Q–S, *Pseudomonoclimacis antiqua* sp. nov.; Q, PŠ3153, sample 52b, upper *leintwardinensis* Biozone; R, PŠ3182, sample 58a, lower *leintwardinensis* Biozone; S, PŠ3102, sample 75, *scanicus–chimaera* Biozone. All specimens from the Všeradice section, except for L30887 (F) from Mušlovka quarry near Řeporyje. All scale bars represent 1 mm.

Neotype (designated herein)

Chemically isolated specimen g.458.3.1 figured by Jaeger (1991, text-fig. 26, fig. 9), from erratic boulder collected at Hiddensee Island near Rügen, Baltic Sea, Germany. Lower Ludlow, *S. chimaera* Biozone.

Material

More than 30 flattened rhabdosomes from the upper *scanicus*–*chimaera*, *leintwardinensis* and *tenuis* biozones of the Všeradice section (Fig. 2).

Diagnosis

Modified from descriptions by Jaeger (1991) and Urbanek *et al.* (2012). Relatively narrow (1.6 mm maximum width), gradually widening pristiograptid; rhabdosome gently ventrally curved up to th 5 at least. Angle between thecal aperture and succeeding theca right or obtuse, distinct apertural lips do not extend onto the ventral wall of the succeeding theca and end near the beginning of the free ventral thecal wall.

Description

The straight, 10- to 30-mm-long rhabdosomes possess a slightly ventrally curved proximal end comprising *c.* 5 proximal thecae. The sicula is 1.7–2.0 mm long and 0.2–0.36 mm wide across the slightly concave aperture. Its apex attains approximately the level of th 2 aperture. The rather short th 1 emerges almost immediately above the sicular aperture; its ventral wall is markedly convex. Subsequent thecae are simply cylindrical, of typical pristiograptid form, with slightly concave apertures, which are mostly perpendicular to the thecal axis. Thus, the angle between thecal aperture and free wall of the subsequent theca (angle β *sensu* Urbanek *et al.* 2012) is right, rather than obtuse, in profile view. Distal thecae overlap for half their length and are inclined at an angle of about 30 degrees to the rhabdosome axis. The width of the rhabdosome varies both throughout the stratigraphical succession and within individual sampling levels. It is 0.65–0.9 mm wide at th 1, 0.8–1.2 mm at th 3 and 1.0–1.45 mm at th 5. The maximum width of 1.2–1.6 mm is attained by theca 8–13. 2TRD increases from 1.2–1.6 mm at th 2, through 1.35–1.9 mm at th 5 to 1.6–2.1 mm in distal thecae, which number 9.5–12.5 in 10 mm.

Discussion

Jaekel's type material of *P. frequens* is lost (J. Maletz, pers. comm.), including the lectotype (Jaekel 1889, pl. 28, fig. 1) designated by Přibyl (1943, p. 22). We designate the specimen illustrated and described by Jaeger (1991) as neotype. The specimen came from erratic boulder of Baltoscandinavian origin, from a stratigraphical level supposedly similar to that of the original material described by Jaekel (1889), and corresponds with the morphological concept of *P. frequens* conserved by Jaeger (1991) and Urbanek *et al.* (2012). Considerable variation in rhabdosome width, thecal length and spacing can be observed in Czech material both within bedding-plane associations and between different sampling levels. No sicular rings

noted by Urbanek *et al.* (2012) have been observed due to the preservation, as is the case as in most other taxa encountered at Všeradice. Urbanek *et al.* (2012) distinguished *P. frequens* from *P. dubius* (Suess, 1851) by its having the sicular rings. The type material of *P. dubius*, however, includes neither the sicula nor the proximal part of the rhabdosome. Also preservation of other topotypical specimens of *P. dubius* from the middle Sheinwoodian of the Prague Synform does not allow for recognition of the sicular rings. The only observable difference between *P. frequens* and its possible successor, *P. dubius postfrequens* (Urbanek *et al.* 2012), is the apertural lip ending near the beginning of the ventral wall of the subsequent theca. *P. dubius ludlowensis* described by Bouček (1936) from the lower Ludlow of the Barrandian Synform falls within the range of broad variability of *P. frequens* in all parameters. It is therefore regarded as a junior synonym of the latter species.

Pristiograptus tumescens (Wood, 1900) Figures 5H, P–R, 6D, K–M; Table 1

1900

Monograptus tumescens Wood, p. 458, pl. 25, fig. 5a, b; text-fig. 11.

cf. 2001

Pristiograptus ?kosoviensis (Bouček); Rickards, pp. 450–451, fig. 1a–h.

1956

Pristiograptus (Pristiograptus) tumescens tumescens (Wood); Tomczyk, p. 54, pl. 7, fig. 2; text-fig. 15b.

2012

Pristiograptus cf. tumescens minor (Wood); Legrand, pp. 664, 666; fig. 4a–d.

2012

Pristiograptus tumescens (Wood); Urbanek *et al.*, p. 606, figs 5n, 12a–f.

Table 1. *Pristiograptus tumescens* (Wood, 1900)

Specimen	Figures	W				2TRD		
		th 1	th 3	th 5	Dist. max./th	th 2	th 5	Dist. th
BU1472, lectotype	See Zalasiewicz <i>et al.</i> (2000)	0.8	?	1.45	1.9/th 9–10	1.6	1.6	2.0
PŠ3187(1)	5H	0.85	1.2	1.65	1.9/th 13	1.1	1.3	1.5
PŠ3187(2)	6D	0.8	1.4	1.65	1.75/th 8	1.25	1.45	1.75
PŠ3184	5P,6M	0.9	1.25	1.6	1.9/th 9–17	1.3	1.5	1.75
PŠ3146	5Q,6K	0.95	1.2	1.6	2.4/th 9–10	1.35	1.65	1.85
PŠ3208	5R,6L	0.8	1.3	1.65	1.95/th 8	1.5	1.3	1.45

Dimensions of figured specimens and lectotype (in mm).

Material

Thirty-six flattened, mostly immature rhabdosomes from the upper *scanicus–chimaera* and lower *leintwardinensis* biozones (samples 70b–58a) of the Všeradice section (Fig. 2).

Description

The rhabdosome is usually 10–15 mm (max. 29 mm) long, with a ventrally curved proximal part, abruptly becoming straight at the level of theca 4–8. Whereas the dorsal wall of the rhabdosome diverges from the longitudinal axis at an angle of 10–12 degrees in its proximal part, the ventral rhabdosome outline maintains an almost straight course. The rhabdosome widens rapidly from 0.8–0.95 mm at th 1 aperture, through 1.2–1.4 mm at th 3 and 1.55–1.85 (max. 2.0) mm at th 5, to 1.65–2.2 (max. 2.4) mm which is attained usually by theca 7–10. One rhabdosome, however, attained its maximum width already at th 5, whereas another one increased widening until th 13. The sicula is conical, straight, 1.5–1.8 mm long (max. value 2.0 mm) with a concave, 0.35- to 0.42-mm-wide aperture possessing a tiny virgella. The sicular apex attains the level of either th 2 aperture or, less commonly, th 3 aperture. The first theca is c. 1 mm long, with a slightly concave ventral wall and everted aperture. Subsequent thecae are straight tubes, inclined at an angle of 35–45 degrees to the rhabdosome and overlapping for one-half to two-thirds their length. Thecal apertures with thickened lips appear perpendicular or slightly introverted depending on the rhabdosome orientation to the bedding plane and mode of its flattening. Thecae are densely spaced, with 2TRD th 2 = 0.95–1.35, 2TRD th 5 = 1.2–1.65 mm and distal 2TRD = 1.45–1.6 (max. 1.85) mm. Distal thecae number 12.5–13.8 in 10 mm.

Discussion

The present material differs from the type collection of Elles and Wood (1911) in having more densely spaced thecae inclined at a higher angle (35–45 degrees compared with c. 30 degrees reported by Elles and Wood, although some specimens figured by the latter authors exhibit thecal inclination up to 40 degrees). The specimens figured by Urbanek *et al.* (2012) exhibit distinct variation in thecal spacing and inclination, which is also observed in our material. Instead, a diagnostic significance was found by Urbanek *et al.* in thecal apertures being perpendicular to the free ventral wall of the succeeding theca and thickened apertural lips reaching high on the succeeding theca. The latter trait, however, can be barely recognized in few of the flattened specimens from Všeradice. Rickards and Wright (2003) pointed out the rapid increase in dorso-ventral width and angular ventral curve of the proximal part involving 4–6 thecae in topotypical collections of *P. tumescens* from the Long Mountain and Ludlow areas of Shropshire. These two features, as well as the straight ventral outline of the relatively wide rhabdosomes, are readily distinguishable in the present material and clearly differentiate *P. tumescens* from pristiograptids of *P. dubius* Group. *P. frequens* and related forms of Gorstian – early Ludfordian age can be further differentiated from *P. tumescens* by having a gently and regularly ventrally curved proximal part of the rhabdosome and shorter, considerably less overlapping thecae.

Genus PSEUDOMONOCCLIMACIS Mikhaylova, 1975

Type species

Pseudomonoclimacis elegans Mikhaylova, 1975; from the Přídolí of Kazakhstan.

Diagnosis

After Lenz and Kozłowska-Dawidziuk (2004, p. 23).

Discussion

The genus *Pseudomonoclimacis* was derived from the *Pristiograptus* stem line in the early Gorstian progenitor Zone. Its long-ranging early representative *P. antiqua* was replaced by the particularly robust *P. kosoviensis* in the *tenuis* Interval Zone, and the whole group further diversified during the Ludfordian. Pseudomonoclimacids can be distinguished from coeval pristiograptid taxa by their more ventrally curved sicula with dorsal apertural tongue, commonly somewhat S-shaped most proximal part of the rhabdosome, and thecae of moderately to strongly geniculated appearance, having well-developed, continuous and arcuate, thickened interthecal septa. The nema is robust and projects well beyond the thecate part of the rhabdosome. Thecal apertures tend to be more complex than in pristiograptids: the proximal thecae of many late mature specimens possess hook- or hoodlike apertural overgrowths as illustrated by Rickards and Palmer (1977) and Manda *et al.* (2012). Such thecae, when flattened, appear hooked in outline.

Pseudomonoclimacis antiqua sp. nov. Figures 5G, O, 6Q–S; Table 2

LSID

urn:lsid:zoobank.org:act:819BA77B-7B13-4725-A75C-C98851775EA6

Table 2. *Pseudomonoclimacis antiqua* sp. nov.

Specimen	Figures	W				2TRD			
		th 1	th 5	th 10	Dist. max./th	th 2	th 5	th 10	Dist. th
PŠ3153	5G,6Q	0.63	1.0	1.25	>1.45	1.6	1.9	2.2	2.3
PŠ3102	5O,6S	0.55	0.85	1.35	1.8/th 16–20	1.25	1.5	1.6	2.0
PŠ3182	6R	0.55	0.75	1.0	>1.45	1.25	1.35	1.55	1.8
PŠ3183	–	0.62	1.5	1.4	>1.55	1.55	1.8	2.0	2.45
PŠ3255	–	0.6	0.95	1.25	1.8	?	1.85	1.95	2.2

Dimensions (in mm) of specimens from sampled part of the section.

1936

Monograptus contumax n. sp., Bouček, pp. 12–13 (*partim*), text-fig. 1i, j (*non* pl. 2, figs 6–8).

1943

Pristiograptus frequens Jaekel, 1889; Přibyl, pp. 22–23, pl. 3, fig. 13; text-fig. 3a.

Derivation of name

Latin, *antiquus*, old, ancient.

Holotype

PŠ3102 (Figs 5O, 6S), from sample 70b, *scanicus*–*chimaera* Biozone, Kopanina Formation, Všeradice section.

Material

Twenty-five flattened rhabdosomes from the upper *progenitor*, *scanicus*–*chimaera* and *leintwardinensis* biozones of the Všeradice section (from stratigraphically below the present log up to sample 50), and specimens figured by Bouček (1936).

Diagnosis

Rhabdosome, straight, widening very gradually from narrow proximal portion. Sacula small, commonly ventrally curved, furnished with dorsal apertural lobe. Simple, pristiograptid thecae are slightly geniculated, with prominent intertheatal septa. Distal thecae overlap for barely more than one-half even in the most mature rhabdosomes.

Description

The straight rhabdosome attains a maximum length of more than 50 mm. It widens gradually and regularly from 0.5–0.63 mm at the level of th 1 aperture, through 0.75–1.05 mm at th 5 and 0.9–1.4 mm at th 10, to the maximum distal width of 1.45–1.85 mm. The sicula is 1.55–1.8 mm long, gently ventrally curved, 0.2–0.3 mm wide across the aperture. The sicular aperture appears to be facing towards the virgella due to a broad dorsal apertural lobe developed in the great majority of our specimens. The sicular apex is situated at about the level of th 2 aperture. Thecae are weakly geniculated, with a prominent interthecal septum and aperture which is almost perpendicular to the thecal tube. Distal thecae are 1.7–2.0 mm long and overlap for about half their length. 2TRD is 1.25–1.6 mm at th 2 and then rapidly increases to 1.35–1.9 mm at th 5 and 1.55–2.25 mm at th 10. Distal thecae number 8–11 in 10 mm (2TRD = 1.8–2.5 mm). The robust nema can project distally well beyond the thecate part of the rhabdosome.

Discussion

Pseudomonoclimacis antiqua sp. nov. is closely similar to *P. kosoviensis* (Bouček, 1931) and '*Monograptus*' sp. of Rickards and Palmer (1977) which share a gradually widening rhabdosome with very rigid nema, pseudomonoclimacid thecae and secondary lateral apertural outgrowths developed in the proximal thecae of some mature rhabdosomes. '*Monograptus*' sp. of Rickards and Palmer (1977) and *Monoclimacis* sp. 1 of Rickards and Jordan (1975) can be distinguished solely by their larger, up to 2.5-mm-long sicula, the apex of which attains a level above the aperture of th 2, and by the wider (up to 2.5 mm) rhabdosome. Also the stratigraphically younger *P. kosoviensis* (Manda *et al.* 2012), including the paratypes of *Pristiograptus contumax* Bouček, 1936 (text-fig. 1i–j), exhibits a more robust rhabdosome with more widely spaced and more overlapping thecae. Přibyl (1943) placed *Pristiograptus contumax* Bouček, 1936 in synonymy with *P. frequens* Jaekel, 1899, but the holotype figured by Bouček (1936, pl. 2, 6–8) matches *Colonograptus colonus* (Barrande) instead. It is marked by a slightly ventrally curved and rapidly widening proximal part, steeply inclined proximal thecae with lateral apertural processes and long, greatly overlapping distal thecae. *P. frequens* and other pristiograptids of the *dubius* group (*sensu* Rickards and Wright 2003; Urbanek *et al.* 2012) can be readily distinguished from *P. antiqua* by their rapidly widening rhabdosome which is significantly ventrally curved in the proximal part, entirely straight thecae and considerably less prominent nema. The sicula of *P. frequens* and its relatives is little curved ventrally, if at all, and typically lacks the dorsal tongue. Mature specimens of *P. antiqua* differ from the typical pristiograptid morphology of *P. frequens* (Figs 5L, N, 6A–C, E, and Jaeger 1991, pl. 25, figs 9, 11, 15), also in their proximal thecal apertures with more or less developed apertural additions which, although known in some other Ludlow monograptids (Jaeger 1978; Rickards 1875; this study), are most commonly seen in this lineage (Rickards and Palmer 1977). This species is regarded as a less advanced, ancestral pseudomonoclimacid that evolved from the pristiograptid stem lineage in the course of the earliest (or early) Gorstian radiation. Thecal geniculation is slightly developed, and interthecal septa appear to be less thickened than in descendent

forms. The ventrally curved sicula with its dorsal lobe, the straight, gradually and steadily widening rhabdosome, as well as occasional apertural additions in proximal thecae suggest its assignment to *Pseudomonoclimacis*.

Pseudomonoclimacis dalejensis (Bouček, 1936) Figures 5E–F, M, 6F, H, J; Table 3

1936

Monograptus dalejensis Bouček, p. 146, text-fig. 2f–i.

1942

Pristiograptus (Colonograptus) dalejensis (Bouček); Příbyl, p. 11, text-fig. 2, figs 7, 8.

1955

Monograptus haupti n. sp., Kühne, p. 365, text-fig. 3a, b, d–f.

1958

Monoclimacis haupti (Kühne); Urbanek, p. 88, figs 59–64, pl. 4, fig. 5.

1967

Pristiograptus ultimus; Koren' and Ulst, p. 250, pl. 29, figs 10, 11.

1974

Pristiograptus (?) *tauragensis*, Paškevičius, p. 130, pl. 17, figs 7–10; text-fig. 3a, b.

1976

Pseudomonoclimacis tauragensis (Paškevičius); Tsegelnyuk, p. 105, pl. 30, figs 8, 9.

1979

Pseudomonoclimacis tauragensis (Paškevičius); Paškevičius, p. 158, pl. 9, figs 8, 9; pl. 24, figs 11–15.

1979

Monograptus haupti Kühne; Jaeger and Robardet, pl. 1, fig. 3.

1986

Monograptus dalejensis Bouček; Jaeger (*in Kříž et al.*), pl. 2, figs 1, 2.

1988

Pseudomonoclimacis tetlitensis Lenz, p. 359, pl. 1i, j; text-fig. 2e–i.

1990

Pseudomonoclimacis dalejensis (Bouček); Lenz, fig. 4v–y, aa.

1990

Pseudomonoclimacis tetlitensis Lenz; Lenz, fig. 3k–m.

1992

Pseudomonoclimacis dalejensis (Bouček); Lenz, p. 206 (*partim*), pl. 3B, E–G (*non* A, C–D).

1993

Monograptus dalejensis Bouček; Rickards *et al.*, p. 127, figs 3a–f, 4a–d.

1995b

Monograptus dalejensis dalejensis Bouček; Rickards *et al.*, p. 46, figs 25d, 26a–e.

1995

Monograptus dalejensis Bouček; Štorch, p. 69, pl. 5, fig. 6; pl. 6, fig. 4; text-fig. 8d–i.

1999

Monograptus? haupti Kühne; Maletz, p. 287, fig. 3a–f.

2004

Pseudomonoclimacis dalejensis dalejensis (Bouček); Lenz and Kozłowska-Dawidziuk, pp. 24–25, pl. 44, figs 4–8, 11–16, 18–29.

2012

Pseudomonoclimacis dalejensis (Bouček); Manda *et al.*, fig. 7i.

Table 3. *Pseudomonoclimacis dalejensis* (Bouček, 1936).

Specimen	Figures	W				2TRD		
		th 1	th 3	th 5	Dist. max./th	th 2	th 5	th 10
PŠ3059	5E	0.65	0.95	1.15	1.4/th 8	1.2	1.35	1.55
L30887, paratype	5F,6H	0.7	1.5	1.3	>1.6/?	1.25	1.4	–
PŠ3049	5M,6J	0.7	0.95	1.3	1.6/th 9	1.15	1.45	1.6
PŠ3055	6F	0.6	0.85	1.15	1.4/th 8	1.0	1.25	1.55

Dimensions of figured specimens, including paratype (in mm).

Material

More than 30 flattened rhabdosomes from the topmost *leintwardinensis* Biozone and *tenuis* Biozone of the Všeradice section (Fig. 2) and specimens from *inexpectatus* and *kozlowskii* biozones (Mandaet *al.* 2012) above the present log; material from Kosov quarry (Štorch 1995a) and the type material figured by Bouček (1936) and Přibyl (1942).

Description

The small, *c.* 10-mm (max. 16 mm)-long, generally straight rhabdosome is characterized by a slightly S-shaped most proximal part comprising the sicula and initial two thecae. This shape results from the prominent ventral curvature of the 1.4- to 1.7-mm long sicula. The curved dorsal wall of the sicula creates a more or less prominent hump in the dorsal outline of the rhabdosome. The sicular aperture is 0.2–0.22 mm wide, introverted towards the virgella and in many specimens furnished with a weakly developed dorsal lobe. The sicular apex attains the level of th 2 aperture, rarely up to half way up th 3.

The rhabdosome widens from 0.55–0.8 mm at th 2, through 0.8–0.95 mm (max. 1.1) at th 3 and 1.0–1.3 mm at th 5, to the maximum width of 1.3–1.6 mm attained by thecae 8–10. Extreme values of maximum dorso-ventral width, 1.0 and 1.75 mm, are due to intraspecific variability further enhanced by different modes of rhabdosome flattening.

The first theca is slightly everted, with a markedly concave, 0.55- to 0.85-mm-long ventral wall. The following thecae are slightly geniculated, with a short supragenicular wall and markedly thickened interthecal septum. The thecal aperture is generally straight and perpendicular to the axis of the theca. Distal thecae are 1.3–1.7 mm long and overlap for one-half to two-thirds their length. 2TRD is 1.0–1.3 mm at th 2, 1.25–1.45 mm at th 5 and 1.5–1.65 mm at th 10. Thecae number 12–13 in 10 mm in the distal part of the rhabdosome.

Discussion

Bouček (1936, text-fig. 2f–h) figured four badly preserved specimens from fragile shale above the limestone bank with *M. baylei* at Mušlovka Quarry. Due to partial decay of the holotype (text-fig. 2 g) and the rather deformed paratype of text-figure 2i, some diagnostic features, such as the slight sigmoidal curvature of the proximal end, ventrally curved sicula and rapid increase in dorso-ventral width within 6 or 7 weakly geniculated proximal thecae, are best seen in the paratype figured in Bouček's text-figure 2f. Several junior synonyms briefly discussed by Štorch (1995a) resulted from limited knowledge of the true appearance, variability and stratigraphical range of *P. dalejensis*. Some specimens from Arctic Canada, assigned to *P. dalejensis* by Lenz (1992, pl. 3, figs A, C–D), differ from the topotypical material in having a protracted, very gradually widening rhabdosome. Instead, these chemically isolated rhabdosomes closely resemble *P. antiqua*.

Pseudomonoclimacis cf. *dalejensis* (Bouček, 1936) Figures 5K, 6G, I

Remarks

Twelve flattened pseudomonoclimacid rhabdosomes with distinct dorsal curvature, from sample 40b (lower *tenuis* Biozone), are generally narrower (max width 1.1–1.35 mm) than *P. dalejensis*, and their maximum width is attained by th 5. Distal thecae are particularly densely spaced in these rhabdosomes (2TRD = 1.2–1.3 mm, c. 16 thecae in 10 mm). Other values do not differ from those measured in *P. dalejensis*. The present material is retained in open nomenclature until more, stratigraphically and morphologically distinct specimens with better preserved siculae are available for further biometric evaluation.

Pseudomonoclimacis kosoviensis (Bouček, 1931) Figures 5A, D, 6P

Remarks

Pseudomonoclimacis kosoviensis has been revised by Manda *et al.* (2012), who included a full synonymy of the species. In the lower Ludfordian part of the Všeradice section robust, more than 50 mm long, straight rhabdosomes, gradually widening to a maximum width of 2.5–2.9 mm, have been collected from the *B. tenuis* Biozone (beginning with sample 40b). They are further characterized by a thick, rigid nema and ventrally curved sicula with a dorsal apertural lobe. Some late mature, possibly even gerontic specimens exhibit also hooklike apertural outgrowths on the most proximal thecae as documented also by Manda *et al.* (2012). Immature colonies of *P. kosoviensis*, those comprising some 12–15 thecae at least, can be distinguished from other species of *Pseudomonoclimacis* by their steadily widening rhabdosome with relatively wide thecal spacing and low thecal inclination.

Remarks

A single, 48-mm-long rhabdosome from the upper *leintwardinensis* Biozone (sample 50) possesses at least twelve hooked or hooded proximal thecae and pristiograptid distal thecae that are more than 3 mm long. This specimen cannot be assigned to any described species with confidence. The sicula is heavily sclerotized, 1.7 mm long, and its apex attains the level of th 2. Proximal metathecae are partly isolated and terminated by a hook- or hoodlike apertural structure which can be distinguished up to th 12 at least. This apertural hook could perhaps be equivalent to the apertural outgrowths recorded in some pseudomonoclimacids. The rhabdosome widens rapidly from 0.93 mm at th 1 (including hook) to 1.6 mm at th 5 and then more gradually until the maximum width of 3.1 mm is attained at th 27. Another gerontic feature of this specimen can be seen in the subsequent gradual narrowing of the rhabdosome to only 2.5 mm near the distal end. Until more and better preserved specimens are found, the present specimen is tentatively assigned to *Pseudomonoclimacis* because of its hooklike apertural outgrowths which are present also in the most proximal thecae of some late mature rhabdosomes of, for example, *P. kosoviensis* (see Manda *et al.* 2012).

Genus COLONOGRAPTUS Přibyl, 1943

Type species

Graptolithus colonus Barrande, 1850; from the lower Kopanina Formation (Ludlow) of Bohemia.

Diagnosis

After Lenz and Kozłowska-Dawidziuk (2004, p. 28).

Colonograptus roemer (Barrande, 1850) Figures 5I–J, 7U–V

Remarks

Two robust rhabdosomes from samples 70b (upper *scanicus–chimaera* Biozone) and 62a (lowermost *leintwardinensis* Biozone) match *C. roemer* in having hooklike lateral apertural processes on th 1 and th 2, and the ventral thecal wall slightly extended beyond the thecal aperture in all subsequent thecae. The thecae are inclined at c. 50 degrees to the rhabdosome axis and overlap for three-quarters of their length which is almost 2 mm at c. th 10. Distal thecae number 13–14 in 10 mm. The two rhabdosomes are 16 and 18.3 mm long, with a ventrally curved proximal portion and straight to weakly dorsally curved distal part. Dorso-ventral width is 1.1 mm at th 1 (without apertural processes), 1.8 mm at th 5 and up to 2.3 mm distally. More common, typical specimens of *C. roemer* have been collected lower in the section, in the upper *progenitor* and in the lower *scanicus–chimaera* biozones.

Genus SAETOGRAPTUS Přibyl, 1943

Type species

Graptolithus chimaera Barrande, 1850; from the lower Kopanina Formation (Ludlow) of Bohemia.

Diagnosis

(Emended from Hutt 1969, Bulman 1970, Maletz 1997 and Lenz and Kozłowska-Dawidziuk 2004.) Straight to dorsally curved monograptids with cylindrical thecae terminated by paired apertural spines developed on all or only the proximal thecae. Th 1 aperture furnished by broad, highly triangular, spinelike lateral lappets; other apertures exhibit ventral notch and laterally to dorso-laterally situated spines separated by a trough from the ventral wall of the next theca. Sricula bears variably formed dorsal apertural tongue; its aperture may be considerably extended, almost trumpetlike, in profile.

Saetograptus chimaera (Barrande, 1850) Figures 7F–H, 8C–D, I, K, 9C–E, G–I; Table 4

1850

Graptolithus chimaera Barrande, pp. 52–53, pl. 4, figs 34, 35.

1899

Monograptus chimaera Barr.; Perner, p. 23, pl. 17, fig. 18a, b.

1911

Monograptus chimaera (Barrande); Elles and Wood, pp. 898–899, pl. 39, fig. 3a–d; text-fig. 266a, b.

1936

Monograptus chimaera (Barrande); Bouček, p. 17, text-fig. 3a–c.

1942

Pristiograptus (Saetograptus) chimaera chimaera (Barrande); Přibyl, pp. 13–14, text-fig. 3, figs 1–3.

1953

Monograptus chimaera; Walker, pp. 370–373, text-fig. 5a–b; text-fig. 6a–c.

1955

Monograptus chimaera (Barrande); Kühne, pp. 372–373, 375–379; text-fig. 6a–h.

1956

Pristiograptus (Saetograptus) chimaera chimaera (Barrande); Tomczyk, pp. 55–56, pl. 8, fig. 2; text-fig. 16b.

1958

Saetograptus chimaera (Barrande); Urbanek, p. 53, text-figs 26–31; pl. 2, figs 1–4; pl. 3, figs 1–3.

1975

Saetograptus (*Saetograptus*) *chimaera chimaera* (Barrande); Berry and Murphy, pp. 76–77, pl. 9, figs 5, 6.

? 1992

Saetograptus ex gr. *chimaera* (Barrande); Lenz, p. 206, pl. 1A–C.

Figure 7. A–B, D, I, K–L, Q, *Saetograptus leintwardinensis* (Jaekel, 1880); A, PŠ3140, sample 52d, *leintwardinensis* Biozone; B, PŠ3252, sample 62b, lower *leintwardinensis* Biozone; D, PŠ3151, sample 52b, upper *leintwardinensis* Biozone; I, PŠ3152, sample 52b, upper *leintwardinensis* Biozone; K, PŠ3210, sample 52a, upper *leintwardinensis* Biozone; L, L31518, *leintwardinensis* Biozone, holotype of *Saetograptus*

linearis figured by Bouček (1936, text-fig. 3u); Q, L17749, *leintwardinensis* Biozone, paratype of *S. leintwardinensis primus* figured by Bouček (1936, pl. 2, fig. 3). C, J, *Saetograptus fritschi* (Perner, 1899); C, L17764, holotype figured by Perner (1899, pl. 17, fig. 15), ?*scanicus–chimaera* Biozone; J, PŠ3230, sample 75, *scanicus–chimaera* Biozone. E, *Saetograptus* sp. B, PŠ3166, sample 46a, upper *leintwardinensis* Biozone. F–H, *Saetograptus chimaera* (Barrande, 1850); F, PŠ3193, sample 68, upper *scanicus–chimaera* Biozone; G, PŠ3253, sample 82, *scanicus–chimaera* Biozone; H, L19973, holotype figured by Barrande (1850, pl. 4, figs 34, 35), ?*scanicus–chimaera* Biozone. M–P, R–S, *Saetograptus clavulus* (Perner, 1899); M, L19867, holotype figured by Perner (1899, text-fig. 15), *leintwardinensis* Biozone; N, PŠ3170, sample 46a, upper *leintwardinensis* Biozone; O, PŠ3223, sample 54d, *leintwardinensis* Biozone; P, PŠ3176; R, PŠ3163; S, PŠ3174, sample 46a, upper *leintwardinensis* Biozone. T, *Saetograptus incipiens* (Wood, 1900)?, PŠ3144, sample 60b, lower *leintwardinensis* Biozone. U–V, *Colonograptus roemeri* (Barrande, 1850); U, PŠ3208, sample 62a, lower *leintwardinensis* Biozone; V, PŠ3083, sample 78, *scanicus–chimaera* Biozone. All specimens from the Všeradice section, except for L17764 (C) and L19973 (H) from Zadní Kopanina, L31518 (L) and L17749 (Q) from Mušlovka quarry near Řeporyje. Scale bar represents 1 mm.

Table 4. *Saetograptus chimaera* (Barrande, 1850).

Specimen	Figures	W				2TRD			
		th 1	th 5	th 10	Dist. max./th	th 2	th 5	th 10	Dist. th
PŠ3193	7F,8K	0.9	1.2	1.6	2.1/th 14	1.0	1.25	1.4	1.45
PŠ3253	7G	0.8	1.2	1.6	2.2/th 10	0.75	?1.3	1.4	?1.8
L19973, holotype	7H,8C	0.85	1.15	1.45	1.7/th 7–8	0.98	1.3	1.6	–
PŠ3089	8I	0.65	1.5	1.35	1.85/th 10	0.97	1.2	1.35	1.45
PŠ3159	8D	0.75	1.1	1.55	2.2/th 13	1.0	1.25	1.25	1.4
PŠ3246(2)	9C	0.75	1.0	1.2	–	1.5	1.25	–	–
PŠ3248(1)	9E	0.9	1.5	1.35	2.1/th 15	1.0	1.15	1.45	1.45
PŠ3247(4)	9H	1.0	1.25	1.5	~1.65/th 9	1.1	1.4	–	–
PŠ3246(1)	9I	0.9	1.5	1.45	–	1.2	1.4	–	–
PŠ3155	–	0.75	1.1	1.55	2.05/th 10	1.0	1.2	1.45	–

Dimensions of figured specimens, including holotype (in mm).

Figure 8. A, E–H, M–O, *Saetograptus leintwardinensis* (Lapworth, 1880); A, PŠ3180, sample 54a; E, PŠ3151; F, PŠ3152, sample 52b; G, PŠ3201, sample 62b; H, L31518, paratype of *S. leintwardinensis primus* figured by Bouček (1936, pl. 2, fig. 3); M, PŠ3140, sample 52d; N, PŠ3149, sample 52b; O, PŠ3210, sample 52a; all specimens from the *leintwardinensis* Biozone. B, *Saetograptus* sp. B, PŠ3166, sample 46a, upper *leintwardinensis* Biozone. C–D, I, K, *Saetograptus chimaera* (Barrande, 1850); C, L19973, holotype figured by Barrande (1850, pl. 4, figs 34, 35), *scanicus–chimaera* Biozone; D, PŠ3159, sample 68, upper *scanicus–chimaera* Biozone; I, PŠ3089; K, PŠ3193, sample 81, *scanicus–chimaera* Biozone. J, *Saetograptus clavulus* (Perner, 1899), L19867, holotype figured by Perner (1899, text-fig. 15), ?upper *leintwardinensis* Biozone. L, *Saetograptus incipiens* (Wood, 1900)?, PŠ3144, sample 60b, lower *leintwardinensis* Biozone. All specimens from the Všerádice section, except for L19973 (C) from Zadní Kopanina, L31518 (H) from Mušlovka quarry near Řeporyje and L19867 (J) from Kosov-Dlouhá Hora near Beroun. All scale bars represent 1 mm.

Figure 9. A–B, F, *Saetograptus leintwardinensis* (Lapworth, 1880); A, PŠ3245(1); B, PŠ3245(2); F, PŠ3245(3); isolated from glacial boulder from Nienhagen near Rostock, north-east Germany (Maletz 1997). C–E, G–I, *Saetograptus chimaera* (Barrande, 1850); C, PŠ3246(2); D, PŠ3246(4); E, PŠ3248(1); G, PŠ3249(2); H, PŠ3247(4); I, PŠ3246(1); isolated from glacial boulder from northern Germany. Scale bar represents 1 mm.

Material

Sixteen flattened rhabdosomes from the upper *scanicus–chimaera* Biozone of the Všeradice section (samples 73–64c), holotype figured by Barrande (1850), specimens illustrated by Perner (1899), Bouček (1936) and Přibyl (1942) and further material collected from the lower part of *scanicus–chimaera* Biozone lower in the Všeradice succession. The flattened Bohemian material has been supplemented by specimens chemically isolated from a glacial erratic boulder from northern Germany.

Description

The otherwise straight rhabdosome, usually 10–15 mm long, is weakly ventrally curved in the proximal part comprising the first 5–7 thecae. Also the sicula is ventrally curved, in particular in its subapertural part. The sicula is 1.55–1.95 mm long; the sicular apex usually reaches the level of th 3 aperture. The sicular aperture is c. 0.3 mm wide, furnished with a more or less prominent dorsal apertural lobe which is either parallel to the sicular axis or slightly introverted. The virgella is short and rather thickened in some mature specimens. The first theca arises 0.1–0.3 mm above the sicular aperture. It is slightly everted, having a concave ventral wall. The ventrally facing aperture of th 1 possesses paired, triangular, ventrally directed lateral lobes terminated by prominent, proximally curved spines. In th 2 and th 3, the lateral apertural lobes get narrower, shift to a dorsolateral position and transform into 0.5- to 0.7-mm-long, ventro-proximally directed spines. The ventral apertural margin forms a prominent step, well seen in flattened specimens. In

turn, a deep notch is developed on the dorsal side of the thecal aperture, just behind the spine. The thecal morphology is better demonstrated in the chemically isolated specimens shown in Figure 9. The number of spinose thecae varies considerably in our specimens (from 5 to 15). Spines are progressively reduced in this interval, and subsequent distal thecae exhibit simple, almost pristiograptid-like apertures without any lateral processes. Mesial and distal thecae attain a length of c. 2 mm (measured without lateral processes), are inclined at c. 45 degrees and overlap for three-quarters of their length. Thecae are densely spaced, numbering 8–9 in the proximal 5 mm and 13.5–14.5 in 10 mm distally (2TRD th 2 – 0.95–1.2 mm, 2TRD th 5 – 1.1–1.4 mm, 2TRD th 10 – 1.25–1.6 mm). The rhabdosome widens rapidly from 0.65–1.0 mm at th 1, through 1.0–1.25 mm at th 3, to 1.2–1.6 mm at th 5 and then more gradually to 1.65–2.2 mm at th 10. The maximum width of flattened specimens, 1.9–2.2 mm, is attained at th 8–16.

Remarks

Saetograptus chimaera occurs only in the upper Gorstian *chimaera*–*scanicus* Biozone. In about the middle part of the biozone (below this section and so not figured), it is accompanied by the superficially similar *Saetograptus salweyi* (Lapworth, 1880), which can be differentiated by having a less robust rhabdosome with a straighter proximal part and apertural spines developed in both proximal and distal thecae. Th 1 of *S. salweyi* is relatively long and steeply inclined which results in the blunt asymmetrical appearance of the proximal end of the rhabdosome. Dorso-lateral apertural spines are generally long and point upwards rather than perpendicular to the rhabdosome axis.

Saetograptus clavulus (Perner, 1899) Figures 7M–P, R–S, 8J, 10A–D, G–J; Table 5

1899

Monograptus clavulus n. sp., Perner, p. 23, text-fig. 15.

1942

Pristiograptus (*Saetograptus*) *leintwardinensis primus* (Bouček); Přibyl, pp. 19–20 (*partim*), text-fig. 3, fig. 21 (*non* 19, 20).

1979

Monograptus fritschi linearis Bouček; Jaeger and Robardet, pl. 1, fig. 6.

cf. 2005

Saetograptus fritschi Bouček; Rickards and Woodcock, fig. 11a–c.

Table 5. *Saetograptus clavulus* (Perner, 1899).

Specimen	Figures	W					2TRD			
		th 1	th 3	th 5	th 10	Dist.	th 2	th 5	th 10	Dist. th
L19867, holotype	7M,8J	0.75	1.0	1.5	1.45	>1.6	1.15	1.25	1.35	–
PŠ3170	7N,10H	0.75	0.9	1.35	1.6	1.95	1.1	1.35	1.3	1.6
PŠ3223	7O	0.8	1.0	1.25	1.45	1.45	1.5	1.25	1.35	?
PŠ3176	7P	0.75	?	0.85	1.4	>1.6	1.2	1.25	1.55	–
PŠ3163	7R, 10B	0.8	?	1.2	1.35	2.3	1.5	1.15	1.35	1.9
PŠ3174	7S	0.75	1.1	1.15	1.6	2.1	1.0	1.1	1.5	1.7
PŠ3173	10A	0.7	0.85	1.1	1.7	1.95	1.2	1.4	1.55	1.7
PŠ3076	10C	0.9	1.15	1.2	1.35	>1.55	1.5	1.5	1.35	–
PŠ3148	10D	0.7	0.95	1.1	–	–	1.5	1.2	–	–
PŠ3169	10G	0.85	1.0	–	–	–	1.0	1.1	–	–
PŠ3254	10I	0.8	0.85	0.95	1.45	–	1.15	1.15	1.8	–
PŠ3077	10J	?	0.95	1.2	1.55	2.4	?	1.25	1.5	1.8

Dimensions of figured specimens, including holotype (in mm).

Figure 10. A–D, G–J, *Saetograptus clavulus* (Perner, 1899); A, PŠ3173; B, PŠ3163; C, PŠ3076; D, PŠ3148; G, PŠ3169; H, PŠ3170; I, PŠ3254; J, PŠ3077; all specimens from the upper *leintwardinensis* Biozone, sample 46a, except for PŠ3148 (D) from sample 52c. E–F, *Saetograptus fritschi* (Perner, 1899); E, PŠ3230, sample 75; F, PŠ3121, sample 73, *scanicus–chimaera* Biozone; all specimens from the Všeradice section. All scale bars represent 1 mm.

Material

Over 70 flattened rhabdosomes from the *leintwardinensis* Biozone of the Všeradice section (samples 58a–46a) and the specimen illustrated by Přibyl (1943).

Description

Medium-sized specimens are commonly 20–30 mm long; the most mature attain a length of 46.5 mm. The rhabdosome is dorsally curved in the proximal part and straight distally. The dorsal curvature comprises 6–12 (rarely up to 26) spinose thecae that rapidly become pristigraptid-like in the straight distal part of the rhabdosome. The rhabdosome widens from 0.7–0.9 mm at th 1 (measured without spines), through 0.8–

1.15 mm at th 3, 0.85–1.35 mm at th 5 and 1.25–1.85 at th 10, to 1.35–2.2 mm at th 15. The maximum width of 1.85–2.4 mm is attained by mature rhabdosomes, the width achieved depending on their mode of flattening. Maximum values are seen in obliquely flattened (as a flattened cardboard box) specimens. The sicula is 1.55–2.1 mm long, slender initially but conspicuously extended and trumpetlike in the apertural part. The sicular apex attains the level of th 3 aperture. Up to four dark bands, the sicular annuli, have been observed in several specimens (Fig. 10G). The sicular aperture is straight or concave, commonly 0.4–0.45 mm wide with rare extreme values of 0.25 and 0.55 mm. Its dorsal margin is furnished with a prominent, dorsally directed or slightly backward bent, up to 0.7-mm-long spinelike structure. This dorsal apertural spine is roughly perpendicular to the approximately equally long virgella which projects from the ventral side of the sicula.

The thecae are biform. The first 10–20 thecae (in one specimen 27) are furnished with conspicuous, 0.6- to 1.2-mm-long, paired apertural spines. These proximal thecae are relatively short and broad. The apertural spines, situated ventro-laterally in the first theca, take a dorso-lateral position on the thecal apertural margin beginning with the second theca. All spines maintain the same direction relative to the rhabdosome, including those in its curved proximal part (Fig. 10C). The spines are smaller when the rhabdosome becomes straight and subsequent, distal thecae become simple pristiograptid-like tubes with a straight or concave profile of the aperture. Distal thecae are 2.5–2.8 mm long, inclined at 50–55 degrees, and overlap for three-quarters to five-sixths their length. Thickened interthecal septa can be observed pressed through in some specimens. Thecae are densely spaced, in particular those in the proximal part of the rhabdosome: 2TRD th 2 = 1.0–1.25 mm, 2 TRD th 5 = 1.05–1.4 mm, 2TRD th 10 = 1.3–1.8 mm. Distal thecae number 10.5–12.5 in 10 mm (2TRD = 1.6–1.9 mm).

Discussion

Monograptus clavulus Perner, 1899 was placed in synonymy with *Monograptus fritschi* Perner, 1899 in the first comprehensive revision of the Ludlow graptolites of Bohemia by Bouček (1936). The two forms are superficially similar, and Perner's *M. clavulus* was based upon a single and incomplete type specimen (refigured on Figs 7M, 8J), albeit preserved in relief and complemented by the counterpart. This holotype by monotypy, associated with the trilobite *M. baylei* (Barrande) and smooth atrypid brachiopods, came from the old locality of Dlouhá Hora, from the *M. baylei* trilobite horizon. Recent studies of several sections document that *M. baylei* is restricted to the upper part of the *linearis* (i.e. *leintwardinensis*) Biozone (Š. Manda and J. Kříž, unpub. data 2007), which is in full accord with the range of *S. clavulus* in the Všeradice section.

The rich and stratigraphically distinct material from the Všeradice section triggered more detailed study and re-evaluation of the long-abandoned *S. clavulus* (Perner, 1899), which we show to be readily

distinguishable in mature and well-preserved material. The new material matches the type specimen in having a rapidly and considerably widening dorsally curved proximal part, rather narrow at th 1 (Table 5), and rapidly increasing thecal length and overlap. Prominent apertural spines retreat in the straight part of the rhabdosome. The same features differentiate immature specimens from those of *S. fritschi* (Perner) which are narrower and have shorter and less overlapping thecae furnished with generally smaller apertural spines. Long, cylindrical, distal thecae of pristiograptid appearance have not been observed in *S. fritschi*. Another saetograptid with a gently dorsally curved proximal end was recognized by Bouček (1936, text-fig. 3g–k) as a subspecies of *S. leintwardinensis*. The selected holotype of *Monograptus leintwardinensis primus* Bouček, 1936 lacks the proximal end and was probably the least suitable of its figured specimens to be designated holotype. Jaeger (1959) correctly placed *M. leintwardinensis primus*, with its weakly curved proximal end and flared sicular aperture, in synonymy with *M. fritschi linearis*, which was described by Bouček in the same paper and which we synonymize with *S. leintwardinensis* (see below). However, one of the specimens figured by Přibyl (1942) as *S. leintwardinensis primus* (Bouček) differs from the others in its greater maximum width, greater thecal overlap, prominent proximal dorsal curvature and suppressed apertural spines distally. This specimen belongs in *S. clavulus* as does the specimen identified as *S. linearis* by Jaeger and Robardet (1979, pl.1, fig. 6) from the Ossa Morena Zone of south-west Spain.

Saetograptus fritschi (Perner, 1899) Figures 7C, J, 10E–F

1899

Monograptus Fritschi n. sp., Perner, p. 24, pl. 17, fig. 15.

1936

Monograptus fritschi Perner; Bouček, pp. 19–20, pl. 1, fig. 1; text-fig. 3l–n.

1942

Pristiograptus (Saetograptus) fritschi fritschi (Perner); Přibyl, pp. 20–21, text-fig. 3, figs 14–16.

non 1975

Saetograptus fritschi fritschi (Perner); **Berry and Murphy**, text-fig. 21c–d.

Material

Twenty-six flattened rhabdosomes from the upper *progenitor*, *scanicus–chimaera* and lower–middle *leintwardinensis* biozones of the Všeradice section (most of the material is from below the level of the present log), the type specimen figured by Perner (1899) and material figured by Bouček (1936) and Přibyl (1942).

Description

The rhabdosome is commonly about 10 mm, max. 20 mm long, dorsally curved throughout its length. Dorsal curvature is accentuated proximally and decreases distally. The rhabdosome is 0.7–0.9 mm wide at the aperture of the first theca (measured without spines) and 0.8–1.05 mm wide (one specimen 1.15 mm) at th 3, 0.95–1.25 mm at th 5 and 1.2–1.35 (max. 1.5) mm at th 10. The dorso-ventral width decreases again in the distal part of mature rhabdosomes. The sicula is 1.5–1.7 mm long and 0.4–0.7 mm broad across the aperture which is extended in a funnellike fashion on the dorsal side. The dorsal margin of the sicular aperture is also lobate in many specimens. The apical part of the sicula, in turn, is very narrow. The apex attains the level of th 3. Thecae are short and relatively broad, steeply inclined (at c. 45 degrees), densely spaced, overlapping for about two-thirds their length. 2TRD increases gradually from 1.0–1.25 mm at th 2, through 1.2–1.4 mm at th 5, to 1.3–1.45 mm at th 10 and attains 1.55 mm in the most distal part in mature rhabdosomes. The ventrally facing aperture of th 1 possesses high-triangular, proximally curved lateral spines. Succeeding thecae exhibit c. 0.5 mm long, dorso-laterally situated apertural spines which gradually retreat in distal thecae. At least 11 spinose thecae have been recorded in specimens from the middle and upper *scanicus–chimaera* Biozone and lower *leintwardinensis* Biozone, while only 3–6 spiny thecae are developed in stratigraphically earlier populations from the upper *progenitor* and lower *scanicus–chimaera* biozones. Distal thecae after c. th 10 do not exhibit progressive elongation any more, and the lateral apertural spines are missing, although the precise outline of the aperture remains unclear in the present flattened specimens.

Remarks

Saetograptus fritschi is a long-ranging species distinguished from other saetograptids by its medium-sized dorsally curved rhabdosome with relatively short sicula which is greatly widened at its flared or trumpetlike aperture which is furnished with a commonly long, dorsally directed dorsal tongue.

Only *S. clavulus* and *S. leintwardinensis* may exhibit a similar sicula. *S. clavulus* could be derived from *S. fritschi* by progressive thecal elongation coupled with markedly later gradual loss of apertural spines which is best manifested in the long, straight and robust distal portion with greatly overlapping, straight tubular thecae terminated by simple apertures, probably concave in lateral outline, without any spines or lateral lappets. Rhabdosomes of *S. leintwardinensis* differ in having gentle, if any, dorsal curvature and apertural spinosity maintained until the distal thecae.

Saetograptus incipiens (Wood, 1900)? Figures 7T, 8L

Remarks

Several saetograptid rhabdosomes from the *scanicus–chimaera* and lower *leintwardinensis* biozones can be distinguished from *S. chimaera* by their less robust and less rapidly widening rhabdosomes, and rapid retreat of the prominent thecal spinosity. The long apertural spines developed in the first three or four

proximal thecae are progressively suppressed in subsequent thecae. Short spines were detected until about th 8. The rhabdosomes widen from 0.7–0.8 mm at th 1 (excluding spines), through 0.95–1.1 mm at th 3, 1.1–1.4 mm at th 5, and 1.8–2.15 mm at th 10, to the maximum of c. 2.3 mm attained by th 12–14. Distal thecae, numbering 10.5 in 10 mm, are less densely spaced than those of *S. chimaera*. The 2TRD ranges from 1.6 to 1.7 mm at th 10, and up to 1.9 mm in subsequent thecae. The sicula is about the same length, c. 1.6 mm long and slightly ventrally curved at its 0.25–0.3 mm wide aperture which is furnished with a dorsal tongue.

Saetograptus leintwardinensis differs from the present form in having a moderately extended sicular aperture, a less robust rhabdosome and shorter thecae. All of its mature thecae are furnished with dorsolateral apertural spines.

The dorsal sicular tongue developed in most of the present specimens and the number of the spinose thecae, which is a little higher than in *S. incipiens* (Wood, 1900), resemble *Saetograptus soperi* Rickards and Woodcock, 2005. The latter species, however, exhibits a more prominent sicular apertural tongue and significant ventral curvature of the proximal part of the rhabdosome. Thecal spinosity can vary and may be preservationally obscured in some specimens. Our specimens are retained without confident identification due to the limited material available.

Saetograptus leintwardinensis (Lapworth, 1880) Figures 7A–B, D, I, K–L, Q, 8A, E–H, M–O, 9A–B, F; Table 6

1873

Monograptus leintwardinensis; Hopkinson, p. 520 (*nom. nud.*)

1880

Monograptus leintwardinensis Hopkinson MS; Lapworth, p. 149, pl. 4, fig. 1a–d.

1911

Monograptus leintwardinensis Hopkinson MS; Elles and Wood, p. 401, pl. 39, fig. 8a–f; text-fig. 268a–c.

1936

Monograptus leintwardinensis var. *primus* n.var. Bouček, pp. 18–19, pl. 2, fig. 3; text-fig. 3g–k.

1936

Monograptus fritschi mut. *linearis* n.mut., Bouček, p. 20, text-fig. 3r–u.

1943

Pristiograptus (Saetograptus) fritschi linearis (Bouček); Přibyl, pp. 21–22, text-fig. 3, figs 17, 18.

1942

Pristiograptus (Saetograptus) leintwardinensis primus (Bouček); Přibyl, pp. 19–20 (*partim*), text-fig. 3, figs 19, 20 (*non* 21).

1956

Pristiograptus (Saetograptus) leintwardinensis leintwardinensis (Lapworth); Tomczyk, pp. 57–58, pl. 8, figs 4, 6a, b; text-fig. 17a–c.

1992

Saetograptus fritschi linearis (Bouček); Lenz, pp. 206–207, pl. 2A–G.

1995a

Saetograptus leintwardinensis Hopkinson in Lapworth; Rickards *et al.*, pp. 73–74, text-fig. 4c.

1995a

Saetograptus fritschi linearis (Bouček); Rickards *et al.*, p. 74, text-figs 4a, b; 9b.

1997

Saetograptus sp. cf. *Saetograptus leintwardinensis* (Lapworth); Maletz, pp. 248–254, figs 1–4.

cf. 2004

Saetograptus linearis (Bouček); Lenz and Kozłowska-Dawidziuk, pp. 28–29, pl. 27, figs 8, 10–18; pl. 38, figs 2, 11 (see for further references to Canadian material assigned to *S. linearis*).

2005

Saetograptus leintwardinensis (Lapworth); Rickards and Woodcock, fig. 11d–l.

2007

Saetograptus linearis (Boucek); Koren' and Sujarkova, text-fig. 2, fig. 4; pl. 1, fig. Q.

2007

Saetograptus leintwardinensis (Hopk.); Koren' and Sujarkova, text-fig. 2, fig. 3.

Table 6. *Saetograptus leintwardinensis* (Lapworth, 1880)

Specimen	Figures	W					2TRD			
		th 1	th 3	th 5	th 10	Dist. max	th 2	th 5	th 10	Dist. th
BU1527, lectotype	See Zalasiewicz <i>et al.</i> (2000)	0.7	?	1.1	1.15	–	~1.3	1.5	1.6	–
BU1529	See Zalasiewicz <i>et al.</i> (2000)	0.8	?	1.3	1.45/th 7	–	1.2	1.2	–	–
PŠ3140	7A,8M	0.8	0.85	1.5	1.3	>1.45	1.2	1.25	1.6	?
PŠ3252	7B	0.85	1.2	1.35	1.65	–	1.2	1.2	1.35	–
PŠ3151	7D,8E	0.7	0.9	1.0	1.4	1.55	1.2	1.55	1.55	1.8
PŠ3152(1)	7I,8F	0.7	0.85	1.1	1.4	1.55	1.5	1.25	?1.5	?
PŠ3210	7K,8O	0.75	0.95	1.3	1.5	1.55	?1.05	1.25	1.7	1.8
L31518	7L,8H	0.8	0.95	1.5	–	–	1.25	1.3	–	–
L17749	7Q	?	0.8	0.9	1.1	–	?0.95	1.1	1.25	–
PŠ3180	8A	0.7	0.85	1.0	1.45	–	1.0	1.25	1.4	–
PŠ3201	8G	0.85	1.2	1.35	1.55	–	1.1	1.15	1.3	–
PŠ3149	8N	0.75	0.95	1.2	1.35	1.55	1.2	1.35	1.55	1.9
PŠ3245(1)	9A	0.7	0.85	1.1	–	–	1.15	–	–	–
PŠ3245(2)	9B	0.8	0.9	0.95	1.25	–	1.1	1.4	–	–
PŠ3245(3)	9F	0.85	0.9	0.9	–	–	1.1	–	–	–

Dimensions of figured specimens and lectotype (in mm).

Material

Forty-two flattened rhabdosomes restricted to the *leintwardinensis* Biozone (samples 62b–46a of the Všeradice section), type material of *M. fritschi linearis* and *Monograptus leintwardinensis primus* described by Bouček (1936) and material of the same species described and figured by Přibyl (1943). Flattened Bohemian material has been supplemented by specimens chemically isolated from a glacial erratic boulder collected from Nienhagen near Rostock (see Maletz 1997 for further details).

Description

The rhabdosome is up to 47 mm long, straight to slightly dorsally curved in the proximal part. The slightly dorsally curved outline can be attributed, for the most part, to the broadened apertural part of the sicula. The sicula is conical, straight, 1.7–1.9 mm long; its apex attains the level of the th 2–3 aperture. The sicular aperture is commonly expanded attaining a width of 0.32–0.42 mm. It is furnished with a tiny virgella and, in some specimens, with a dorsal apertural tongue. Thecae are simple tubes without apparent geniculation. Thecal apertures possess prominent paired, up to 1 mm long, ventrally to proximo-ventrally directed spines. The spines are situated laterally at the aperture of th 1, whereas subsequent thecae exhibit dorso-laterally situated apertural spines, separated by a narrow groove in the apertural margin from the ventral wall of the subsequent theca. This groove is commonly hidden in a flattened rhabdosome, and the spines then appear to be appressed on the ventral wall of the subsequent theca (hence their dorso-lateral position

on thecal aperture), which matches illustrations of topotypical *S. leintwardinensis* (see e.g. Elles and Wood 1911). Apertural spines are developed in all mature thecae. Th 1 is 0.9–1.0 mm long, inclined at an angle of 30–40 degrees to the rhabdosome. Thecal inclination attains 40–45 degrees in subsequent thecae which overlap for more than half their length. Thecae are densely spaced, with 2TRD th 2 = 1.0–1.25 mm, 2TRD th 5 = 1.1–1.55 mm, and 2TRD th 10 = 1.25–1.7 mm (max. 1.8 mm). The distalmost thecae number about 11 in 10 mm. The width of the rhabdosome, excluding spines, increases from 0.7–0.85 mm at th 1 (0.95 mm in one specimen) to 0.8–1.2 mm at th 3, 0.9–1.35 mm at th 5 and 1.1–1.65 mm at th 10. A maximum width of 1.7–1.95 mm has been recorded in the distal part of mature rhabdosomes.

Discussion

The proximal part of the rhabdosome ranges from straight to slightly but distinctly dorsally curved in the Bohemian material, and it is that that provoked the recognition of two different taxa. Bouček (1936) recognized *M. fritschi linearis*, differentiated from the nominal subspecies *M. fritschi fritschi* Perner, 1899 by its nearly straight rhabdosome. Other features have been reported as identical in Bouček's brief comment although the sicula is missing from the poorly preserved holotype of *M. fritschi linearis* (Fig. 7Q). Paratypes exhibit a longer and less flaring sicula and less densely spaced thecae compared with *S. fritschi* (cf. Fig. 7J) and exhibit closer affinity to *S. leintwardinensis* (Lapworth) except for being weakly dorsally curved. Both the morphology and measurable traits match the isolated *Saetograptus* cf. *leintwardinensis* figured by Maletz (1997). Specimens with typical flaring sicula and dorsal sicular apertural tongue isolated by Maletz are shown on Figure 9A–B, F. *M. leintwardinensis primus* described by Bouček (1936) from about the same level of the same Mušlovka quarry was characterized by the rhabdosome being markedly dorsally curved in the proximal part. However, its holotype lacks a proximal end. The paratypes of *M. leintwardinensis primus* are preserved as internal moulds with largely damaged spines and do not exhibit some important features of saetograptid morphology. Jaeger (1959) had good reason to include *M. leintwardinensis primus* Bouček, 1936 in the synonymy of *M. fritschi linearis* Bouček, 1936.

Our re-examination of the type material of *M. leintwardinensis primus* and *M. fritschi linearis* has revealed that both taxa belong in the same species, which is furthermore conspecific with the senior synonym *S. leintwardinensis* (Lapworth, 1880). Only one specimen, with a rapidly widening and curved proximal part and almost pristiograptid distal thecae, assigned to *S. leintwardinensis primus* by Přibyl (1942, text-fig. 3, fig. 21), belongs to *S. clavulus* (Perner), emended above. The thecal shape, spacing and spinose apertures of the specimens housed in the National Museum, Prague collection and those from the Všerádice section match the *S. leintwardinensis* types re-figured by Zalasiewicz *et al.* (2000). The only differences from the English material are the slightly shorter sicula and greater rhabdosome width after th 5. The slight dorsal curvature of the most proximal part can barely be taken as a diagnostic feature as is obvious from the illustrated specimens (Figs 7, 9). The majority of English specimens

of *S. leintwardinensis* are immature rhabdosomes, which may explain their lesser dorso-ventral width after th 5–7 (see Table 6 for comparison with Bohemian material).

Specimens assigned to *S. linearis* in Arctic Canada (Lenz and Melchin 1986, Lenz 1988, 1990, 1992 and Lenz and Kozłowska-Dawidziuk 2004) differ from our specimens in their more flaring sicular aperture with dorsally projecting dorsal tongue (or process) and bifurcating or trifurcating thecal apertural spines. The rhabdosome is generally wider at th 1, which is more steeply inclined and gives the rhabdosome's proximal part a more robust appearance. The Canadian material may represent a palaeogeographically distinct subspecies.

Saetograptus sp. A Figure 6N

Remarks

Two 15- and 27-mm-long specimens from sample 54a (*leintwardinensis* Biozone) can be distinguished from other saetograptids by their robust rhabdosomes widening regularly from 0.85 mm at th 1 to a maximum of 2.3 mm attained at about th 15–17. Thick dorso-lateral apertural processes are developed in all thecae. The sicula is c. 1.6 mm long, 0.26 mm wide at the aperture and its apex attains the level of th 2 aperture. 2TRD increases from 1.05 mm at th 2, through 1.2 mm at th 5 and 1.35 mm at th 10, to 1.45 mm in distal thecae numbering 13–14 in 10 mm. Distal thecae are 2.1 mm long and overlap for two-thirds of their length or a little more.

Saetograptus sp. B Figures 7E, 8B

Remarks

Three specimens tentatively designated as *Saetograptus* sp. B came from two separate levels (sample 70b from the uppermost *scanicus–chimaera* Biozone and sample 46a from the uppermost *leintwardinensis* Biozone). The S-shaped appearance of the rhabdosome is caused mainly by the 1.7-mm-long sicula which protrudes somewhat from the dorsal margin of the rhabdosome. The sicular aperture is 0.3 mm wide and in one rhabdosome is furnished with a slight dorsal lobe. The sicular apex attains the level of th 4. Thecae are strongly inclined and possess paired dorso-lateral apertural spines with apparent branching. Distal thecae are only 1.6–1.7 mm long, overlapping for two-thirds to three-quarters their length. The rhabdosome is 0.85 mm wide at th 1, 1.1–1.15 mm wide at th 3 and 1.5–1.55 mm at th 5. The maximum width of 1.8–1.95 mm, still excluding apertural spines, is attained by th 10. 2TRD is 0.85–1.0 mm at th 2, 1.15 mm at th 5 and c. 1.3 mm at th 10. Distal thecae number 15 in 10 mm. The greater dorso-ventral width of the rhabdosome and the densely spaced thecae differentiate this form from the most similar species, *S. leintwardinensis*, which exhibits a similarly shaped proximal end with the sicula emerging from the dorsal outline of the rhabdosome.

Genus NEODIVERSOGRAPTUS Urbanek, 1963

Type species

Monograptus nilssoni Lapworth, 1876, *sensu* Urbanek, 1954 and Palmer 1971; from the Gorstian of the Welsh Borderland, UK.

Diagnosis

After Urbanek (1963, p. 149).

Neodiversograptus sp. Figures 11G, 12E

Remarks

Several fragments of straight, slender rhabdosomes possess simple thecal tubes inclined at 10–13 degrees to the rhabdosome axis. The thecal aperture occupies more than two-thirds the rhabdosome width, which ranges from 0.35 to 0.45 mm. The aperture is either perpendicular to the straight ventral thecal wall or is slightly everted. Thecae overlap only a little, and the metatheca forms only a short, distal portion of the thecal tube. The thecae number 7 in 10 mm with 2TRD ranging from 2.9 to 3.05 mm. The present material differs from similar fragments of *Linograptus posthumus* (R. Richter, 1875) in its ventral thecal walls without any geniculum and straight and everted thecal apertures. The thecal apertures of *L. posthumus* occupy a lesser proportion of the dorso-ventral width of the stipe. In turn, the thecal form, dimensions and stratigraphical occurrence of the present material at about the top of the *leintwardinensis* Biozone correspond with the data provided by Urbanek (1963) for *Neodiversograptus beklemishevi*. The ultimate taxonomic assignment of the Bohemian specimens, however, is left open due to the absence of evidence on proximal rhabdosome structures (sacula, its dorsal apertural spine and th 1) which enable *N. beklemishevi* (Urbanek, 1963) to be distinguished from its closely similar ancestor *N. nilssoni* (Lapworth, 1876) *sensu* Urbanek (1954).

Figure 11. A, J–K, *Lobograptus* aff. *cirrifer* Urbanek, 1966, sample 54a, *leintwardinensis* Biozone; A, K, PŠ3177b (A, distal thecae in detail from section of rhabdosome labelled a in K); J, PŠ3177a, proximal thecae in detail. B, *Cucullograptus hemiaversus* Urbanek, 1960?, PŠ3148, sample 52b, *leintwardinensis* Biozone. C, O, *Cucullograptus* cf. *aversus* Eisenack, 1942; C, PŠ3171, inset of the distal fragment, sample 46a; O, PŠ3125, sample 44d, upper *leintwardinensis* Biozone. D–E, I, *Lobograptus scanicus* (Tullberg, 1883) s. l.; D, PŠ3205, distal fragment, sample 62a, lower *leintwardinensis* Biozone; E, PŠ3198, mesial fragment; I, PŠ3158, sample 68, *scanicus–chimaera* Biozone. F, *Egregiograptus* cf. *rinellae* Koren' and Sujarkova, 2004, PŠ3067, sample 32, *tenuis* Biozone. G, *Neodiversograptus* sp., PŠ3136, sample 44b, lower *tenuis* Biozone. H, L–N, *Cucullograptus rostratus* Urbanek, 1960. H, L, PŠ3126, sample 44c; H, mesial thecae from section of rhabdosome labelled h in L; M, PŠ3132, sample 40c; N, mesial fragment, PŠ3127, sample 40c; all specimens from the *leintwardinensis* Biozone of the VŠeradice section. All scale bars represent 1 mm.

Figure 12. A–B, F, G, *Egregiograptus* cf. *rinellae* Koren' and Sujarkova, 2004; A, PŠ3065, sample 34c; B, PŠ3235b, sample 34d; F, PŠ3067, sample 32; G, PŠ3060, sample 30b, *tenuis* Biozone. C, O, *Bohemograptus praecornutus* Urbanek, 1970?; C, PŠ3141, sample 60b; O, PŠ3204, sample 62a, lower *leintwardinensis* Biozone. D, H, *Lobograptus scanicus* (Tullberg, 1883) s. l.; D, PŠ3205, distal thecae in detail, sample 62a, lower *leintwardinensis* Biozone; H, PŠ3158, mesial thecae in detail, sample 68, *scanicus–chimaera* Biozone. E, *Neodiversograptus* sp., PŠ3136, sample 44b, lower *tenuis* Biozone. I, L, *Cucullograptus rostratus* Urbanek, 1960; I, PŠ3132, sample 40c; L, PŠ3126, sample 44c, *leintwardinensis* Biozone. J, *Bohemograptus cornutus* Urbanek, 1970, PŠ3064, sample 28c, upper *tenuis* Biozone. K, *Bohemograptus tenuis* (Bouček, 1936), PŠ3134, sample 40d, *tenuis* Biozone. M–N, *Cucullograptus* cf. *aversus* Eisenack, 1942; M, PŠ3172; N, PŠ3168, sample 46a, upper *leintwardinensis* Biozone. P, *Lobograptus* cf. *cirrifer* Urbanek, 1966, PŠ3177b, sample 54a, *leintwardinensis* Biozone. Q, *Korenea sherwini* Rickards et al. 1995b?, PŠ3117a, mature rhabdosome with prominent ventro-lateral apertural lobes, sample 64b, upper *scanicus–chimaera* Biozone. All specimens from the Všeradice section. All scale bars represent 1 mm.

Genus BOHEMOGRAPTUS Přibyl, 1967

Type species

Graptolithus bohemicus Barrande, 1850; from the Kopanina Formation (Ludlow) of Bohemia.

Diagnosis

After Urbanek (1970, p. 265).

Bohemograptus bohemicus (Barrande, 1850) Figure 13D

Discussion

Robust bohemograptid rhabdosomes with a 1.5- 2.2-mm-long sicula, the apex of which reaches well above the th 1 aperture, are typical of Gorstian strata in the Všeradice section although the same morphotype persists high into the lower Ludfordian *leintwardinensis* Biozone, and Manda *et al.* (2012) reported *B. bohemicus* as high as in the middle Ludfordian *inexpectatus* Biozone.

Figure 13. A, *Korenea sherwini* Rickards *et al.* 1995b?, PŠ3117a, prominent ventro-lateral lobes developed in mesial thecae of mature rhabdosome, sample 64b, upper *scanicus*–*chimaera* Biozone. B–C, F, H, *Egregiograptus* cf. *rinellae* Koren' and Sujarkova, 2004, *tenuis* Biozone; B, PŠ3235b, sample 34d; C, PŠ3133, distal part, sample 40c; F, PŠ3070, proximal part bearing sicula, sample 30c; H, PŠ3060, sample 30b. D, *Bohemograptus bohemicus* (Barrande, 1850), PŠ3138, proximal part of large rhabdosome with apertural additions, sample 60b, lower *leintwardinensis* Biozone. E, *Bohemograptus praecornutus* Urbanek, 1970?, PŠ3141, sample 60b, lower *leintwardinensis* Biozone. G, *Bohemograptus tenuis* (Bouček, 1936), PŠ3134, sample 40d, *tenuis* Biozone. I, *Bohemograptus cornutus* Urbanek, 1970, PŠ3064, sample 28c, upper *tenuis* Biozone. All specimens from the Všeradice section. Scale bar represents 1 mm.

Small, presumably microfusellar additions to the ventro-lateral apertural margin of the proximal thecae (Fig. 13D) occur in several rhabdosomes collected from the *scanicus*–*chimaera* and *leintwardinensis* biozones. No microfusellar apertural structures (Koren' and Sujarkova 2004) or extremely rare ones (Urbanek 1970) have previously been reported in *B. bohemicus*. These challenge the

previous proposal of Urbanek (1970) regarding the timing of bohémograptid evolution and suggest that microfusellar apertural additions evolved quite early in the *Bohemograptus* stem lineage.

Bohemograptus tenuis Bouček, 1936 Figures 12K, 13G

Remarks

This slender *Bohemograptus*, which has its lowest occurrence in the upper *scanicus–chimaera* Biozone and becomes common in the *tenuis* Biozone in the Všeradice section, is characterized by its relatively low position of the sicular apex (at about the level of th 1 aperture), a little less enrolled proximal end and thecae inclined at a relatively low angle to the dorsal wall of the rhabdosome. The rhabdosome widens from 0.4–0.5 mm at th 1, through 0.5–0.75 mm at th 3 and 0.55–0.85 mm at th 5, to the maximum c. 0.85 mm attained at about th 10. Although the maximum length of our specimens did not exceed 30–40 mm, measured values of the rhabdosome width have got close to maximum reported values. The width of the sicular aperture and the form of its dorsal lobe can be barely differentiated from those of *B. bohemicus*. The apertural lobe is largely missing in later populations of *B. tenuis* described from the *inexpectatus* and *kozłowskii* biozones of the Kosov Quarry section (Štorch 1995a).

Bohemograptus praecornutus Urbanek, 1970? Figures 12C, O, 13E

Remarks

Several relatively slender and gently ventrally curved rhabdosomes with ventro-lateral apertural elevations in their robust, steeply inclined proximal thecae have been encountered in the lowermost *leintwardinensis* Biozone and also in the upper *tenuis* Biozone. The sicula is 1.4–1.7 mm long, 0.28–0.4 mm wide at the aperture, and its apex attains about the middle of the length of th 2. Metathecae show a distinct tendency to isolation, and slight ventro-lateral elevations are developed on thecal apertures. These specimens are more slender than the topotypical specimens of *B. praecornutus* illustrated by Urbanek (1970) and specimens from the *inexpectatus* and *kozłowskii* biozones of the Kosov Quarry section (Štorch 1995a) but correspond with early populations of *B. praecornutus* from the *linearis* (*leintwardinensis*) Biozone of Tien Shan illustrated by Koren' and Sujarkova (2004, fig. 21a–d). We have assigned our specimens questionably to *B. praecornutus* as the diagnostic characters are not fully developed in the limited material available.

Bohemograptus cornutus Urbanek, 1970 Figures 12J, 13I

Remarks

A *Bohemograptus* having paired apertural processes, a blunt proximal end, a generally robust rhabdosome, and c. 1.5-mm-long sicula with its apex reaching well above the aperture of th 1 was found in the upper *tenuis* Biozone (sample 28c). The rhabdosome widens rapidly from 0.6 mm (without apertural processes) at th 1 to 1.25 mm at th 5. The maximum width of about 1.5 mm is attained by th 11. A distinct tendency to isolation of the proximal metathecae can be observed along with everted thecal apertures furnished with paired, more than 1 mm long, ventrally directed tapelike structures (Fig. 12J). Apertural structures, considered as diagnostic of *B. cornutus* by Urbanek (1970) and Koren' and Sujarkova (2004), arise from the ventro-lateral part of the apertural lip. Further details of these apertural additions are not seen in our specimen. Based on the rich material from the Mielnik core, Urbanek (1970) placed the origin of *B. cornutus* from its ancestor *B. praecornutus* in the stratigraphical interval that roughly corresponds with the upper *tenuis* Biozone of our biozonation. Koren' and Sujarkova (2004), however, recorded *B. cornutus* Urbanek as low as in the lowermost *linearis* Biozone, roughly equivalent to our *leintwardinensis* Biozone, and suggested that the relatively gracile early populations of *B. cornutus* were derived from *B. tenuis*.

Genus KORENEA Rickards, Packham, Wright and Williamson, 1995b?

Type species

Korenea sherwini Rickards, Packham, Wright and Williamson, 1995b; from the Ludlow part of the Panuara Formation, Quarry Creek area, New South Wales, Australia.

Diagnosis

After Rickards *et al.* (1995b, p. 54).

Korenea sherwini Rickards, Packham, Wright and Williamson, 1995b? Figures 12Q, 13A

Remarks

A mature rhabdosome, at least 70 mm long, found in the uppermost *scanicus–chimaera* Biozone (sample 64b) matches *K. sherwini* in thecal shape and principal parameters. The specimen possesses prominent lateral apertural lobes imitating monograptid metathecal hooks in lateral outline. These apertural lobes, which occupy nearly half the rhabdosome width, are present on at least twelve proximal thecae and then retreat gradually until about th 20. It is not clear, however, whether these lateral lobes (or lappets) are composed of fusellae (as claimed for *Korenea*) or microfusellar additions as recognized in the *B. tenuis* lineage and rarely in *B. bohemicus* (Urbanek 1970). The present rhabdosome, lacking the sicula and initial thecae, is 1.5 mm wide proximally, including lobes, and 1.8 mm wide distally. Thecae, inclined at an angle of 25–30 degrees, overlap for almost half their length and number 9 in 10 mm in the distal part. Proximal 2TRDs (2.1–2.2 mm) correspond with c. 9.5 thecae in 10 mm. Although the present rhabdosome

resembles *K. sherwini* in most parameters, the missing sicula and proximal thecae as well as the poor preservation of the apertural lobes do not allow for its definite assignment.

Genus EGREGIOGRAPTUS Rickards and Wright, 1997

Type species

Monograptus egregius Urbanek, **1970**; from the upper part of the Siedlce Beds (Ludlow) of the Mielnik borehole, Poland.

Diagnosis

After Koren' and Sujarkova (2004, p. 368).

Egregiograptus cf. *rinellae* Koren' and Sujarkova, 2004 Figures 11F, 12A–B, F–G, 13B, C, F, H

cf. 2004

Egregiograptus rinellae Koren' and Sujarkova, pp. 372, 374; figs 25a–g, 26.

Material

Twenty-four flattened rhabdosomes, including several complete specimens with th 1 and sicula, from about the middle part of the *tenuis* Biozone (samples 40c–26b).

Description

Mature rhabdosomes are ventrally coiled, reaching 270–360 degrees of a circle which ranges between 10 and 18 mm in maximum diameter. The proximal end is straight or even slightly dorsally recurved. The sicula is small, only 1.05–1.25 mm long, slightly ventrally curved, having a 0.17–0.2 mm wide, almost straight aperture and a tiny virgella. Th 1 is a 3.6- to 4.6-mm-long tube arising c. 0.3 mm above the sicular aperture. It is only 0.18 mm across when measured above the sicular apex. The rhabdosome then widens gradually from 0.2–0.27 mm at the aperture of th 1, through c. 0.45 mm at th 3 and 0.55–0.7 mm at th 5, to the maximum of 0.85–1.35 mm attained near the distal end of the most mature specimens. All thecae are long, narrow tubes without an apparent geniculum. Distal thecae possess a straight aperture and overlap for more than half their length. Thecal inclination does not exceed 10 degrees. Distal 2TRD varies between 2.6 and 3.5 mm. Further details of this markedly thin-walled rhabdosome are barely recognizable due to insufficient preservation.

Discussion

This species is characterized by a particularly small sicula among egregiograptids and its slender, almost straight th 1 which is commonly dorsally recurved or broken near the apical end of the sicula. The poor preservation and presence of this species only on very smooth bedding planes are due to the extremely

thin periderm of the rhabdosome. For this reason, some details and characters of the species are not discernible in the present material. The lesser width of the rhabdosome at the level of the first thecal aperture is a major difference between the present specimens and those described by Koren' and Sujarkova (2004). Thecal spacing is rather irregular even within a specific rhabdosome; thecal overlap is rarely seen, but it is about half the thecal length. *Eggregiograptus egregius* (Urbanek, 1970) can be differentiated by its 1.4- to 1.5-mm long sicula, and considerably longer, c. 5.7-mm-long th 1. *E. egregius byrnesianum* Rickards and Wright, 1997 with its short sicula and 3.7-mm-long th 1 is very similar and may prove to be a senior synonym of *E. rinellae*. It is based, however, upon a single, unfavourably preserved juvenile specimen with few characters to compare. *Eggregiograptus klishevichi* Koren' and Sujarkova, 2004 has a rapidly widening and more tightly coiled rhabdosome. The only species similar to *Eggregiograptus* in the Bohemian succession – *Polonograptus chlupaci* Štorch, 2012 (in Manda *et al.* 2012; see also Štorch 1995a) from the *inexpectatus* and *kozłowskii* biozones – can be distinguished by its 1.3- to 1.7-mm-long sicula, equally short th 1 and more overlapping and elongated distal thecae.

Genus LOBOGRAPTUS Urbanek, 1958

Type species

Monograptus scanicus Tullberg, 1883; from the Ludlow of the Scania region, southern Sweden.

Diagnosis

After Urbanek (1958, p. 12).

Lobograptus scanicus (Tullberg, 1883) s. l. Figures 11D–E, I, 12D, H

1883

Monograptus scanicus Tullberg, pp. 26–27, pl. 2, fig. 44 (*non* figs 40, 42).

?1913

Monograptus scanicus Tullberg; Elles and Wood, pp. 433–434, pl. 44, fig. 2a–d; text-fig. 207a–d.

1936

Monograptus scanicus Tullberg; Bouček, pp. 21–22 (*partim*), pl. 2, fig. 9; text-fig. 4e, h (*non* f–g, i).

1953

Monograptus scanicus Tullberg; Bulman, pp. 131–136, figs 1, 2.

1955

Monograptus scanicus Tullberg; Kühne, pp. 391–392, fig. 14.

1958

Lobograptus scanicus (Tullberg); Urbanek, pp. 72–74 (*partim*), pl. 2, fig. 4 (*non* fig. 5).

1960

Lobograptus scanicus scanicus (Tullberg); Urbanek, fig. 13d.

1966

Lobograptus scanicus scanicus (Tullberg); Urbanek, pp. 444–452, pl. 27, pl. 47, fig. 2; text-figs 11, 12.

1997

Lobograptus scanicus (Tullberg); Zhang and Lenz, p. 1234, figs 6j–k, ?l.

2004

Lobograptus scanicus (Tullberg); Lenz and Kozłowska-Dawidziuk, p. 37 (*partim*), pl. 32, figs 6, ?8, 9, 10 (*non* figs 5, 7, 11, 12).

Material

Twelve flattened, more or less fragmentary rhabdosomes from the middle *chimaera–scanicus* Biozone through to the lowermost *leintwardinensis* Biozone, and further material from beds below the logged section.

Description

The most complete specimen is 53 mm long, yet lacks a distal end, sicula and initial thecae. The ventral curvature of the rhabdosome is accentuated in its mesial part, whereas the distal part and long, slender proximal portion are almost straight. Proximal thecae are c. 2.1 mm long, but only 0.12-mm-wide tubes, terminated by a small isolated metatheca with roughly kidney-shaped lateral apertural lobes. The ventral termination of the lobe is prominent in outline; the dorsal termination is in contact with the ventral wall of the subsequent protheca. Proximal thecae are widely spaced with a 2TRD of 3.1–3.8 mm (5.5–6.5 thecae in 10 mm), and they overlap for one-fifth their length. The ventral prothecal wall is inclined very weakly (at 0.5 degrees) to the rhabdosome axis. The dorso-ventral width measured across the apertural lobe is 0.25–0.35 mm.

Thecal overlap increases markedly in the mesial part of the rhabdosome accompanied by gradual widening to about 0.4–0.6 mm. The 2TRD decreases to 2.5–2.7 mm (thecae number 7.5–8 in 10 mm). Distal thecae are 2.1–2.65 mm long, 0.25–0.28 mm wide, inclined at 6–9 degrees, overlapping for more than half their length, and numbering 8.5–10.5 in 10 mm (Fig. 12D), 2TRD ranges from 1.9 to 2.3 mm. Metathecæ are tightly appressed without any isolation. The ventral parts of the lateral apertural lobes are more expressed

than the dorsal ones, which are seldom discernible against the ventral side of the subsequent protheca. The rhabdosome attains a maximum width of 0.9–1.1 mm.

Discussion

The present material is from the upper part of the *scanicus–chimaera* Biozone. Urbanek (1966) recognized several closely similar lobograptids at about the same level in the Mielnik borehole of eastern Poland. The two collections are hard to compare. The Polish material is chemically isolated with well-preserved siculae, initial thecae and thecal apertural structures. It is rather fragmentary, however, and the general form of the rhabdosome remains unknown. The flattened Czech material, in turn, reveals the flagellate general form of the rhabdosome as well as the thecal outline, whilst some diagnostic details of the complex apertural apparatus are barely discernible and siculae have not been found. *Lobograptus expectatus* Urbanek, 1960 can be readily distinguished from the present material by having symmetrical apertural lobes projected into beaklike, ventrally directed processes incurved over a ventral incision in the aperture. The distal thecae of *L. parascanicus* (Kühne, 1955) exhibit less asymmetrical apertural lobes with less prominent ventral extension. Apertural lobes are more appressed on the ventral wall of the succeeding protheca. *L. amphirostris* Urbanek, 1966, the presumed ancestor of *L. scanicus*, can be distinguished by its less asymmetrical apertural lobes with ventral process tightly incurved to form a large ventral extension. The latter feature is barely distinguishable in Czech specimens which are thus referred to *L. scanicus* s. l. *Lobograptus* cf. *cirrifer* Urbanek, 1966 Figures 11A, J–K, 12P

Remarks

A single, S-shaped rhabdosome with distinctive ventral curvature in its distal part and a dorsally curved proximal part comprising five thecae came from the middle *leintwardinensis* Biozone, sample level 54a. The more than 35-mm-long rhabdosome widens regularly from 0.3 mm at th 1, through 0.45 mm at th 5, to a maximum of 0.96 mm attained by th 30. The relatively rapid increase in dorso-ventral width is a distinctive feature of this specimen. The widely spaced proximal thecae (2TRD 2.8 mm, c. 7 thecae in 10 mm) with a markedly isolated subapertural part are terminated by dorso-ventrally extended elliptical lateral apertural lobes, are inclined at 10–15 degrees and overlap for nearly half their length. Distal thecae number 10–10.5 in 10 mm (2TRD – 1.9–2.0 mm). The limited material does not allow for definite identification. Apertural lobes, although badly preserved, resemble those of *S. scanicus* in outline except for the several barely recognizable, irregularly curved processes which suggest some similarity with less advanced forms of *L. cirrifer* (Urbanek; see Urbanek 1966, pp. 470–471). The rapidly widening, markedly S-shaped rhabdosome and more densely spaced thecae differentiate this form from *L. scanicus*.

Genus CUCULLOGRAPTUS Urbanek, 1954

Type species

Cucullograptus pazdroi Urbanek, 1954; from Ludlow limestone erratics from the Gdansk area, Poland.

Diagnosis

After Urbanek (1958, p. 12).

Cucullograptus hemiaversus Urbanek, 1960? Figure 11B

Remarks

Rhabdosomes are fragmentary, straight distally, with slight ventral curvature observed in mesial fragments. Thecae are long tubes, inclined at 2–6 degrees to the rhabdosome, having a slightly convex ventral wall and an asymmetrical aperture covered by dorso-ventrally extended apertural lobe. The apertural lobe has a slightly convex distal outline and a sub-semi-elliptical dorso-proximally facing margin. Thecae overlap for two-fifths to half their length. Only a small subapertural part of the metatheca may exhibit some isolation. The maximum width of the rhabdosome, measured across the apertural lobe, is 0.5–0.9 mm. 2TRD ranges from 1.7 to 2.5 mm generally decreasing towards the most distal thecae in concert with a gradual increase in the dorso-ventral width.

Cucullograptus hemiaversus can be distinguished from its ancestors and other, nonrelated cucullograptids by its asymmetrical thecal apertures with hypertrophied left apertural lobe bent over the aperture in the form of a simple sub-semi-elliptical structure. Thecae exhibit markedly greater overlap and lesser isolation than those of the presumed successors *C. aversus* (Eisenack) and *C. rostratus* Urbanek.

Cucullograptus cf. *aversus* (Eisenack, 1942) *sensu* Urbanek, 1966 Figures 11C, O, 12M–N

1966

Cucullograptus aversus cf. *aversus* Eisenack; Urbanek, pp. 492–495, text-fig. 17.

Material

Fourteen flattened incomplete specimens lacking proximal ends from a short interval in the uppermost part of the *leintwardinensis* Biozone and lowermost part of the *tenuis* Biozone (most specimens are from samples 46a and 44d, some poorly preserved rhabdosomes as high as from samples 44a and 42b).

Description

The rhabdosome is straight distally, with slight ventral curvature in its mesial part. The sicula and most proximal thecae have not been found. Based upon the 35- to 45-mm-long distal fragments and the gradual increase in dorso-ventral width, a complete mature rhabdosome must have exceeded 100 mm long. Thecae

exhibit laterally asymmetrical apertures covered by the left apertural lobe. The distal outline of the dorso-ventrally extended lateral apertural lobe is straight, parallel or everted to the thecal apertural margin hidden behind the lobe. The dorsal termination of the apertural lobe is tightly appressed to the ventral wall of the subsequent protheca. The dorso-ventral width measured across the apertural lobe is 0.3–0.4 mm in the most proximal regions preserved and reaches 0.5–0.9 mm in distal thecae. Prothecal tubes are 0.1–0.12 mm wide in proximal thecae (width measured above the preceding thecal aperture) and 0.28–0.3 mm wide in distal thecae. Distal thecae overlap for c. one-third their length; ventral prothecal walls are inclined at 1–2 degrees in proximal thecae and 5–10 degrees in distal thecae. Proximal thecae are widely spaced (2TRD 2.65–3.4 mm), distal thecae number c. 10 in 10 mm (2TRD 1.8–2.4 mm) although thecal spacing considerably varies between the thecae.

Remarks

Bohemian specimens best match the *C. aversus* cf. *aversus* illustrated and described by Urbanek (1966) which differs from *C. aversus* (Eisenack) and *C. cf. aversus sensu* Kühne (1955) in having metathecae without any apparent isolation. The dorsal termination of the dorso-ventrally extended left lateral apertural lobe is appressed to the ventral wall of the next theca. The distal outline of the lobe is nearly straight, and no rostrum is developed on the ventral termination in contrast to *C. rostratus* Urbanek. Definite assignment of the present material to Eisenack's (1942) *C. aversus* is not advisable until more and better preserved specimens with proximal thecae are found.

Cucullograptus rostratus Urbanek, 1960 Figures 11H, L–N, 12I, L

1954

Monograptus aversus Eisenack; Urbanek, pp. 297–300, figs 9–12.

1958

Cucullograptus aversus (Eisenack); Urbanek, pp. 70–72, figs 36–39.

1960

Cucullograptus aversus rostratus Urbanek, pp. 216–218, pl. 3, figs 1–5; text-figs 13 g, 14d, 21a–c.

1966

Cucullograptus aversus rostratus Urbanek; Urbanek, pp. 495–518, pls 37–42, pl. 47, figs 5–10; text-figs 18–24.

1990

Cucullograptus aversus rostratus Urbanek; Tomczyk *et al.* in Pajchlowa ed., pp. 390–393, pl. 185, fig. 11; pl. 186, fig. 1.

Material

Eleven flattened, more or less fragmentary rhabdosomes from the lower part of the *tenuis* Biozone (samples 44c–40c).

Description

The rhabdosome is very slender, flagellate, for the most part weakly dorsally curved. The longest two specimens, although incomplete without sicula and initial thecae, are 23 mm long. No sicula has been preserved. Thecae are composed of a long protheca and a short but very isolated metatheca with an asymmetrical, highly elaborate apertural structure. The aperture is covered completely by the large, incurved left apertural lobe, which is roughly semicircular in outline and oriented obliquely to the rhabdosome axis. The ventral (right) side of the lobe is projected into a 0.4- to 0.6-mm-long, dorsally curved, hornlike rostrum in mesial and distal thecae, whereas the dorsal (left) side of the lobe is only slightly extended in a much shorter process (Fig. 11H, e.g. the lowest theca).

Proximal thecae are extremely slender, prothecae being only 0.11 mm wide, inclined at an extremely low angle (1–2 degrees) to the rhabdosome. The dorso-ventral width of the rhabdosome, if measured from the ventral side of the lobe to the dorsal wall of the rhabdosome, is only 0.2 mm in proximal thecae. 2TRD ranges from 1.7 to 2.5 mm in the proximal part of the rhabdosome. In the mesial part of the rhabdosome, thecal spacing varies considerably with 2TRD ranging from 2.7 to 3.8 mm. Dorso-ventral width increases to 0.3–0.4 mm. Distal thecae becoming shorter (2TRD 2.3–2.5 mm, 8–9 thecae in 10 mm), and more isolated, with prothecae inclined at an angle of 10–13 degrees. The rhabdosome attains its maximum width of 0.5–0.63 mm measured across the metathecal lobe excluding processes. Initial parts of prothecae are 0.2–0.25 mm wide in distal thecae.

Remarks

Cucullograptus rostratus can be differentiated from *C. aversus* and *C. hemiaversus* by its lesser thecal overlap and more isolated metathecæ with proximo-ventrally directed or upwards incurved rostrum (cf. Urbanek 1966, fig. 22) and smaller process on the opposite side of the apertural lobe. We have raised *C. rostratus* to species rank because of its morphological and stratigraphical distinctiveness.

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