Ten graptolite species have been recognized by a general revision of all the material (both historical and new) collected from the Králův Dvůr Formation of the Prague Basin. One species belongs to the diceranograpid genus *Dicellograptus* and the remaining are biserial taxa assigned to the diplograptid genera *Diplograptus* and *Anticostia*, the lasiograptids *Parapielegmatograptus* and *Phormograptus*, the climacograptid *Styracograptus*, and the neodiplograptid genera *Normalograptus* and *Metabolograptus*. Although graptolite specimens are rare in these strata, there does appear to be a regular succession among the species, which results in a relatively low diversity of graptolites throughout the formation. The maximum species diversity is in the upper part preceding the distinct carbonate Perník Bed sedimentation. Three of the four species that occur in the lower part of the formation are endemic to the study region, however, *Anticostia teres* occurs in *P. linearis* Zone strata in Baltica (Bornholm and Sweden). Three of the four species that occur in the middle and upper part of the unit are more widely distributed species that occur also in the late Katian of the paleotropics. The uppermost Králův Dvůr Formation is marked by impoverishment that reduced the fauna to a single cosmopolitan species that occupies a narrow interval below the first early Hirnantian diamicrite. This graptolite distribution pattern appears to reflect changing global environmental conditions, including a late Katian climate amelioration (with expanded geographic ranges of several paleotropical graptolite species) followed by cooling and climate deterioration during latest Katian and early Hirnantian interval. Based on the new data, a biostratigraphic scheme has been modified and the Králův Dvůr Formation is inferred to be of mid Katian (*P. linearis*) to the earliest Hirnantian (early *M. extraordinarius*) age.

Key words: graptolite, Ordovician, Katian, Hirnantian, Prague Basin, biostratigraphy.

**Petr Kraft, Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague, Albertov 6, 128 43 Praha 2, Czech Republic; kraft@natur.cuni.cz • Petr Štorch, Institute of Geology v.v.i., Academy of Sciences of the Czech Republic, Rozvojová 269, 165 00 Praha 6, Czech Republic; storch@gli.cas.cz • Charles E. Mitchell, Department of Geology, University at Buffalo-SUNY, Buffalo, NY 14260-3050, USA; cem@geology.buffalo.edu**

Graptolite faunas are rare to absent in the majority of the Upper Ordovician successions of north-western peri-Gondwana. An exception within this graptolite “desert” is the middle Katian to lowermost Hirnantian graptolites of the Králův Dvůr Formation (Prague Basin, Barrandian area, central Bohemia, Fig. 1). Generally rare but locally common biserials and dicellograptids were discovered in this area in mid-19th century. Barrande (1870, p. 126, *Diplograptus teres, nomen nudum*) first noted their presence in association with his investigations at the historical Ježškov locality (Fig. 1) and his concept of “colonies”, *Dicellograptus aniceps* (= *D. laticeps* herein) was mentioned by Marr (1880). All graptolite material from the 19th century, including Barrande’s collection but excluding collections by J. Scharý, was subsequently described in a monograph by Perner (1895). Until Přibyl’s (1949) revision of biserial taxa, only a few notes on the stratigraphic occurrences of the faunas were published. The most recent systematic revision of graptolites from the Králův Dvůr Formation (Štorch 1989) focused exclusively on the upper part of the formation. The present paper benefits from substantial recent progress in the general knowledge of taxonomy and systematics of the Upper Ordovician graptoloids (Chen et al. 2005, Mitchell et al. 2007, Mitchell et al. 2009, Mclchin et al. 2011, Štorch et al. 2011). Here we re-examine all available specimens of graptoloids from the Králův Dvůr Formation, including a number of new collections, in an effort to bring these occurrences to broader attention, to up-date their taxonomic treatment and refine the biostratigraphic and biogeographic relationships of the fauna in the light of these revisions. We do not include rare dendroids *Ptilograptus* sp. and *Callograptus* sp. also known from this unit (unpublished fragments and Havlíček & Vaněk 1966).
The Upper Ordovician Králův Dvůr Formation crops out in a belt that surrounds the Silurian to Middle Devonian core of the Prague Basin volcano-sedimentary infill (Fig. 1). The Králův Dvůr Formation was also encountered in several boreholes in the central part of the basin relic below the overlying systems (e.g. in Tobolka near Koněprusy and Praha-Ořech). A prominent change in sedimentation, traceable across the whole “Mediterranean Province” (Havlíček 1989), can be observed at the base of the formation where the black shale lithofacies of the underlying Bohdalc Formation (Fig. 2) is replaced by greyish to greenish shales with micritic carbonate nodules. A prominent faunal change also occurs at this level: the Aegiromena-Drabovia brachiopod fauna of underlying units is replaced by low-diversity associations assigned to the relatively deep-water and soft-bottom Foliomena Fauna.

A complete list of fossil taxa of the Králův Dvůr Formation (e.g. Havlíček & Vaněk 1966) indicates that this interval records one of the more diverse fossil assemblages recovered from any formation of the Bohemian Ordovician. The fauna is dominated (roughly in order of decreasing species diversity) by benthos such as trilobites, bivalves, rhychoconelliform brachiopods, gastropods, ostracods, echinoderms, hyolithids, linguliform brachiopods, conulariids and others. The stratigraphic distribution of fossils is highly irregular and patchy, however, and portions of the formation are distinct both paleogeographically and stratigraphically. Based on those differences and typical species of trilobites and brachiopods, several faunal associations have been defined and described by Budil et al. (2011b).

The Králův Dvůr Formation is 25–200 m thick (Havlíček 1981, fig. 15; Havlíček in Chlupáč et al. 1998), and is composed of monotonous, commonly bioturbated shales. Their greyish to greenish color reflects a low content of organic matter (total organic C usually ranges between 0.1 and 0.3%). In the uppermost part of the formation, a carbonate-rich, 5–20 cm thick mudstone layer is developed in the great majority of sections (clayey carbonate according to Havlíček in Chlupáč et al. 1998). The overall faunal diversity increases abruptly in this level. Because of its correlative potential and specific fossil content, Brenchley & Štorch (1989) formalized the local jargon name, “Perník Bed” (i.e. gingerbread bed), for this
distinctive layer. The Perník Bed is overlain by 0.3–6 m of shale at the top of the Králův Dvůr Formation (Štorch & Mergl 1989), below the lower diamictite bed, which marks the base of the Kosov Formation (Fig. 3). Above the Perník Bed the overall faunal diversity decreased dramatically in response to global climatic changes driven by early Hirnantian glaciation.

Preservation of graptolites

Rhabdosome preservation ranges from completely flattened to almost full-relief. In flattened specimens some internal structures, such as the nema, lists or rods are often visible, pressed through the thecal walls. In moderately flattened rhabdosomes with three-dimensionally preserved external structures, some internal structures are discernable. Rhabdosome walls are generally well preserved (fusellar rings are evident in some specimens) but easily flake off in weathered material. In all the degrees of flattening rhabdosomes may be more or less distorted due to irregular soft-sediment distortion. Some rhabdosomes are bent or twisted non-parallel to bedding. Depending on the orientation of compression, i.e. position of specimens in the sediment, different features are affected. Besides usual lateral flattening, scalariform, sub-scalariform and box-flattened (a special case of lateral flattening in which one lateral surface of the rhabdosome and one apertural surface is in profile while the other apertural surface is presented in scalariform view) preservation is common. Some flattened rhabdosomes were identified to be aseptate because of the style of distortion in the proximal-distal direction. Most species show some preferential type of flattening, usually perpendicular to the broadest cross section of rhabdosome (i.e. the profile with maximal hydrodynamic drag). In the case of rhabdosomes that are elliptic or nearly circular in cross section (e.g., Normalograptus angustus), there is no preferential orientation to the bedding plane. Purely obverse or reverse profile views of rhabdosomes of these species are rare and sub-scalariform or scalariform orientations predominate. This is why the number of specimens appropriate for biometric study is low in N. angustus compared to the amount of collected material of this common species.

Stratigraphy and correlations

There are no known continuous sections through the Králův Dvůr Formation. The ranges of graptolites, shown in Fig. 3, are inferred from partial sections compiled over all accessible localities. Thus, the composite section through the formation is tentative and illustrates our current knowledge on the species co-occurrence and succession. The
lower part of formation is less well known than the upper part where more data are available and thus reliability of the proposed results (e.g. stratigraphic chart and diversity analyses) for that interval is much higher. Detailed reconstruction of the succession is further biased by lateral changes in biofacies and shale lithology. In spite of those restrictions, the new data presented here justify the revision and formal re-definition of the previous graptolite biostratigraphy of the Králův Dvůr Formation.

There have been several previous attempts to establish a biostratigraphic subdivision of the Králův Dvůr Formation strata based on graptolites. Bouček (1928) mentioned that Dicellograptus anceps (= D. laticeps herein) is frequent in the upper part of the formation, and Diplograptus teres (= Anticostia teres herein) and Diplograptus lobatus (Bouček appears to have included several species within this name) occur in the lower part. In his stratigraphic table, Bouček (1928) used only “D. anceps” as an index species and thus he considered the whole of the formation to belong to that single graptolite zone, with direct correlations to Scotland and Sweden where D. anceps was used as an index species. Bouček’s (1928) conception of a single graptolite zone through the entire Králův Dvůr Formation was adopted by other authors such as Přibyl (1949), Havlíček & Vaněk (1966) and Havlíček & Marek (1973). In contrast, Chlupáč (1951a, b, 1953), concluded from his study of several localities in the south-eastern flank of the outcrop belt that the Králův Dvůr Formation contained a succession of several faunally distinct “horizons”. In the upper part of the formation, below the Perník Bed, he recognized an interval characterized by the occurrence of “Climacograptus angustus”. In the uppermost beds of the formation Chlupáč (1951a, 1953) reported a very rich fauna that he said was characterized by the common occurrence of “Glyptograptus teres” concentrated in the layer just above the Perník Bed (“pelocarbonatic intercalation” according to Chlupáč 1951a). His detailed descriptions of the localities (Zadní Třebaň and Liteň) and the graptolite occurrences (see below), however, clearly indicate that the graptolite species that he had in these collections was Metabolograptus ojsuensis. Earlier misidentification and consequent extension of the stratigraphic range of “Glyptograptus teres” led Havlíček & Vaněk (1966) to recognize but a single biozone in the Králův Dvůr Formation. Subsequently, apparently because of his revised understanding of Anticostia teres and the stratigraphic position of the Lejškov locality, Havlíček in Chlupáč et al. (1992) returned to a stratigraphical concept similar to that of Bouček (1928) with a lower Glyptograptus teres Zone and an upper Dicellograptus anceps Zone. At around the same time, Storch & Mergl (1989) studied the upper part of the formation and noted that it was difficult to form a detailed graptolite biostratigraphy for the unit. They kept the concept of informal “horizons” and distinguished the “Climacograptus angustus Horizon” in the lower portion of the upper Králův Dvůr Formation and a separate “Glyptograptus aff. teres Horizon” within the uppermost portion of the formation. This model also was adopted by Storch (1989) who reassigned G. aff. teres material to Glyptograptus cf. ojsuensis. Havlíček in Chlupáč et al. (1998) critically synthesized all previous concepts into a stratigraphic chart in which he used a succession of three loosely defined zones: “Glyptograptus teres” in the lower part, “Scalarigraptus angustus” in the middle part, and “Glyptograptus cf. ojsuensis” in the uppermost part of the formation. This informal zonation is further updated and refined herein.

In the lower part of the Králův Dvůr Formation no well-defined biozone can be established due to the scarcity of graptolite data and sufficiently exposed sections. Several graptolite species occur in this part of the formation but specimens are rare and, for the most part, have been collected from different, isolated localities. Thus, it is not possible to establish their stratigraphic relationships. An informal interval with Anticostia teres and Styracograptus lobatus (Fig. 3) appears to be the best solution for the time being.

The middle and upper portions of the Králův Dvůr Formation are characterized by relatively common occurrences of Normalograptus angustus. Although the species characterizes a laterally persistent and restricted stratigraphic interval in the Prague Basin, its known stratigraphic range is extremely long, as shown in many successions in other parts of the world (e.g. Goldman et al. 2011). Dicellograptus laticeps occurs with N. angustus through most of its range in the Králův Dvůr Formation. Despite its low abundance, we prefer D. laticeps as an index taxon because of the much longer stratigraphic range of N. angustus in other areas and we establish the Dicellograptus laticeps Taxon-range Zone (Fig. 3). Its base, although not yet recorded in a continuously sampled section, is defined by the lowest occurrence of D. laticeps, Diplograptus rigidus? occurs in the lower part of the biozone, and Paraplagmatograptus uniformis and Phormograptus chuchlensis occur in the upper part, however all these species are quite rare.

The youngest known specimen of D. laticeps has been found several meters below the Perník Bed, slightly below the last occurrence of Normalograptus angustus (specimen CGS SZ 181). Thus, the top of the Dicellograptus laticeps Biozone lies within the upper part of the shaly succession, a few meters below the Perník Bed. The biozone is overlain by approximately 2–5 meters of shale that hosts the last occurrences of N. angustus. A subsequent interval of mottled shale, ca 2 m thick and devoid of graptolites, is topped by the calcareous Perník Bed (Fig. 3).

The shale immediately above the Perník Bed is characterized by locally abundant occurrences of Metabolo-
**graptus ojsuensis**, which is associated with and succeeded by common specimens of the trilobite *Mucronaspis*. A formal *Metabolograptus ojsuensis* Taxon-range Zone can be recognized in this level (Fig. 3). Its base, defined by the lowest occurrence of the index species, coincides with the basal layer of the shale overlying the Perník Bed. Its upper limit, defined by the highest occurrences of *M. ojsuensis*, lies in shales between the Perník Bed and the basal diamictite of the overlying Kosov Formation. The *Metabolograptus ojsuensis* Zone is usually only a little more than 10 cm thick. The shale succession above this zone is barren of graptolites until the lowest occurrences of *Metabolograptus persculptus* in the uppermost part of the Hirnantian Kosov Formation.

Although the number of graptolite species present in the Králův Dvůr Formation is somewhat higher than that of other units of the Upper Ordovician in the Prague Basin, individual occurrences have relatively low diversity. The maximum number of species coexisting in any portion of the formation (four) is inferred to have occurred in the upper part of the formation (Fig. 3). The diversity in the lower part cannot be reliably evaluated and the maximum illustrated for that interval (Fig. 3) is a composite of ranges recorded from separate localities. We suppose that these species overlapped in time but direct evidence of this is slim and they have never been found together, unlike the small multispecies assemblages of the *D. laticeps* Zone. The abundance of graptolite specimens in the formation (in distinction from number of species) fluctuates, but overall is higher in the upper beds. However, this rise is purely a product of the relatively common *Normalograptus angustus* and less common *Dicellograptus laticeps* in the upper part of the *D. laticeps* interval, and by the locally abundant monospecific occurrences of *Metabolograptus ojsuensis* in the uppermost part of the formation.

The paleobiogeographic distribution of the species exhibits a more distinct trend. Three of the four species of the lower part of the formation are so far known only from the Prague Basin. Although *Anticostia teres* has not previously been reported from outside the study region, this appears to reflect the poor state of knowledge of the species rather than its original range. One of us (CEM, in collaboration...
with Daniel Goldman) has found A. teres commonly in the Pleurograptus linearis Zone of the Dicellograptus Shales at Laeså, Bornholm (Denmark; Goldman collections), and in the Fjåka Shale at Gulleråsen, Dalarn region, Sweden (unnumbered slab, Törnqvist collection, Lund University). Graptolites with a somewhat wider range of palaeogeographic distribution appear in the middle part of the formation, dominate in the upper part and became exclusive in the uppermost portion.

The changes in diversity and biogeographic distribution discussed above may reflect the effects of Late Ordo-vician climatic fluctuation. The shift toward slightly more common graptolite occurrences with an increasingly cosmopolitan fauna in the D. laticeps Zone may represent a local expression of the late Katian temporary warming episode (accompanied by poleward invasion of paleotropical species) known as the Boda Event (Fortey & Cock 2005; see recent summary in Melchin et al. 2013). That interval contains a peak in the diversity of diplograptine graptolites as it does here in the Prague Basin, and is followed in most parts of the paleotropics by an abrupt replacement of this diverse diplograptine fauna in the earliest Hirnantian by a low diversity assemblage entirely dominated by Neograp-tina species, and in this case by the monospecific Metabolo-graptus ojsuensis occurrence in the upper-most Králův Dvůr Formation. We turn below to a discussion of the probable age of these Králův Dvůr Formation occurrences.

Several authors have used graptolites to correlate the Králův Dvůr Formation (e.g., Přibyl 1949, Štorch 1989, and Brenchley & Štorch 1989). However, it is difficult to correlate the Královodvorní graptolite faunas and biozones even with diverse faunas and zonal schemes of low-latitude palaeogeographic realms. Correlation is possible only with limited precision because of the lack of sufficient diversity of widespread species with relevant correlative potential. Other mid- and high-latitude palaeogeographic realms do not yield reliable correlative graptolite taxa at all.

The lower part of the formation has hitherto yielded solely species with limited palaeogeographical extent, as noted above, however, the new records of Anticostia teres in undoubted Pleurograptus linearis Zone strata in the Baltic region (discussed above) dramatically changes this situation. Thus, the strata of the interval with A. teres and Styracograptus lobatus were most likely deposited in mid-Katian time — probably early in the Ashgill or the late Caradoc, early Harju, and late Eastonian series or stage equivalents, or the Ka3 to Ka4 time slices of Bergström et al. (2009).

Normalograptus angustus appears to have a very long stratigraphic range (Koren’& Sobolevskaia in Koren’ et al. 1983), but middle Katian records from the paleotropics (e.g. Chen et al. 2005) previously identified as N. angustus are actually referable to Styracograptus (Goldman et al. 2011) and many Rhuddanian occurrences belong to other normalograptid species. Reliable records of N. angustus range from mid-Katian (Pleurograptus linearis Zone; Skoglund 1963), through the Hirnantian Metabolograptus extraordinarius and Metabolograptus persculptus zones and possibly lowermost Rhuddanian (e.g., Chen et al. 2005, Apollonov et al. 1980).

Dicellograptus anceps, closely related to D. laticeps, is the index species of the uppermost Katian zone in the east-Laurentian southern Scotland (e.g. Williams 1982). Diplograptus rigidus is known from the Paraorthograptus pacificus Zone of Nevada, western Laurentia (Štorch et al. 2011) and from approximately upper Dicellograptus complexus and lower P. pacificus zones of South China (Yangtze Platform, Mu et al. 1993). Parapleogrammatograptus uniformis and Phormograptus chuchlensis (which is probably the senior name of Phormograptus connectus) have been found in the D. complexus, P. pacificus and M. extraordinarius (former M. extraordinarius–M. ojsuensis) zones of South China (Chen et al. 2000), the Dicellograptus ornatus and P. pacificus zones in western Laurentia (Štorch et al. 2011), and in the D. anceps Zone of eastern Laurentia (Williams 1982). Thus, on the basis of species ranges, the Bohemian D. laticeps Zone corre-sponds roughly to D. anceps Zone of eastern Laurentia, D. ornatus to P. pacificus Zone of western Laurentia and D. complexus to P. pacificus Zone of South China.

Rickards (2002) and Zalasiewicz. et al. (2009) reported D. laticeps (identified as D. praeanceps) from the Pleurograptus linearis Zone of England, i.e. preceding the D. anceps Zone. Although the zonal assignment of the assem-blage in which it occurs relied in part on several doubtful specimens of Pl. linearis, many of the other elements of that fauna are commonly regarded as indicative of the Pl. linearis Zone. The associated Conochitina rugata Zone and younger chitinozoan faunas (Vandenbroucke et al. 2005), on the other hand, suggest correlation with the D. anceps Zone interval in Baltica (Ainsaar et al. 2010), consistent with the inferences above about the age of the D. laticeps-bearing interval in the upper Králův Dvůr Formation.

As mentioned above, the D. laticeps Zone of the Králův Dvůr Formation contains the highest graptolite faunal diversity (per occurrence) and specimen abundance of any interval in the Late Ordovician succession in the Prague Basin and also includes a relatively cosmopolitan fauna. These features, combined with the ranges of the taxa present, suggest that the D. laticeps Zone may actually corre-spond to some part of the late-phase Boda Event climatic warming in which black shales became widespread in the paleotropics during the P. pacificus Zone (Armstrong et al. 2009a, Page et al. 2007, Melchin et al. 2013).

Biostratigraphic correlation of the monospecific assem-blage of the zonal index Metabolograptus ojsuensis is also somewhat ambiguous. M. ojsuensis is a secondary marker of the base of the Hirnantian (Chen et al. 2006) and
its lowest occurrences with respect to those of the primary marker *Metabolograptus extraordinarius* vary in different areas as discussed by Legrand (2011). It seemed that in the Prague Basin the problem could be solved as Mitchell et al. (2011) reported a specimen of *M. extraordinarius* associated with *M. ojsuensis* from Zadní Třeň. Our examination of this specimen, however, shows that it is rather broad specimen of *M. ojsuensis*, furthermore preserved in a specific box-flattened partial relief mode. Thus, *M. extraordinarius* has thus far not been recovered in the peri-Gondwana Europe. Indirect evidence of an Hirnantian age for the shale interval between the Perník Bed and the first diamictite is provided by the earliest occurrence of the *Hirnanti Fauna* 5–7 cm below the diamictite at the base of the overlying Kosov Fm. as documented by Mergl (2011a, b) and by the positive excursion in δ13Corg through this interval shown by Mitchell et al. (2011; Fig. 2). The steep rising limb of this excursion passes through the Perník Bed and δ13Corg values peak immediately below the lowermost Kosov Fm. diamictite. This part of the δ13Corg curve at Vinini Creek, Nevada (LaPorte et al. 2009, Storch et al. 2011) and at several other sites (most notably at Mirny Creek, Siberia; Kaljo et al. 2012) contains the base of the *M. extraordinarius* Zone. These data suggest that the *M. ojsuensis* Biozone of the uppermost Králův Dvůr Formation is most likely early Hirnantian in age.

Havlíček & Vaněk (1966) established several stratigraphical “horizons” based on the apparent stratigraphical succession of some typical benthic faunal associations, especially trilobites, revealed by the detailed field studies by Chlupač (1951a, b, 1953). This scheme has been modified and gradually transformed into a model of trilobite associations that reflect both the stratigraphical succession and regional facies distribution (e.g. Shaw 2000) and was also combined with a similar model of brachiopod associations (or assemblages or communities) by several authors (e.g. Havlíček & Vaněk 1966, Havlíček 1982, Havlíček in Chlupač et al. 1998). Recent revision of trilobite associations by Budíl et al. (2011b) suggests that the main part of the stratigraphic range of *Amphitriton-Klouceckia* Association falls within the *Dicellograptus laticeps* Biozone because the index species, as well as *Dicellograptus anceps*, are usually found in shales with benthic elements typical for that association. The *Metabolograptus ojsuensis* Biozone occupies the lowermost part of the stratigraphic range of the *Mucronaspis* Association. It corresponds to layers with the richest fossil content of this benthic association, the composition of which is generally considered to be a response to cooling (Storch & Mergl 1989).

Special attention has been paid to the so called Lejškov facies (Budíl et al. 2011b) occurring in the lower part of the Králův Dvůr Formation because of its abundant and characteristic fossils collected mainly in 19th century. Havlíček & Vaněk (1966) called this assemblage the “Lejškov” fauna association (biofacies, in current usage). The typical historical material came from dark grey shale (Fig. 3). Budíl et al. (2011b), however, did not recognize the Lejškov facies as a formal faunal association. Recent field research at Lejškov suggests that the typical fauna of the dark shale has a wider stratigraphic range reaching higher in the Králův Dvůr Formation than supposed before (Budíl et al. 2011a). However, the historical Lejškov material that preserved in the characteristic dark shale lithofacies contains only *Anticostia teres* and apparently belongs to a limited stratigraphic interval in the lower part of the formation.

The Králůdvorían and its delimitation

Havlíček & Marek (1973) originally established the Králůdvořían Stage as a Series of regional value, corresponding to the Králův Dvůr Formation. Although this unit has been used subsequently in the Mediterranean realm of peri-Gondwana (Gutiérrez-Marco et al. 2002), its loose definition has relied on distinctive lithology and benthic faunas. Thus, the Králůdvorían represents an interval characterized by both facies that are different from underlying as well as overlying units and by a specific succession of faunal associations that reflect distinct conditions widespread in the peri-Gondwana Europe of that time. These are criteria irrelevant to the definition of a formal chronostratigraphic unit because of their heterochronous nature. Any redefinition of Králůdvořían as a regional chronostratigraphic unit should be based upon isochronous markers. As is obvious from the above, graptolites are of low value to resolve this task. However, the upper limit of the Králůdvořían can be recognized by the first appearance of *Metabolograptus ojsuensis* immediately followed by typical elements of benthic Hirnantian fauna (Fig. 3).

Systematic part

Despite approximately 150 years of research and fossil collecting in the Králův Dvůr Formation, the graptolite material is quite limited and housed in only a few collections: National Museum in Prague (specimens with prefix NM), Faculty of Science, Charles University in Prague (FSCU), Czech Geological Survey in Prague (CGS), West Bohemian Museum in Pilzen (WBM), and the J. Schary Collection repositioned in the Agassiz Museum of Comparative Zoology, Harvard University (MCZ). The present revision further benefits from the authors’ own collections, discovery of “forgotten” material in historical collections at the Faculty of Science, and overlooked material in the Schary Collection. For descriptions in the following chapter we use biometric features as characterized by Storch et al. (2011; fig. 7 for *Dicellograptus* and fig. 13 for biserials).
Genus *Dicellograptus* Hopkinson, 1871

**Type species.** – *Didymograptus elegans* Carruthers, 1867, p. 369, pl. 2, fig. 16a; subsequently designated by Gurley 1896, p. 70.

**Dicellograptus laticeps** Štorch, 1989

Figures 4B–F; 11A–B, F–G

1895 *Dicellograptus anceps* Nicholson. – Perner, p. 43, pl. 7, fig. 17; pl. 8, figs 2–4; text-figs 3–6; non pl. 8, fig. 1 (distorted *Normalograptus angustus*).

1989 *Dicellograptus cf. anceps* (Nicholson). – Štorch & Merkl, pl. 4, fig. 5.

1989 *Dicellograptus laticeps* sp. n.; Štorch, pp. 175–177, pl. 1, figs 1, 2, 6, 8; text-fig. 1A–C, E–G.

1989 *Dicellograptus cf. morrisi* Hopkinson. – Štorch, pp. 175–177, pl. 1, figs 4, 5; text-fig. 1D, H.

2002 *Dicellograptus praeaniceps* sp. nov.; Rickards, pp. 6–7, text-fig. 5.

**Holotype.** – Specimen NM L27514 from Králův Dvůr designated and figured by Štorch (1989) on pl. 1, fig. 8 and text-fig. 1B; previously also figured by Perner (1895) on text-fig. 5.

**Material.** – 21 specimens (NM L27511, L27514, L27523, L27533, L27761, L27762, L40983; FSCU 909, 5169, 5173 – counterpart to NM L27533, 5174, 5175, 1 specimen without number – counterpart to part of CGS BB653/1; CGS BB653/1 – 2 specimens, CGS P5311, PŠ312, PŠ314; WBM S 05148; MCZ 196546, 196547, 2 specimens without numbers) with proximal part and several stipe fragments. The specimens include individuals preserved in moderate relief as well as flattened. Generally specimens have been recovered as single individual colonies. Only at the Králův Dvůr historical locality have multiple specimens (often complete) been found together, where they comprise largely non-specific accumulations of specimens of different size. Occasionally rhabdosomes were accompanied by specimens of *Normalograptus angustus*.

**Description.** – Sicula 0.16–0.24 mm wide, apical part resorbed during colony growth; all adult rhabdosomes display only sicular residua 0.55–0.8 mm long. Nearly complete sicula recorded in one juvenile specimen (Fig. 4C; possessing 3 thecae in stipe) is 1.2 mm long. Nema not observed. Virgella 0.35 to 0.45 (max. 0.5) mm long. Stipes usually more than 20 mm long; longest recorded: 67.5 mm (Fig. 11F). The stipes initiate with narrow, 1.25–1.4 mm wide axil in which th1 and th2 grew sub-horizontally to slightly reclined, then, behind mesial spines, turned sharply upward (dorsally) forming relatively narrow, rounded axil. Initial angle of divergence (first one to two centimeters) ranges between 20° and 40°. Three unusual specimens exhibit stipe divergence of 65° to as much as 83°. Thus, proximal shape highly variable, ranging from narrow to less frequently open. Proximal stipe segments of variable length, usually straight to almost straight, becoming slightly dorsally flexed distally, or less commonly slightly dorsally flexed throughout. Long stipes form narrow and high double helix accompanied by rotation of the stipes. Depending on growth stages of stipes and their distortion on bedding planes, angle of divergence and orientation of thecae change in the distal portion (e.g., Figs 4B, 11F) as thecal apertures continually faced outward from the helix. Thickened proximal part of stipes combined with resorbed sicula form a narrow U-shaped dorsal arch. Exceptionally, a small membrane fills the axil of mature rhabdosomes (Fig. 4E with tiny, probably initial membrane, 4F with advanced, sickle-like membrane) to an observed maximum height of 0.45 mm in the sicular axis. Stipes 0.45–0.5 mm wide at th1 and 12, 0.45–0.5 mm at th2, 0.45–0.55 mm at th2 and gradually broaden to 0.5–0.65 mm at th3 and th4, 0.6–0.7 mm at th5, 0.6–0.75 mm at th6, 0.75–0.8 mm at th7, 0.75–0.85 mm at th8 and th9, 0.8–0.95 mm at th10, reaching maximum of 0.9–0.95 mm usually at the level of th9 to th12; maximum observed stipe width is 1.1 mm in a long stipe fragment. Stipe expansion curve (for method see Cooper & Fortey 1982) has almost linear trend and a low slope. Thecae dicellograptid with angular genicula; apertures introverted and weakly to strongly introtorted. Thecae 1 and 2 are 0.5–0.65 mm long; distal thecae reach 1.6–1.8 mm in length and overlap for less than one half their length. Interthecal septa inclined at 18–25°, and supragenicular ventral walls parallel to slightly inclined to stipe axis. Basal spines developed in th1 and 1 are 0.2 to 0.3 mm long (max. 0.35) and 0.04–0.09 mm wide at their base. Much shorter mesial spines occur on convex supragenicular ventral thecal walls up to th6 to th11. Specimen NM L40983 exhibits a genicular rim resembling a short spine but this is a preservational artifact. Thecal spacing (2TRD) increases from 1.25–1.5 mm at th2, through 1.75–1.9 mm
A–Diplograptus rigidus (Lee in Wang, 1974)?: FSCU 5165 (external mold). • B–F – Dicellograptus laticeps Storch, 1989: B – NM L27514 (holotype, relief specimen); C – WBM S 05148 (flattened juvenile specimen with preserved sicula); D – FSCU 5169 (relief specimen, partly exfoliated); E – FSCU 5175 (specimen in partial relief with initial membrane); F – FSCU 5173 (low relief external mold, specimen with advanced membrane), figured by Perner (1895, pl. 8, fig. 3) and counterpart of the specimen, NM L27533, figured by Perner (1895, pl. 7, fig. 17) and refigured by Štorch (1989, fig. 1A). All specimens from Králův Dvůr, except C from Praha-Radotín – highway tunnel. All figures × 6, except C × 10. Scale bars equal 1 mm.

Figure 4. A – Diplograptus rigidus (Lee in Wang, 1974)?: FSCU 5165 (external mold). • B–F – Dicellograptus laticeps Storch, 1989: B – NM L27514 (holotype, relief specimen); C – WBM S 05148 (flattened juvenile specimen with preserved sicula); D – FSCU 5169 (relief specimen, partly exfoliated); E – FSCU 5175 (specimen in partial relief with initial membrane); F – FSCU 5173 (low relief external mold, specimen with advanced membrane), figured by Perner (1895, pl. 8, fig. 3) and counterpart of the specimen, NM L27533, figured by Perner (1895, pl. 7, fig. 17) and refigured by Štorch (1989, fig. 1A). All specimens from Králův Dvůr, except C from Praha-Radotín – highway tunnel. All figures × 6, except C × 10. Scale bars equal 1 mm.
Table 1. Dicellograptus laticeps Štorch, 1989. Dimensions of illustrated, type and other selected specimens (in mm): L – length, W – width. References on previously figured specimens only in cases not mentioned in the text or explanations of figures.

<table>
<thead>
<tr>
<th>Specimen No.</th>
<th>Figures</th>
<th>Sicula L</th>
<th>Axil W</th>
<th>Number of spinose thecae</th>
<th>Stipe W</th>
<th>2TRD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>th1</td>
<td>th3</td>
</tr>
<tr>
<td>NM L27514</td>
<td>4B (holotype)</td>
<td></td>
<td>1.4</td>
<td>–10</td>
<td>0.6</td>
<td>0.65</td>
</tr>
<tr>
<td>NM L40983</td>
<td>–</td>
<td>0.8 (partly absorbed)</td>
<td>1.45</td>
<td>8</td>
<td>0.55</td>
<td>0.6</td>
</tr>
<tr>
<td>WBM S 05148</td>
<td>4C</td>
<td></td>
<td>1.2</td>
<td>?</td>
<td>0.5</td>
<td>–</td>
</tr>
<tr>
<td>FSCU 5167</td>
<td>4D, 11B</td>
<td>absorbed</td>
<td>1.25</td>
<td>–9</td>
<td>0.55</td>
<td>0.6</td>
</tr>
<tr>
<td>FSCU 5175</td>
<td>4E</td>
<td>absorbed</td>
<td>1.25</td>
<td>–9</td>
<td>0.5</td>
<td>0.55</td>
</tr>
<tr>
<td>FSCU 5173</td>
<td>4F</td>
<td>membrane</td>
<td>1.45</td>
<td>–11</td>
<td>0.6</td>
<td>0.55</td>
</tr>
<tr>
<td>MCZ 196546</td>
<td>11A</td>
<td>absorbed</td>
<td>–0.9</td>
<td>? (only 2 visible)</td>
<td>0.45</td>
<td>0.55</td>
</tr>
<tr>
<td>MCZ 196547</td>
<td>11F, G</td>
<td>0.6 (partly absorbed)</td>
<td>1.3</td>
<td>? (~7–8)</td>
<td>0.4</td>
<td>0.55</td>
</tr>
<tr>
<td>CGS BB 653/1 (Štorch 1989, text-fig. 1D)</td>
<td>0.5 (part missing)</td>
<td></td>
<td>1.25</td>
<td>clearly visible in 3</td>
<td>0.45</td>
<td>0.5</td>
</tr>
<tr>
<td>CGS BB 653/2 (Štorch 1989, text-fig. 1H)</td>
<td>0.6 (partly absorbed and surrounded by minute membrane)</td>
<td></td>
<td>1.2</td>
<td>only in 1st pair visible</td>
<td>0.45</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Remarks. – This species characteristically has a narrow, U-shaped axil, small basal spines on first thecal pair followed by a number of spiny thecae. Thecae are relatively closely spaced compared to stipe width and strongly geniculate. The general shape of the rhabdosome on bedding planes varies depending on the orientation of the different growth stages of double helical rhabdosome prior to flattening. The stipes may be straight or flexed in different ways as a whole or in part as a result of that distortion. The angle of divergence also ranges over a very wide interval. Williams (1981) has shown that primary variability in stipe angle is enhanced by the preservational effects of stipe flattening in different orientations. The orientation of stipes and thecae also influence the preservation of mesial spines, ranging from fully preserved series to no spines preserved. In addition, preservation of spines can differ between stipes on a single specimen. Thus, divergence and course of stipes and mesial spines, combined with original variability have to be assessed based on a sufficient number of specimens to show the range of both primary and preservational variations. Their misinterpretation, in general, can bias the identification and classification of dicellograptids.

Only a few dicellograptid species exhibit spinose proximal thecae beyond the first pair. Among them are D. gurleyi Lapworth in Gurley, 1896 and D. flexuosus Lapworth, 1876, which are considerably older and markedly different in form. A conspicuous sicula is preserved in adult colonies in both taxa and the former is much more slender. Some similarities in biometric features can be traced in the latter species but their thecae are more widely spaced and the stipes are more strongly divergent, forming an open arched proximal end. Only two coeval species, D. anceps Nicholson, 1867 and D. morrisi Hopkinson, 1871 have numerous spinose thecae beyond the first pair. The more open, almost symmetrical proximal end together with narrower stipes, slightly longer distal thecae and denser thecae proximally represent significant differences from the very similar D. anceps. The biometric parameters of D. morrisi are even closer to those of D. laticeps but the key difference is in the position of its mesial spines as suggested by Rickards (2002). D. laticeps (as well as D. anceps) has spines situated usually slightly above the half length of supragenicular wall while D. morrisi possesses supramesial spines positioned subaperturally. The latter species also has more open axil and much wider angle of stipe divergence in most specimens. Štorch (1989) assigned two specimens (Fig. 1D, H therein) to D. cf. morrisi. The shape of the rhabdosome in these specimens does resemble that of D. morrisi, but the preserved mesial spines are not as high on the supragenicular wall as in that species. It should be noted that the spines on the left stipe of the specimen figured by Štorch (1989, fig. 1D) appear to occupy slightly higher positions than typical of D. laticeps but we regard this as a preservational artifact and consider the specimen to be within the variability of that species.

Rickards (2002) described D. praeances D. praeances as a descendant of D. morrisi and an ancestor of D. anceps. The overall shape and biometric data of the type specimens of D. praeances fit with those of D. laticeps. We consider D. praeances to be conspecific with D. laticeps and the deduced lineage to be questionable due to the doubtful correlation of the biostratigraphic ranges (Rickards 2002).

Occurrence. – Králov Dvůr, Levin, Litén, Praha-Malá Ohrada, Praha-Radotín – highway tunnel, Praha-Velká Chuchle; middle and upper part of Králov Dvůr Formation. In addition to Bohemia, the species is known from England.

A stipe fragment in dark grey shale reposited in the National Museum (without inventory number) from Lejškov was identified as undeterminable Dicellograptus. It is
poorly preserved but several thecae in oblique orientation at one end manifest typical dicellograptid thecal excava-
tions. Its stratigraphic position is unknown but it supports
the concept of Budil et al. (2011a), discussed above, on the
apparently wider stratigraphic range of the locality than
supposed before.

Superfamily Diplograptoidae Lapworth, 1880; emend. Mitchell et al., 2007
Family Diplograptidae Lapworth, 1873; emend. Mitchell et al., 2007

Genus Diplograptus McCoy, 1850, emend. Mitchell et al., 2009

Type species. – Prionotis pristis Hisinger, 1837, p. 114, pl 35, fig. 5; subsequently designated by Gurley 1896, p. 78.

Diplograptus rigidus (Lee in Wang, 1974)?

Figure 4A

1974 Orthograptus rigidus; Lee in Wang, p. 746, pl. 29, figs 10, 11.
1988 Orthograptus rigidus Lee. – Li & Cheng, pp. 168–169, pl. 1, fig. 7; text-fig. 2a, b.
1993 Orthograptus rigidus Lee. – Mu et al., pp. 191–192, pl. 42, figs 1–3.
1993 Orthograptus aquecens sp. nov.; Li in Mu et al., pp. 193–194, 347, pl. 43, figs 5, 6, 9, 14, 15.
1993 Orthograptus yangtziensis sp. nov.; Li in Mu et al., pp. 194, 347–348, pl. 43, figs 8, 10, 11, 16.
2009 Diplograptus rigidus (Lee). – Mitchell et al., fig. 21.

Holotype. – Not traced.

Material. – Three poorly preserved specimens, one box-flattened, preserved as a distorted, semi-relief external mold with proximal end (FSCU 5165), the other two as partly exfoliated flattened molds without proximal end on a single slab (NM L28041). All situated on bedding planes coated with limonite. It could be that some crumpled rhabdosomes compressed in axial direction, i.e. with significant distortion component reducing the length of the colony (NM without number) belong to the same taxon.

Description. – The studied specimens attain length of 16.5 mm. Rhabdosome relatively robust, widens rapidly from 1.6 mm at the first thecal pair, through 1.85 mm at th2, 2.0 mm at th3, 2.1 mm at th4 and 2.3 mm at th5 to maximum 3.3 mm at th15. Mode of flattening accounts for rather rectangular cross section with subrounded ventral thecal profile in figured specimen. Sicula not observed but short virgella present. Proximal end wide, blunt and weakly asymmetric. Th1 and th2 turn outwards and only slightly upwards from sicula initially but turn sharply upwards at the level of short, robust mesial spines developed on both thecae. The subsequent thecae are sharply geniculate proximally with short supragenicular wall becoming weakly geniculate distally. Apertural excavations 0.5–0.6 mm high throughout; supragenicular walls become shorter in distal thecae (Fig. 4A) where height of the apertural excavation equals the length of the supragenicular wall. Two-thecae repeat distance (2TRD) in measurable portions of the limited material: 1.45 mm at th2; 1.7 mm at th5. Thecae number 13 in 10 mm proximally and 10 in 10 mm distally. Rhabdosome seems to be partially aseptate. Specimens compressed axially, and assigned to this taxon only with reserve (NM without number; see material), display distortion that suggests median septum not present. In the best-preserved, almost complete box-flattened specimen (Fig. 4A), however, a trace of a low ridge in the external mold indicates the presence of septum beginning at th11.

Remarks. – Despite poor preservation three fragments match well with emended characteristics of Diplograptus, including thecal style, short virgella and distal shortening of the supragenicular wall (Mitchell et al. 2009). Although many species of Diplograptus are septate, the appearance of the median septum is generally delayed, often considerably. The present aseptate specimens may have such a delayed development of the septum. The architecture of the very broad proximal end and the closely spaced thecae, discussed by Štorch et al. (2011), are typical of D. rigidus and all measurable biometric parameters agree with this species. Thus, we assign the three specimens to this taxon with reservation simply because of the unfavorable preservation of the limited material available for study. The assignment of other distorted rhabdosomes is more doubtful. The thecae of these distorted rhabdosomes more closely resemble those of Anticostia.

Occurrence. – Králův Dvůr; middle part of the Králův Dvůr Fm., questionably also from its lower part. D. rigidus also occurs in South China and western Laurentia (Ne-

Diplograptus fritschi Perner, 1895

Figures 7K, 10A–E, 12A, 13A, E

1895 Diplograptus rugosus Emmons var. Fritschi mihi; Perner, p. 29, pl. 8, fig. 7.

**Holotype.** – Specimen NM L27520 from Králův Dvůr (Königsfohr) figured by Perner (1895) pl. 8, fig. 7, refigured by Přibyl (1949) pl. 3, fig. 7 and herein Fig 1OC; designated by Přibyl (1949) by monotypy.

**Material.** – Two solitary specimens (WBM S 05151, WBM S 05152) and two clusters of several specimens with a few moderately well-preserved rhabdosomes (NM L27520, WBM S 05155), however most material is partially obliquely compressed longitudinally or laterally box-flattened.

**Description.** – Partly septate, robust rhabdosome usually *ca* 30 mm long, but up to 48.5 mm. Rhabdosome widens gradually from 1.15–1.35 mm at first thecal pair, 1.3–1.7 at th2, 1.3–2.0 mm at th3, 1.75–2.2 mm at th5 to 2.35–2.5 mm at th10. Width 2.6 mm at 18th thecal pair and 3.25 mm at the end of the largest specimen. Proximal end rather asymmetrical and V-shaped, with first pair weakly curved and moderately to strongly inclined outward. Sicula 0.25–0.3 mm wide across a straight aperture from which virgella, up to 0.95 mm long, projects. Sicula exposed on obverse side until enclosed by th2\(^2\) protocha. Thin nema (0.03 mm wide) free in the aseptate portion. Downward-grown portion of th1\(^1\) about 0.6 mm long, descends along the sicula and turns upward slightly below the level of the sicular aperture. After hook-like bend, upward-grown portion extends upward and outward for another 0.65–0.9 mm. Thl\(^2\) emerges from dorsal outline of sicula 0.25–0.3 mm above the sicular aperture and extends upwards and outwards. Length of thl\(^2\) is 0.5–0.9 mm. Subsequent thecae of the aseptate portion of the rhabdosome possess a convex infragenicular ventral wall with rounded geniculum and convex supragenicular wall; supragenicular walls become rapidly shorter over the first 6–8 thecae as infragenicular walls develop long triangular concavity (*i.e.*, acquire a pseudogenicular structure; Figs 7K, 10E). The median septum appears from the level of thl\(^1\)–10\(^1\). Thecae in the sepa- tate part become nearly straight with slight ventral convexity, distinct in prothecal part and fading towards the aperture. Thecal length increases from 1.3–1.8 mm at th3 through 1.65–2.0 mm at th5 to 2.5 mm at th10. Intertheal septa are developed as thecae overlap for half their length or slightly more in the distal, septate part of the rhabdosome. Thecae incline at an angle of around 20° to the rhabdosome axis (measured values vary between 16° and 26°). Thecal density decreases from 9.5–12 in 10 mm proximally to 8–9 in 10 mm distally. Accordingly, the 2TRD increases from 1.5–1.7 mm at th2, through 1.65–2.15 mm at th5 and 2.0–2.25 mm at th10 to distal maximum 2.65–2.7 mm. Thecal apertures are 0.35–0.6 mm wide, approximately perpendicular to thecal axis to weakly everted. Thecae alternate regularly in aseptate portion of the rhabdosome, become subalternating to almost opposite in the distal, septate portion.

**Remarks.** – This species is the largest biserial graptolite re- corded in the Králův Dvůr Formation. The large, continuously widening rhabdosome with its steadily lengthening theca, the character of these biform thecae, proximal shape and aseptate proximal portion all fit the combination of characters of *Diplograptus* (Mitchell et al. 2009). The proximal structure of the available material appears to be quite simple and resembles Pattern G or H rather than other more complex patterns, which also is consistent with assignment to *Diplograptus*. The lack of subapertural spines on the first pair of thecae is atypical for species of that genus, however. On the other hand, the preservation of the available specimens is generally unfavorable (the best is that shown in Fig. 7K), and so the full character of the thecae and development of proximal spines is somewhat uncertain. The thecal spines in the type species *D. pristis* (Hisinger, 1837) are relatively small and similar spines might be missed in the present material or they may indeed be absent. Apart from the proximal thecal spines, the present species differs from *Diplograptus rarithecatus* (Ross & Berry, 1963), which is the most widespread species of the genus, in that rhabdosomes of *D. fritschi* widen more rapidly and possess slightly longer thecae. Again excepting the proximal spine configuration *D. fritschi* is most similar to material reported from South China (Mu et al. 1993), and particularly to *Diplograptus palaris* Lin in Mu et al., 1993, which matches the present form in all its
dimensions as well as in the general rhabdosome shape and structure. D. palaris, however, is based on mildly structurally deformed material and, like D. fritschi, relatively few specimens, so the precise relationship of these taxa is unclear.

Occurrence. – Králův Dvůr (one slab with type specimen), Praha-Vršovice (Eden, construction site), Praha (probably Vršovice); uppermost Bohdalec Formation (?) and lower Králův Dvůr Formation. The species is known only from Bohemia. Furthermore, this species has not been found in association with any other graptolite taxon and its precise location within the stratigraphic succession is uncertain. Based on the accompanying fauna it seems to occur in a relatively deep-water biofacies. Several features of the D. fritschi occurrences help to locate them within the Králův Dvůr succession: the facies character of the shale in which it occurs is slightly darker than that is usual in the middle and upper parts of the formation, the absence of Normalograptus angustus or Dicellograptus laticeps (which might be expected in the upper part of the Králův Dvůr Formation), the stratigraphic context of the localities from which the material was collected and, finally, the accompanying poor and low diversified shelly fauna. These features suggest that D. fritschi may have been a contemporary of Anticostia teres and Styracograptus lobatus within the lower part of the Králův Dvůr Formation.


Type species. – Anticostia macgregorae Stewart & Mitchell, 1997, pp. 221–225, figs 5A–M, pl. 1; by original designation.

Anticostia teres (Perner, 1895)
Figures 5A–G, 11E

1870 Diplograptus teres Barrande; p. 126; nomen nudum.
1895 Diplograptus (Glyptograptus) teres Barrande (in litt.). – Perner, p. 28, pl. 8, figs 13a, b.
1949 Glyptograptus teres (Perner). – Přibyl, pp. 11–12, pl. 2, figs 12, 13.

Holotype. – Specimen NM L27529 from Lejškov figured by Perner (1895) pl. 8, figs 13a, b, refigured by Přibyl (1949) pl. 2, fig. 12 and herein Fig. 5E; designated by Přibyl (1949) by monotypy.

Material. – 12 fragmentary rhabdosomes (NM L27529, L28043, L40986 – 2 specimens, L40987 and 4 specimens without number; FSCU 5158, PK 25 and 1 specimen without number) from Lejškov and possibly one incomplete relief specimen from Podolí Ore Horizon at the base of the Králův Dvůr Formation (NM without number). All specimens flattened, periderm partly exfoliated. All specimens from Lejškov. Arrows point to apertural lappets. All figures × 10, scale bar equals 1 mm.

Description. – All available specimens are relatively small colonies up to 16.5 mm long. Aseptate rhabdosome with glyptograptid thecae that bear prominent apertural cusps;
arching th12 crosses the sicula slightly obliquely at the subapertural spine of 0.15 and 0.4 mm in length. Gradually censing portion 0.55–0.75 mm long and bearing a mesial to virgella before turning sharply upward in a narrow arc; Anticostia species with a Pattern G proximal structure than the Pattern K th12 and th21 (visible in reverse view, Fig. 5D, F) is relatively long and appears to extend across the sicular axis very close to th12. That species also shares with A. teres the occasional presence of a subapertural spine on th12 and a relatively broadly rounded proximal end (Stewart & Mitchell 1997, fig. 8). Rhabdosomes of A. teres are relatively robust compared to those of most other Anticostia species, including those of A.? lorrainensis, which is markedly narrower and has significantly more closely spaced thecae.

Anticostia fastigata (Davies, 1929), Anticostia lata (Elles & Wood, 1906) and the type species, A. macgregoriae Stewart & Mitchell, 1997, all possess much narrower rhabdosome in the proximal part and generally lower 2TRD, especially 2TRD2. The rate of rhabdosome widening differentiates A. teres from the almost parallel-sided rhabdosomes of Anticostia uniformis (Mu & Lin in Mu et al., 1993), which are also more slender. Perhaps the most similar species is Anticostia hudsoni (Jackson, 1971), 3D material of which is nearly as broad as the present material but has more strongly inclined thecae that are also slightly more closely spaced. The first two thecae in A. hudsoni colonies are less strongly upwardly directed than in A. teres, which results in a slightly more bluntly rounded proximal end. Finally, A. hudsoni rhabdosomes lack a spine on th12.

Based on the distortion style of several aseptate rhabdosome fragments from Králův Dvůr deposited in NM and FSCU (axially compressed specimens in greyish-green shale) it is possible that these specimens (all without numbers) may also belong to A. teres.

One fragment of an aseptate rhabdosome with thecae resembling those typical of Anticostia was found in the oolitic carbonate-rich bed of the Podolí Iron Ore “Horizon” at Praha-Braník (Pod Zemankou Street). The fragment has its basal part covered inside the rock and is fully three-dimensionally preserved. The mode of preservation makes determination difficult because characteristic features are not visible and biometric features are not comparable with those of flattened specimens. However, recalculated parameters are similar. Thus, it is classified as A. teres?.

Table 3. Anticostia teres (Perger, 1895). Dimensions of type and illustrated specimens (in mm); W – width. References of previously figured specimens mentioned in the text and explanation of figures.

<table>
<thead>
<tr>
<th>Specimen No.</th>
<th>Figures</th>
<th>th1</th>
<th>th3</th>
<th>th5</th>
<th>th10</th>
<th>dist. max.</th>
<th>th2</th>
<th>th5</th>
<th>th10</th>
<th>dist. th</th>
</tr>
</thead>
<tbody>
<tr>
<td>NM L27529</td>
<td>5E (holotype)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2.05</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2.1</td>
</tr>
<tr>
<td>NM L28043</td>
<td>5B</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.8</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2.1</td>
</tr>
<tr>
<td>NM L40986a</td>
<td>5F</td>
<td>1.35</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>NM L40986b</td>
<td>5G</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.75</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.9</td>
</tr>
<tr>
<td>NM L40987</td>
<td>5C</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2.1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.95</td>
</tr>
<tr>
<td>FSCU 5158</td>
<td>5D, 11E</td>
<td>1.2</td>
<td>1.5</td>
<td>1.75</td>
<td>(th7)</td>
<td>–</td>
<td>1.8</td>
<td>1.8</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>FSCU PK 25</td>
<td>5A</td>
<td>1.25</td>
<td>1.4</td>
<td>1.8</td>
<td>(th7)</td>
<td>–</td>
<td>1.4</td>
<td>–2.0</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
the base of the unit since this iron ore “horizon” is locally developed at the base of the formation.

Occurrence. – Lejškov, probably Praha-Baník and old material from Králův Dvůr; lower part of the Králův Dvůr Formation. The species has been recorded only in the Prague Basin, but material collected from the Fjäka Shale at Gulleråsen, in the Dalarna region of central Sweden by S.L. Törnquist (held in the collections of Lund University) includes several specimens that closely resemble A. teres (unpublished observation of C.E. Mitchell). D. Goldman & CEM (unpublished observations) have recently discovered numerous specimens of A. teres in the lower part of the Pleurograptus linearis Zone of the Dicellograptus Shales at Laeså, Bornholm (see Hadding 1915, Bruvo 2005, for information on the site and its graptolite fauna, which is currently under revision by Goldman and Mitchell). These specimens agree with A. teres in all respects (rhabdosome form, thecal apertures, spacing and proximal structure, including the presence of spines on both th1 and th12). At Laeså, A. teres is associated with Styracograptus styloides (Elles & Wood, 1906) and Normalograptus angustus, among other graptolites.


Genus Paraplegmatograptus Mu, 1963

Type species. – Paraplegmatograptus uniformis Mu in Wang, 1978, p. 210, pl. 51, figs 1, 2; subsequently designated by Mu & Lin 1984, p. 66.

Paraplegmatograptus uniformis Mu in Wang, 1978

Figures 6D, 11D


1982 Plegmatograptus? craticulus sp. nov.; Williams, pp. 44–45 (partim), text-fig. 13a, h-k, non text-fig. 13g (text-fig. 13b-f, l uncertain).

1983 Paraplegmatograptus uniformis Mu. – Wang et al., pl. 4, fig. 3.

1983 Paraplegmatograptus gracilis Mu. – Wang et al., pl. 3, fig. 10; pl. 11, fig. 4.

1984 Paraplegmatograptus uniformis Mu. – Mu & Lin, pp. 65–66, pl. 7, fig. 3.

1984 Paraplegmatograptus uniformis Mu. – Li, p. 502, pl. 92, fig. 14.

1989 Plegmatograptus (?) chuchlensis Přibyl. – Štorch & Mergl, pl. 4, fig. 1.

1989 Paraplegmatograptus? chuchlensis Přibyl. – Štorch, pp. 183–184 (partim), pl. 1, figs 3, 7, text-fig. 3A, B.

1993 Paraplegmatograptus uniformis Mu. – Mu in Mu et al., pp. 240–241, pl. 53, fig. 9; pl. 55, figs 5–7; pl. 56, figs 1, 2; text-fig. 44a–c.

1993 Paraplegmatograptus gracilis Mu. – Mu in Mu et al., pp. 241, pl. 56, figs 3–8, text-fig. 45a–c.

1993 Paraplegmatograptus formosus Mu. – Mu in Mu et al., pp. 241–242, pl. 57, figs 1–4; p. 59, fig. 7; pl. 60, fig. 1; text-fig. 46a–c.


Holotype. – Not traced.

Material. – Two incomplete flattened rhabdosomes (CGS PS320, PS321) in respective sub-scalariform and slightly oblique orientations, solitary on bedding planes, figured by Štorch (1989) in figs 3A, B, respectively.

Description. – The longer rhabdosome attains length of 12.9 mm. Sicula, nema and thecal details not visible in the specimens. In both fragments only reticulum and lacinia are preserved, clathria cannot be identified with certainty. The box-flattened, more complete rhabdosome (Figs 6D, 11D) is more than 1.0 mm wide at its proximal end where only reticulum is preserved. The more or less planar reticulum widens gradually to 1.65 mm at the first visible lacinial strand. Overall width is 2.9 mm, including lacinia at this level. Rhabdosome 3.7 mm wide distally with 2.1–2.15 mm wide reticulum. Reticulum in measurable portions of the second specimen 2.6 mm wide proximally and 3.2–3.5 mm in distal part. Loops marking apertural separations by lacinial loops of similar appearance such that apertures alternate with similarly shaped lacinial orifices. Distance between main sub-horizontal apertural/lacinial loops varies from 0.65 to 0.9 mm; inferred mesial 2TRD: 1.5 to 1.65 mm and density approximately 12.5 thecae in 10 mm. Width of lacinia depends on rhabdosome orientation being 0.6–0.8 mm and 1.0–1.15 mm in individual specimens. Lacinial lists are slender, 0.03–0.04 mm wide. Reticular bars are thinner at the proximal end (0.02–0.025 mm) and become thicker (0.03–0.04 mm, exceptionally 0.05 mm) in mid and distal regions. Reticulum exhibits polygonal to almost circular openings. Diameter of openings variable: 0.25–0.7 mm throughout, however, 0.25–0.5 mm prevail in proximal whilst 0.35–0.7 mm in distal parts.

included three principal specimens and several fragments in the material referred to that species. One specimen was Přibyl’s (1949) holotype and two specimens, both figured, were from his new material, one of which is re-illustrated here (Figs 6D, 11D). Despite very limited material and unfavorable preservation of lasiograptids in the Králův Dvůr Formation, new insights into lasiograptid morphology (see Štorch et al. 2011) allow for substantial reclassification of these rhabdosomes. The two specimens figured by Štorch (1989, figs 3A, B) can be assigned to Paraplegmatograptus uniformis whereas the other material belongs to Phormograptus chuchlensis. Colonies of Paraplegmatograptus are characterized by a complex planar reticulum that forms the obverse and reverse walls of the colony and a relatively simple lacinia connected only to the thecal margins (lateral strands) and thecal apertures. Internally the nema is free from any structural connection to the thecal frame/reticulum. In contrast, as Štorch et al. (2011, pp. 346–348) noted, Phormograptus rhabdosomes have a strongly reduced thecal frame that lacks a well defined reticulum but is regularly connected to the nema by crossbars (e.g., Figs 6B, 11H) and possess a deep, complex lacinial mesh that entirely surrounds the rhabdosome, including its obverse and reverse sides. The determination that two studied specimens belong to Parap. uniformis is based on the concordance of dimensions, character of the lacinia and the presence of a dense reticulum. Because of the preservation in the available material, these specimens of Parap. uniformis also resemble some specimens of Plegmatograptus Elles & Wood, 1908, especially those of its type species, P. nebula Elles & Wood, 1908. However, P. nebula exhibits a more slender rhabdosome and distinctly finer reticulum, as noted by Štorch (1989). Additionally, colonies of P. nebula combine the deep, all-encompassing lacinia seen in Phormograptus with a well-developed clathrium that bears a planar reticulum (Štorch et al. 2011).

Occurrence. – Liteň; upper Králův Dvůr Formation. The species appears to be widely distributed being recorded from South China, eastern Laurentia (southern Scotland), western Laurentia (Nevada) and northern Gondwana (Bohemia).

Genus Phormograptus Whittington, 1955

Type species. – Phormograptus sooneri Whittington, 1955: pp. 847–850, pl. 83, figs 4, 5; text-figs 15–19; by original designation.

Phormograptus chuchlensis (Přibyl, 1949)

Figures 6A–C, 11H

1949 Plegmatograptus(?) chuchlensis nov. spec.; Přibyl, pp. 35–37, text-figs 1, 2.
non 1974 Arachniograptus chuchlensis (Přibyl). – Obut & Sobolevskaya, p. 118, pl. 43, fig. 17.
?1978 Paraplegmatograptus connectus Mu; Wang (in Stratigraphy Research Group of the Yangtze Gor-
Holotype. – Specimen NM L31783 from Praha-Velká Chuchle – slope above the hippodrome, designated and figured by Přibyl (1949) text-fig. 1a, b.

Material. – Two incomplete rhabdosomes with traceable clathria and lacinia (NM L27762, L31783, subscalariform and scalariform views, respectively) and one individual sicula (NM L27762) were studied. In addition, several fragments of undifferentiated parts of mesh were found. Several such fragments are associated with the Ph. chuchlensis holotype together with specimens of Normalograptus angustus, and one fragment was encountered on another slab with four rhabdosomes of N. angustus (NM without number).

Description. – Maximum length of the largest incomplete rhabdosome is 10.5 mm (Figs 6B, 11H). In scalariform view, the narrow sicular region rapidly widens from 1.15 mm near sicular aperture to 2.5 mm at third theca, above the sicular apex. Maximum width of 5.45 mm attained around th5–th6. Sicula slender, straight or slightly bent, only 0.15–0.20 mm wide at the aperture. An incomplete sicula is 0.65–0.85 mm long; in one specimen it seems to be almost complete and 1.25 mm long. Virgellar robust, straight to slightly curved, 0.5 to slightly more than 1.0 mm long. Antivirgellar spines seen in one specimen are antero-dorsally oriented, 0.35–0.8 mm long. Th1 buds near the sicular aperture; forms minute fusellar prothecal hood above the sicular foramen. This part has its dorsal edge 0.2–0.25 mm above the sicular aperture and its opening is ca 0.05 mm above the same. Thus, the preserved th1 protheca is 0.15–0.2 mm long and 0.1 mm wide at the opening (Fig. 6A). Framework of th1 continues with a 0.4 mm long median ventral list that arcs gently out from base of virgella and terminates in apertural loop (Fig. 6C). Structure of th2 not clearly visible. Clathria composed of well developed dorsal and apertural lists along with segments of the apertural spine and lacinia. All the structures are arranged along prominent straight nema and supported by well developed crossbars. Crossbars straight, perpendicular or almost perpendicular to the nema, diverging at one point to both obverse and reverse directions, linking dorsal lists of inner thecal framework (first node outwards) and, beyond that, pleural threads of lacinia (Fig. 6B). Crossbar spacing is variable. Except for the first pair of rods, which are 0.75 mm apart, next crossbars irregularly spaced at 0.95–1.25 mm, with most values near the minimum and maximum of this range and repeating irregularly. Clathria is enfolded by prominent, sparse lacinia. Lacinial mesh composed of polygonal openings of variable sizes, but mostly large, some around 1 mm, developed especially on the obverse and reverse sides. Lacinia reduced in sicular region, and widens notably above sicula, i.e. from second thecal pair. Linear structural units of the colony are all of similar thickness. Differences are only slight in absolute values: nema is the most robust, being 0.03–0.04 mm wide, crossbars are slightly thinner, reaching 0.03–0.035 mm, and main lists and bars of clathria and lacinia are 0.02 mm wide. Based on measurement of dorsal lists and transversal rods, 2TRD is 2.1–2.3 mm (exceptionally 1.7 mm) in region above sicula, thecae number 9.5–11.5 in 10 mm.

Remarks. – The proximal clathria fits well with the original diagnosis of the genus by Whittington (1955), based on the well-preserved type species Ph. sooneri Whittington, 1955. Our material resembles the type species also in the dimensions of the sicula, sicular spines and width of the proximal end. The size of the rhabdosome and its width in respective portions, as well as thecal spacing and architecture of Ph. chuchlensis, all match those of Ph. connectus (Mu in Wang, 1978). Thus, it appears likely that the material referred to Ph. connectus belongs to Ph. chuchlensis. All the differences between these taxa are fully attributable to preservational artifacts, which strongly affect the density of the lacinial mesh and the configuration of thecal framework elements (see Štorch et al. 2011 for a detailed discussion). Nevertheless, the material upon which Ph. chuchlensis is based is very incomplete and exceptionally rare. Thus, although the name Plegmatograptus (?) chuchlensis Přibyl, 1949, has clear priority, we hesitate to refer Ph. connectus to Ph. chuchlensis; that is, to replace such a well-known and widely distributed taxon by another that is comparatively poorly known and difficult to study further in its type area.

Occurrence. – Králův Dvůr, Praha-Velká Chuchle; upper Králův Dvůr Formation. Material referred to Ph. connectus is widely known in late Katian strata (Dicellograptus complexus and Paraothoargrapthus pacificus zones) outside Bohemia, including several regions in South China, the western United States, NW Canada, and Scotland where it is a regular element of the late Katian Dicellograptus complexus and...
Paraorthograptus pacificus zones faunas or their local equivalents. Material reported as Arachniograptus chuclensis (Sobolevskaya, 2011) from Taimyr may also represent this species as well as specimens of Arachniograptus sp. from Kazakhstan (Apollonov et al. 1980) and Siberia (Koren’ et al. 1983), and also the material that Brussa et al. (2003) reported as Plegmatograptus sp.

Superfamily Climacograptoidea Frech, 1897; emend Mitchell et al., 2007
Family Climacograptidae Frech, 1897

Genus Styracograptus Štorch et al., 2011

Type species. – Climacograptus tubuliferus Lapworth, 1876; by original designation.

Styracograptus lobatus (Perner, 1895)

Figures 7B–D, I; 12B–D

1876 Styracograptus lobatus n. sp.; by original designation.

1895 Diplograptus (Glyptograptus) lobatus n. sp.; Perner, p. 28, pl. 7, fig. 15; non pl. 8, fig. 15 [= Normalograptus angustus (Perner, 1895)].

1949 Climacograptus angustus (Perner). – Přibyl, pp. 7–9 (partim).

Holotype. – Specimen NM L27532 in scalariform view from Králův Dvůr (Königshof) figured by Perner (1895), pl. 7, fig. 15; by monotypy. Two specimens were included in the original description; as one belongs to a different species it is no longer a syntype because it is not a component of the name-bearing type; the remaining single specimen becomes a holotype.

Material. – Four incomplete, solitary rhabdosomes (NM L27532, WBM S 05149, S 06566, S 06567).

Description. – Medium-sized, aseptate rhabdosome, maximum 26.5 mm long; proximal end only slightly asymmetric, rounded and relatively narrow. Widens from 0.7 to 0.85 mm at first thecal pair, through 0.9–1.0 mm at the second, 1.05–1.25 mm at third, to 1.2–1.35 mm at fifth thecal pair and attains the maximum width of 1.6–1.7 mm at ca 12th thecal pair. Maximum width in scalariform view is 1.8 mm. From values of width in lateral and scalariform orientations, and from length of apertures and depth of apertural excavations, a sub-rectangular to even rounded square cross-section can be inferred. Crossbars and slender nema observed in some specimens (Fig. 7B, 1). Sicula about 1.5 mm long, with aperture 0.2 mm wide. Virgella 1.15 mm long, relatively wide at its base, slightly deflexed across sicular aperture. Ventral wall of upward-grown portion of th1 forms a rounded arc 0.40–0.55 mm long. Th12 crosses sicular outline near sicular aperture and reaches 0.6–1.0 mm in length. Subsequent thecae with strong angular genicula; supragenicular walls usually slightly convex, subparallel to rhabdosome axis; 0.5–0.7 mm long proximally and 0.6–0.9 mm long distally. Thecal density decreases from 12–14.5 thecae in 10 mm proximally to 9.5–10 distally. Accordingly, 2TRD increases from 1.2–1.3 mm at th2, through 1.5–1.75 mm at th5, and 1.6–1.8 mm at th10 to the maximum 2.05 to 2.1 mm. Thecal excavations small, proximally 0.1 to 0.2 mm high, 0.1–0.15 mm deep and distally 0.2–0.3 mm high, 0.15–0.2 mm deep, semicircular in profile. The whole excavation, including thecal aperture and geniculum of next theca, possesses a 0.015–0.03 mm wide selvage. Thecal excavations in the second series [i.e., th(n)2] situated against lower half of supragenicular portion of the opposite th(n + 1)1. In the scalariform oriented rhabdosome (Fig. 12B), thecal excavations have narrow-ellipsoidal shape, 0.7–0.85 mm wide proximally, widen to 0.9–1.0 mm in the middle part of the rhabdosome and then narrow to the width of 0.8–0.85 distally. Width/height ratio of aperture 2.6–6.1 (mean = 4.6). These ratios show decreasing trend of values from proximal to distal end with maximum values recorded in mid part of the rhabdosome. However, apertural shape differences along the colony may be affected by preservational artifacts.

Remarks. – Perner (1895) described this species based on a single scalariform rhabdosome NM L27532 and a small slab bearing two clearly- and one faintly-preserved specimens (NM L27537 and its counterpart NM L27986). He figured the scalariform rhabdosome on pl. 7, fig. 15 and the shorter one of the two distinct rhabdosomes on pl. 8, fig. 15. Přibyl (1949) synonymized S. lobatus with Climacograptus angustus (now Normalograptus angustus) and refigured the latter specimen on his pl. 2, fig. 7. Přibyl’s (1949) assignment of the latter specimen to N. angustus is correct. In addition, the second (longer) clearly preserved rhabdosome on the same slab can be also assigned to N. angustus. The only questionable specimen is a faintly preserved, laterally flattened distal fragment, that was neither described nor figured by Perner (1895) or Přibyl (1949). It displays some similarities in its thecal excavations, although its preservation is too poor for positive identification. On the other hand, Přibyl (1949) misinterpreted the scalariform specimen that exhibits features sufficient for its differentiation from N. angustus, especially the thecal excavations and general robustness of the rhabdosome. Whereas the two distinct subscalariform specimens on the slab NM L27537 exhibit rather high, narrow, open, oval excavations and slightly inclined supragenicular walls, the scalariform specimen NM L27532 possesses low, wide, slit-like excavations showing very different width/height ratio.
Figure 7. A, E–G, J – *Metabolograptus ojsuensis* (Koren’ & Mikhaylova in Apollonov et al., 1980): A – CGS PŠ 1163 (low relief specimen, partly exfoliated); E – CGS PŠ 1168 (partial relief reverse view, juvenile rhabdosome); F – WBM S 05153 (flattened, partly exfoliated rhabdosome); G – CGS PŠ 1170 (obverse proximal part preserved in relief); J – CGS PŠ 1167 (flattened juvenile rhabdosome). • B–D, I – *Styracograptus lobatus* (Perner, 1895): B – WBM S 05149 (low relief specimen in subscalariform view); C – WBM S 06566 (low relief subscalariform specimen, with exfoliated proximal portion); D – WBM S 06566 (partial counterpart of C); I – WBM S 06576 (subscalariform flattened specimen). • H – *Styracograptus* sp.: WBM S 05150 (full relief external mold proximally, becoming compressed distally). • K – *Diplograptus fritschi* Perner, 1895: WBM S 05155 (mature rhabdosome preserved in low relief, distal part continues as indicated). A, E–G, J from Zadní Třebaň; B, H from Vráž–D5 highway exit 14 (lower in the slope); C, D, I from Švinaře; K from Praha (probably Vršovice). Figures A–D, F–I, K × 6, figures E, J × 10. Scale bars equal 1 mm.
ratio in comparison with that of *N. angustus*. Recent finds of several rhabdosomes proved the existence of *S. lobatus* that can be distinguished from *N. angustus* by its strongly geniculate, more densely spaced thecae and shallow, slit-like apertural excavations with longer apertural margins and high width/height ratios. The proximal end of *S. lobatus* is blunt, heavily sclerotized and almost symmetrical. Like other species of *Styracograptus*, *S. lobatus* bears nema cross-bars at the base of the interthecal septa, which also helps to distinguish it from *N. angustus*, and is an especially useful feature in scalariform to subscalariform view. Thus, only the scalariform specimen from type series actually belongs to *S. lobatus* and so becomes the holotype by monotypy despite its preservation in an unfortunate orientation.

*S. lobatus* can be unequivocally distinguished from other biserial taxa of the Králův Dvůr Fm. by its slit-like apertural excavations combined with its stylacogirapid rhabdosome and by other, mainly biometric features. *S. lobatus* differs from the equally robust *Styracograptus styloideus* (Elles & Wood, 1906) only by its slightly narrower rhabdosome with more densely spaced thecae. From another, similarly large species *Styracograptus mississippiensis* (Ruedemann, 1908), *S. lobatus* can be distinguished by less prominent, more gradual widening of the rhabdosome and narrower, more closed, symmetric apertural excavations. *S. lobatus* can be readily distinguished also from *Styracograptus putillus* (Hall, 1865) (= *Pseudoclimacograptus clevensis* Skoglund, 1963; see Goldman & Bergström, 1997, which is probably also synonymous with *Pseudoclimacograptus chiai* Mu, 1949), which possesses a zig-zag median septum, is slightly narrower throughout and has more open apertural excavations relative to its rather short supragenicular thecal walls.

**Occurrence.** – Králův Dvůr (historical material, type specimen), Vráž – D5 highway exit 14 (low in the slope, one specimen), Svinaře (two specimens); lower and probably mid-slope parts of the Králův Dvůr Formation. The species has been recorded only from Bohemia.

**Styracograptus sp.**

Figures 7H, 11C

**Material.** – Single oblique-oriented specimen preserved in relief (WBM S 05150).

**Description.** – The only available specimen 7.3 mm long, preserved in relief but slightly distorted due to oblique reverse orientation on the bedding plane. Rhabdosome with prominent zig-zag septum, 0.73 mm wide at first thecal pair, widens slowly through 0.86 mm at second pair, 0.9–0.95 at third and fifth pairs to maximum 1.2 mm at eighth thecal pair. Proximal end narrow, rounded, and seems to be almost symmetrical. Upward-grown portion of th1 at least 0.35 mm long. Th1 crosses sicula nearly horizontally above its oblique aperture leaving a short, tooth-like free dorsal part of the sicula. Th1 turns up in a wide bend immediately distal from its crossing canal portion. Th1 0.75 mm long, gives rise to a dicalycal th2. Thecae of climacograptid type with angular genicula. Length of their supragenicular walls range between 0.65 and 0.8 mm. Thecal excavations 0.2 mm high (exceptionally 0.4 mm), rimmed by tiny, thickened lips. 2TRD at th2 1.4 mm increasing rapidly to 1.75–1.95 mm at th5. Thecae number 11.5 in 10 mm in proximal part.

**Remarks.** – The rhabdosome may be referred to *Styracograptus* because of its simple, rounded proximal end without any antivirgellar and thecal spines and climacograptid, sharply geniculate thecae. Septal cross-bars express themselves in small pits visible along the axial part of the lateral wall of the rhabdosome. The zig-zag line in the axial part of the lateral wall, however, indicates the presence of a *Pseudoclimacograptus*-like septum. The subscalariform orientation of the rhabdosome partly obscures some critical features such as the thecal style (particularly sharpness of the geniculum), apertural excavations and details of the proximal end. In addition, the specimen is the only climacograptid from the Králův Dvůr Formation that is preserved in relief. As the other specimens assigned to that group, which all belong to *Styracograptus lobatus*, are flattened, the differences in preservation do not allow more detailed comparisons of the preserved features. Despite the high variability of *S. lobatus*, the present specimen differs especially in thecal parameters, having longer supragenicular walls, wider thecal spacing (higher 2TRD in proximal part) and possibly a narrower distal colony width and strongly zigzag median septum. In all these respects the present form strongly resembles *Styracograptus putillus* (Hall, 1865) (for comment on its synonymy see above). Considering the mentioned uncertainties and the fact that we have only a single specimen for study, we leave this taxon in open nomenclature.

**Occurrence.** – Vráž – D5 highway exit 14 (lower in the slope); lower Králův Dvůr Formation.

Infraorder Neograptina Štorch et al., 2011
Family Normalograptidae Štorch & Serpagli, 1993, emend. Melchin et al., 2011

**Genus Normalograptus** Legrand, 1987, emend. Melchin et al., 2011

**Type species.** – *Climacograptus scalaris* var. *normalis* Lapworth, 1877, p. 138, pl. 6, fig. 31; by original designation.
Normalograptus angustus (Perner, 1895)
Figures 8A, B, 9A–F, 13B, F, G

1895 Diplograptus (Glyptograptus) euglyphus Lapworth var. angustus mihi; Perner, p. 27, pl. 8, figs 1, 14a, b.
1895 Diplograptus (Glyptograptus) lobatus n. sp.; Perner, p. 28 (partim), pl. 8, fig. 15.
1949 Climacograptus angustus (Perner). – Přibyl, pp. 7–10, pl. 2, figs 2–9.
1963 Climacograptus angustus (Perner). – Skoglund, pp. 40–42, pl. 3, figs 1, 2, 4–6; pl. 4, fig. 7, pl. 5, fig. 6.
1983 Climacograptus angustus (Perner). – Koren’ & Sobolevskaya in Koren’ et al., pp. 106–108, pl. 27, figs 1–5, text-fig. 34.
1989 Climacograptus angustus (Perner). – Storch & Mergl, pl. 4, figs 3, 4.
2005 Normalograptus angustus (Perner). – Chen et al., pp. 252–255, text-fig. 5D, I, K, Q, DD.
2007 Normalograptus angustus (Perner). – Loydell, pp. 30, 32–33, pl. 1, fig. 3, text-fig. 15L, M.
2011 Normalograptus angustus (Perner). – Storch et al., p. 369, figs 25G, Q, 26H.

Holotype. – Specimen NM L27552 from Králův Dvůr (Königshof) figured as incomplete rhabdosome by Perner (1895), pl. 8, figs 14a, b and refigured complete by Přibyl (1949), pl. 2, fig. 8; designated by Přibyl (1949) by monotypy.

Storch (1989) mentioned and Loydell (2007) also figured specimen NM L27507 as the holotype. Although in type collection of J. Perner, this specimen has never been figured by him but by Přibyl (1949) pl. 2, fig. 6 for the first time. In addition, this specimen is not marked as original on the label. On the other hand, there is clearly stated on the label of the specimen NM L27552 that it is the original No. 67. This fits the datum in the explanation of pl. 8, fig. 14a, b by Perner (1895).

Material. – About 50 specimens studied and measured. The most abundant species known in tens of specimens, which occur either solitary or in small monospecific clusters. At some localities, the rhabdosomes were found clustered with other graptolites (Dicellograptus laticeps or Phormograptus chuchlensis) or shelly debris, especially material of ostracods, rhynchonelliform brachiopods and trilobites.

Description. – Slender, septate rhabdosome, commonly about 10 mm, occasionally up to 20 mm long; oval to almost circular in cross section. Widens slightly from 0.8 to 0.95 mm at first thecal pair, through 0.85–1.0 mm at...
with no theca or only with th1₁, 1.55–2.0 mm long and 0.25 to 0.4 mm wide at aperture. Virgella prominent, up to 3.9 mm (usually 0.5–0.8 mm) long. Nema 0.04 to 0.055 mm, exceptionally 0.06 mm, wide. Sicula exposed on obverse side for 1.0–1.05 mm before becoming enclosed by second thecal pair. Th₁² initially grew downward 0.4 mm along sicula and extended 0.2–0.25 mm below the sicular aperture, forming 0.6–0.65 mm long descending portion. Upward grown part sharply turned upward and 1.0–1.05 mm long (exceptionally 0.9 to 1.2 mm). Prosoblastic th₁² buds just above the sicular aperture and its crossing canal emerges from dorsal sicular outline 0.1–0.4 mm above sicular aperture. Upward grown part of the th₁² 0.75–0.95 mm long. Asymmetric, V-shaped form of the proximal end well visible in reverse view, th₁² with slightly, and smoothly, rounded ventral wall (Fig. 9B, C). Subsequent thecae moderately geniculate, 1.25–1.5 mm long, overlapping for one third their length or slightly more. Thecae appear less strongly geniculate, nearly glyptograptid, when preserved as internal molds in relief, in particular those in oblique orientation on the bedding plane. Infragenicular thecal wall short, concave and arched forming an open aperture. Supragenicular walls straight to slightly convex, 0.5 to 0.7 mm long, parallel to very slightly outwardly inclined. Thecal apertures subhorizontal, often weakly everted and slightly concave, facing markedly asymmetrical apertural excavations. Apertural width 0.25–0.4 mm, maintained in all thecae except narrower th₁², which is only 0.2–0.25 mm wide. Thecae regularly subalternate throughout whole rhabdosome; apertures above th₁² situated slightly above geniculum of opposite thecae. Thecal spacing increases from 2TRD₂ 1.6–1.85 mm, through 2TRD₅ 1.85–2.05 mm to the maximum 2.0–2.2 mm attained with 2TRD₁₀. Thecae number 10.5–11.5 in 10 mm. In scalariform view, depending on distortion, apertural excavations usually suboval with more vaulted infragenicular and flatter apertural arches but oval to almost circular projections of apertural excavations also present in some specimens. In this view, excavations 0.5–0.6 mm wide and 0.3–0.4 mm high; width/height ratio 1.12–2.35 (proving subcircular to prolonged ellipsoid; mean = 1.6).

Median septum complete, generally slightly undulose in its whole course. It begins from sicular apex, i.e. approximately from the level of aperture of th₁¹, but rarely delayed to the aperture of th₂¹ (Fig. 8B). Th₂¹ dicalycal in the former and th₂² in the latter case.

Remarks. – This long-ranging and cosmopolitan species is characterized by its narrow colony with rather widely spaced thecae relative to rhabdosome size, and smooth, unadorned genicula. Other typical features are its parallel-sided rhabdosome and slightly protracted proximal end. The morphology of the Bohemian population is conserva-
tive and biometric variability is quite low. Specimens of _Normalograptus normalis_ (Lapworth, 1877) described by Elles & Wood (1906) resemble _N. angustus_ but most of these belong to _Normalograptus aijeri_ (Legrand, 1977). True _N. normalis_ is a more robust form (Loydell 2007). _N. aijeri_ is wider than _N. angustus_, also having slightly more densely spaced thecae. Downward growing portion of its th1 is shorter. Perner (1895, pl. 8, fig. 1) incorrectly figured a distorted fragment of dicellograptid stipe (_D. laticeps_) as an example of the thecae of _N. angustus_. Přibyl (1949) incorrectly synonymized _N. angustus_ with _Styracograptus lobatus_ (see comment in remarks for that species). Finally, _N. angustus_ has also previously been widely confused with _Climacograptus miserabilis_ Elles & Wood (1906), which it closely resembles in its colony dimensions, but that species has recently been recognized as a distinct species of _Styracograptus_ on the basis of differences in proximal structure and the presence of nema cross bars at the base of the interthecal septa (Goldman et al. 2011).

**Occurrence.** – Karlík, Králův Dvůr, Leškův, Levin, Liteň, Praha-Malá Ohrada, Praha-Nusle, Praha-Radotín – highway tunnel and cut of the road to Třebotov, Praha-Velká Chuchle, Praha-Zličín, Tobolka near Koněprušy – borehole (depths 1118.0 and 1356.6 m), Vráž – D5 highway exit 14 (higher in the slope), Zadní Třebaň; middle (?) and upper Králův Dvůr Formation. It is a cosmopolitan species. In addition to occurrences in northwestern Gondwana (Bohemia), northern Gondwana (Jordan), South China, Avalonia (England), Baltic (central Sweden), Siberia (north-eastern Siberia) and Laurentia (Nevada, southern Scotland) as noted in the synonymy, a further Laurentian occurrence in Arctic Canada was reported by Melchin et al. (2011). Koren’ & Sobolevskaya in Koren’ et al. (1983) listed other occurrences from Siberia (Ural-Tianshan belt and Gorny Altai).

**Superfamily Retiolitoidea Lapworth, 1873, emend. Melchin et al., 2011**

**Family Neodiplograptidae Melchin et al., 2011**

**Genus Metabolograptus Obut & Sennikov, 1985, emend. Melchin et al., 2011**

**Type species.** – _Diplograptus modestus sibiricus_ Obut, 1955, p. 138, pl. 59, figs 5–8; by original designation.

**Metabolograptus ojsuensis** (Koren’ & MIkhaylova in Apollonov et al., 1980)


1973 _Diplograptus tariti_ Legrand; Mikhaylova, p. 16, pl. 3, figs 7, 8.

1980 _Glyptograptus ojsuensis_ sp. nov.; Koren’ & Mikhaylova in Apollonov et al., pp. 143, 145, pl. 41, figs 1–8; pl. 42, figs 1, 2, text-fig. 43.

1983 _Glyptograptus? ojsuensis_ Koren’ & Mikhaylova, – Koren’ & Sobolevskaya in Koren’ et al., pp. 142,
Figure 11. A, B, F, G – Diplocraterurus laticeps Storch, 1989; A – MCZ 196546 (proximal part of large rhabdosome in partial relief, mostly exfoliated external mold); B – FSCU 5169 (detail of proximal part in partial relief); F, G – MCZ 196547 (large rhabdosome preserved in relief, G – detail proximal part). • C – Styracograptus sp.; WBM S 05150 (full relief external mold proximally, becoming compressed distally; the image is left-right reversed to simulate a cast and facilitate interpretation of its proximal part in reverse view). • D – Parapaleognathograptus uniformis Mu in Wang, 1978: CGS P Š 321, specimen figured by Storch (1989, fig. 3B). • E – Anticostia teres (Perner, 1895): FSCU 5158 (periderm mostly exfoliated). • H – Phormograptus chuchlensis (Přibyl, 1949); NM L 31783 (holotype). A, B, F, G from Králův Dvůr; C from Vráž – D5 highway exit 14 (lower in the slope); D from Liteň; E from Lejtíkov; H from Praha-Velká Chuchle. Black scale bars equal 1 mm, white scale bar equals 10 mm.

Description. – Robust septate rhabdosome of rectangular cross section, commonly more than 20 mm long (maximum recorded 35.5 mm); 0.95–1.45 mm wide at first pair of thecae, widens rapidly to 1.45–1.85 mm at th3 and 1.7–2.0 mm at th5 (with extreme value 2.55 mm). Subsequently widens slowly to 2.0–2.1 mm at th10 (range: 1.7 and 2.9 mm), and a maximum of 2.2–2.9 mm reached by 10th pair or later (at 18th pair in one specimen).

Sculca 1.8–2.3 mm long and 0.25–0.4 mm wide at aperture, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface, furnished with 0.4–2.8 mm long virgella. Asymmetric proximal end of pattern H astogeny, composed of th11 growing 0.15–0.35 mm downward along ventral surface.
diverts to form prominent step with obtuse angle between its ventral wall and downward portion of th1. Dorsal wall of sicula exposed for 0.1–0.5 mm (Fig. 7F, J). Upward-growing metathecae of both th1 and 1 straighten near their apertures. Length of th1 0.7 to 1.0 mm. Apertural widths of first theca ca 0.25 mm. Both th1 and 1 diverge forming rather narrow proximal end.

Proximal 2–4 thecal pairs in flattened material strongly geniculate, nearly of climacograptid type. Subsequent 2–3 pairs change gradually to more rounded genicula of glyptograptid type which typify the reminder of the rhabdosome. Number of strongly geniculate thecae probably varies independent of influence of taphonomic effects. Infrageniculate walls concave in profile. Suprageniculate walls, 0.70 to 0.75 mm (exceptionally 0.6 mm) long, straight or slightly convex in distal part of rhabdosome. Ventral walls almost parallel to colony axis proximally (in climacograptid thecae) becoming markedly inclined in distal (glyptograptid) thecae. Thecal apertures 0.45 to 0.65 mm wide, subhorizontal. Distal thecae 1.9–2.2 mm long, overlapping for one half their length or slightly more. Thecae regularly alternate, 2TRD increases from 1.55 to 1.9 mm at th2, through 1.6 to 2.0 mm at th5 to 1.9–2.1 mm at th10 and 2.2–2.3 mm a little higher. Theca number 10–11 in 10 mm proximally.

Median septum complete, straight or slightly undulate begins at the second thecal pair as th1 is usually dicalycal, but exceptionally delayed, beginning at th5 in one specimen (Fig. 13K). Nema rather thick, projected well beyond the thecate part of the rhabdosome.

Remarks. – The rhabdosome dimensions of this species are quite variable. Considerable variation may be observed in many examined parameters of the rhabdosome, in particular the rhabdosome width, which varies with the degree of flattening. Nevertheless, the rhabdosome remains typically

---

Figure 12. A – Diplograptus fritschi Perner, 1895: WBM S 05155 (mature rhabdosome preserved in low relief). • B–D – Styracograptus lobatus (Perner, 1895): B – NM L27532 (holotype, largely exfoliated scalariform specimen); C – WBM S 06567 (subscalariform flattened specimen); D – WBM S 06566 (low relief subscalariform specimen, with exfoliated proximal portion). A from Praha (probably Vršovice); B from Králík Dvůr; C, D from Svinaře. Scale bars equal 1 mm.
robust. The switch from climacograptid to glyptograptid profile in the proximal part of rhabdom is typical and fits well the typeп material.

The close morphologic affinities of M. ojsuensis, Metabolograptus extraordinarious (Sobolevskaya, 1974) and Metabolograptus persculptus (Elles & Wood, 1907) have been discussed in many papers. We refer to those of Koren' & Mikhailova in Apollonov et al. (1980), Storch (1989) and Storch et al. (2011). In this connection, it is worth noting that a few specimens (e.g., Fig. 13D, J) widen more rapidly than typical in M. ojsuensis and are distally wider. Mitchell et al. (2011) referred to one of these usually large specimens as M. extraordinarious. However, taking into account all measured specimens and continuous ranges of their biometric features, they appear to be extreme cases within the range of a single, unimodal population of M. ojsuensis specimens.

Occurrence. – Karlik, Liteň, Nesvačily, Praha-Zličín, Zadní Třebař; uppermost part of the Králuv Dvůr Formation. Cosmopolitan species reported from northern Gondwana (Bohemia, Niger), north-eastern Gondwana (Tibet), South China, Kazakhstania (southern Kazakhstan), Siberia (north-eastern Siberia), western Laurentia (Nevada, Arctic Canada) and eastern Laurentia (southern Scotland) as partly shown by the synonymy list above.

Acknowledgements

We appreciate detailed and helpful reviews by M.J. Melchin (St. Francis Xavier University, Antigonish), F. VandenBerg (Museum Victoria, Melbourne) and Zhang Yuandong (NIGPAS, Nanjing). We are grateful to our colleagues who helped us during our study of material housed in their institutions, especially V. Turek and M. Valen (National Museum, Prague), P. Budil (Czech Geological Survey, Prague) and J. Cundiff (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts). This paper was funded by Grant Agency of Academy of Sciences of the Czech Republic through project IAA301110908 and by project PRVOU P44 to P. Kraft as well as by a grant from the National Science Foundation (EAR 0958372) to C.E. Mitchell. This is contribution to the IGCP project No. 591 (The Early to Middle Paleozoic Revolution).

References


ceedings of the Belfast Naturalists’ Field Club, 1876–1877, 125–148.


NICHOLSON, H.A. 1867. On some fossils from the Lower Silurian rocks of south of Scotland. Geological Magazine 4(33), 107–113. DOI 10.1017/S0016756800205293

