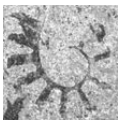
Graptolites from the Rhuddanian–Aeronian boundary interval (Silurian), Prague Synform, Czech Republic

PETR ŠTORCH



Forty-five graptolite species belonging to nineteen genera collected from loose rocks in the field at Všeradice and assigned to the upper *vesiculosus*, *cyphus*, *triangulatus* and lower *pectinatus* biozones of late Rhuddanian and early Aeronian age are described and discussed. Of 16 species recorded for the first time in the Czech Republic, five species are new (*Normalograptus parvus*, *Normalograptus frydai*, *Glyptograptus perneri*, *Pseudorthograptus mitchelli* and *Pernerograptus pribyli*); eight species are left in open nomenclature. The generic diagnoses of *Pseudorthograptus* Legrand, *Demirastrites* Eisel and *Pernerograptus* Přibyl are emended. The sedimentary and faunal succession in the Všeradice area is reconstructed by correlation with the biostratigraphically well dated graptolite-rich sections elsewhere on the southern limb of the Prague Synform. • Key words: graptolite, Silurian, Rhuddanian, Aeronian, Barrandian area, taxonomy, biostratigraphy.

ŠTORCH, P. 2015. Graptolites from the Rhuddanian–Aeronian boundary interval (Silurian), Prague Synform, Czech Republic. *Bulletin of Geosciences 90(4)*, 841–891 (18 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received June 2, 2015; accepted in revised form August 31, 2015; published online November 10, 2015; issued November 30, 2015.

Petr Štorch, Institute of Geology of the Czech Academy of Sciences, Rozvojová 269, 165 00 Praha 6, Czech Republic; storch@gli.cas.cz

The current efforts of the International Subcommission on Silurian Stratigraphy devoted to the restudy of the stratotypes of some Silurian stages and series include searching for a new GSSP (Global Boundary Stratotype Section and Point) for the middle Llandovery Aeronian Stage. The Aeronian and underlying upper Rhuddanian succession is well represented and exposed in the Prague Synform in central Bohemia (Barrandian area). Multi-proxy stratigraphical research devoted to relevant Rhuddanian–Aeronian boundary sections available in the Prague Synform (Štorch 2006, Frýda & Štorch 2014, Štorch *et al*. 2014) has revealed the necessity for modern taxonomic revision of the rich graptolite fauna of this interval, which has never been systematically studied and published in a monographic manner although there are several partial studies on selected genera (Přibyl 1941, 1942; Přibyl & Münch 1941; Bouček 1944; Štorch 1983, 1985, 1988).

The lower and middle Llandovery (Rhuddanian and Aeronian stages) are developed as a black-shale succession assigned to the Želkovice Formation (see Bouček 1953, and Štorch 1986, 2006 for details). Graptolites preserved in black shales, black silty-micaceous laminites and black siliceous shales exposed *in situ* in all relevant sections unfortunately do not exhibit some of the fine details and features inevitably needed for proper identification of many graptolite taxa. However, particularly well preserved graptolites of the Rhuddanian–Aeronian boundary strata comprising the upper *Cystograptus vesiculosus*, *Coronograptus cyphus* and *Demirastrites triangulatus* biozones have been found in bleached loose rocks and subcrops in the field at the northern periphery of Všeradice village (Fig. 1), 49° 52´ 36.3˝ N, 14° 6´ 12.9˝ E, 10 km south of Beroun. These specimens are flattened but their fine apertural details, spines, ancorae and membranous structures are well preserved and internal structures such as thecal septa and sutures are pressed through similarly to those in the middle Aeronian specimens from Tmaň described by Štorch (1998). In total 45 species have been identified, including some tiny taxa with complex morphology, which would be barely recognizable in black shales exposed in sections studied for stratigraphic purposes. Thus, the present material, although collected from loose rocks, helps to provide the taxonomic framework for the detailed biostratigraphical analysis of the Rhuddanian–Aeronian boundary beds in the Prague Synform. Several taxa, tentatively known as abundant in the black shales, have been determined with certainty thanks to the material from Všeradice. Conversely, some rare taxa represented in new large bed-by-bed collections from Hlásná Třebaň section are either missing or too fragmentary to be described

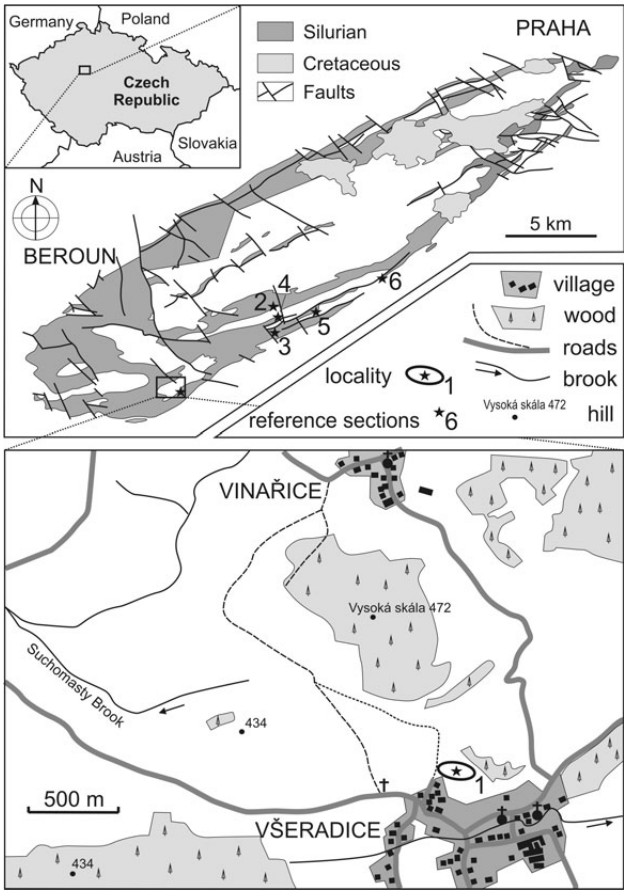


Figure 1. Map showing the location of loose lower Silurian rocks in the field at the northern periphery of Všeradice (1) and the location of reference sections used for better biostratigraphical interpretation of the Všeradice graptolite fauna. 2 – Vočkov section, 3 – Běleč section, 4 – Zadní Třebaň section, 5 – Hlásná Třebaň section, 6 – Karlík section.

from the Všeradice collections, which form the basis of this paper.

Material and preservation

Ca 1000 determinable graptolite specimens have been collected from bleached loose rocks and subcrops in the field at the northern periphery of Všeradice during the last 15 years. The graptolites are preserved in several sub-types of black-shale lithology, thermally affected by a neighbouring middle Silurian sill of doleritic alkaline basalt and subsequently bleached by humid, sub-tropical weathering during the late Neogene and early Quaternary. The graptolite rhabdosomes are flattened, with well preserved juvenile specimens, fine apertural details, spines, ancorae, and membranous structures. Also some internal structures, such as interthecal and rhabdosome septa and nemata are seen pressed through. Specimens from Všeradice have been compared with stratigraphically well dated, though commonly less favourably preserved specimens from the Běleč, Vočkov, Zadní Třebaň, Hlásná Třebaň and Karlík sections (Fig. 2) described by Štorch (1986). Most of the material from Všeradice belongs to the Rhuddanian upper *vesiculosus* and *cyphus* biozones. Less common are slabs assigned to the lower Aeronian *triangulatus* Biozone. Of the latter the majority can be assigned to the lower part of the biozone. Higher levels (*pectinatus* Biozone) are represented by a few slabs only.

All illustrated and measured specimens (prefixed PŠ) are housed in the palaeontological collections of the Czech Geological Survey, Prague.

Biostratigraphy

Each loose rock collected in the field has been treated as a bulk sample and its graptolite association correlated with graptolite range charts and assemblages known from numerous sections through the Rhuddanian–Aeronian black shale succession of the Prague Synform (Bouček 1953, Štorch 1994 and subsequent updates). This approach allowed for discrimination of six, stratigraphically distinct assemblages in the Všeradice material (see Fig. 2), which can be identified in all stratigraphically relevant sections of the Prague Synform briefly described by Štorch (1986, 1994, 2006). Correlation of the present "isolated" assemblages with exposed sections and the standard *Akidograptus ascensus*, *Parakidograptus acuminatus*, *Cystograptus vesiculosus*, *Coronograptus cyphus*, *Demirastrites triangulatus* and *Demirastrites pectinatus* assemblage biozones has been achieved, for the most part with intrazonal resolution. Biostratigraphical correlation is further supported by lithologies since the same sub-types of black shale lithology are known from corresponding levels in the "*in-situ*" sections.

The stratigraphically lowest assemblage (assemblage No. 1 in Fig. 2) is preserved in thin shales without lamination and corresponds to the *Akidograptus ascensus* and lower–middle *Parakidograptus acuminatus* biozones. The assemblage, comprising *Normalograptus trifilis* (Manck), *Normalograptus longifilis* (Manck), *Normalograptus* cf. *ajjeri* Legrand, *Normalograptus* sp., aff. *angustus* (Perner), *Cystograptus ancestralis* Štorch, *Neodiplograptus lanceolatus* Štorch & Serpagli, *Akidograptus ascensus* (Davies) and *Parakidograptus acuminatus* (Nicholson) is not included in the systematic part of this paper. Most species have been fully described and discussed by Štorch & Serpagli (1993) and Štorch (1996).

No species indicating the upper part of the *acuminatus* Biozone and lower–middle *Cystograptus vesiculosus* Biozone have been found in the Všeradice samples which is consistent with the unconformity and stratigraphical gap

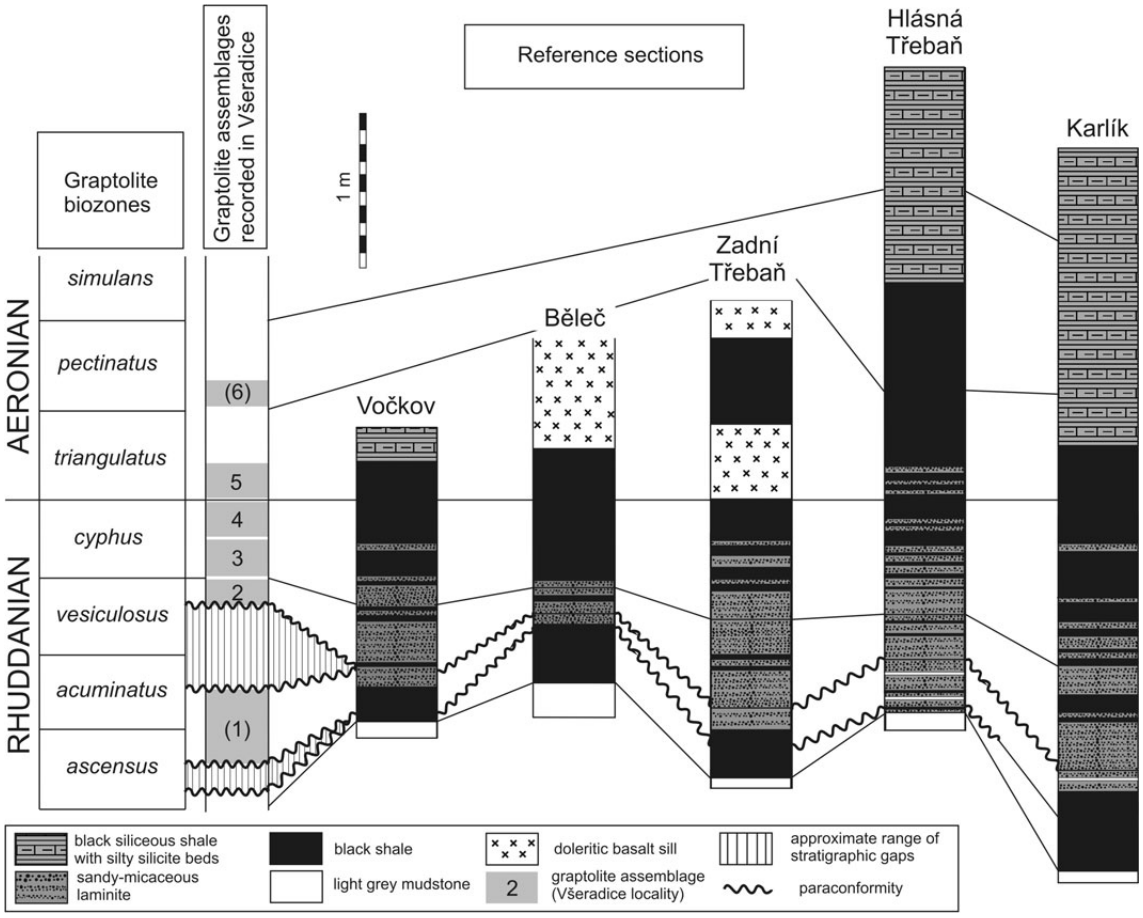


Figure 2. Correlation of the presumed stratigraphical range of the graptolite assemblages from loose rocks from Všeradice with the principal Rhuddanian–Aeronian boundary sections exposed in the southern limb of the Prague Synform. 1 – graptolite assemblage of the upper *ascensus* and lower-middle *acuminatus* biozones (not described in the systematic part), 2 – upper *vesiculosus* Biozone assemblage, 3 – lower *cyphus* Biozone assemblage, 4 – upper *cyphus* Biozone assemblage, 5 – lower *triangulatus* Biozone assemblage, and 6 – lower *pectinatus* Biozone which is poorly represented in the present material. Section logs after Štorch (1986), revised and updated. The missing graptolite assemblages of the lower *ascensus* and upper *acuminatus*-middle *vesiculosus* biozones match the gaps in sedimentation identified by Štorch (2006) from "*in situ*" sections.

present in all sections on the southern flank of the Prague Synform (Štorch 1986, 2006).

The upper part of the *vesiculosus* Biozone (Fig. 2, assemblage 2) is typically represented by a rich fauna comprising *Cystograptus vesiculosus* (Nicholson), *Cystograptus penna* (Hopkinson), *Dimorphograptus confertus* (Nicholson), *Normalograptus parvus* sp. nov., *Metaclimacograptus* aff. *slalom* Zalasiewicz, *Paraclimacograptus innotatus* (Nicholson), *Glyptograptus* sp. B, *Atavograptus atavus* Jones, common *Atavograptus*? *pristinus* (Hutt), *Huttagraptus acinaces* (Törnquist) and common *Huttagraptus billegravensis* Koren' & Bjerreskov. *Rickardsograptus lautus* (Štorch & Feist) and *Huttagraptus* cf. *lunata* (Chen & Lin) are rare. The long-ranging species *Rhaphidograptus toernquisti* (Elles & Wood) and *Korenograptus nikolayevi* (Obut) have their lowest occurrences in the upper *vesiculosus* Biozone. The graptolite assemblage of the upper *vesiculosus* Biozone in the Prague Synform is correlatable with the lower part of the *Huttagraptus acinaces* Biozone of the British Isles in the sense of Zalasiewicz *et al*. (2009).

The lower part of the *Coronograptus cyphus* Biozone (Fig. 2, assemblage 3) can be distinguished by the common occurrence of *Coronograptus cyphus* (Lapworth) accompanied by *Pseudorthograptus mitchelli* sp. nov. (the earliest *Pseudorthograptus* found in the Prague Synform), *Normalograptus frydai* sp. nov., *Pernerograptus austerus* (Törnquist) – the first monograptid with hooked proximal thecae, and *Cyst. penna* associated with rare *Pseudorthograptus physophora* (Nicholson). Less common elements inherited from the *vesiculosus* Biozone interval are *Paracl. innotatus*, *A.*? *pristinus*, *H. acinaces* and *H. billegravensis*. *Rh. toernquisti* is abundant in association with the lowest occurrences of *Neodiplograptus fezzanensis* (Desio), *Pseudorthograptus obuti* (Rickards & Koren'), *Coronograptus*? sp. B, rare *Hercograptus* cf.

introversus Melchin and the long-ranging *Coronograptus gregarius* (Lapworth).

Some of the species listed above become more abundant in the upper part of the *cyphus* Biozone (Fig. 2, assemblage 4), notably *Neodipl. fezzanensis*, *Rh. toernquisti*, *C. cyphus* and less so *C. gregarius*. *Ps. mitchelli* and *A.*? *pristinus*, in turn, became less abundant in the upper *cyphus* Biozone. *Cyst. penna*, *P. austerus*, *H. acinaces* and *H. billegravensis* disappear in about the middle of the biozone. New elements, highly indicative of the upper *cyphus* Biozone assemblage comprise common *Pseudorthograptus obuti* (Rickards & Koren'), *Pernerograptus pribyli* sp. nov. and *Pernerograptus* cf. *vulgaris* (Hutt). The uppermost part of the biozone is marked by abundant *Pernerograptus difformis* (Törnquist) – possibly the ancestor of the triangulate monograptids. Normalograptids and metaclimacograptids are surprisingly rare in the upper Rhuddanian of the Barrandian area. Earlier observations (*e.g*. Bouček 1953, Štorch 1994) based upon abundant but badly preserved specimens from black silty-micaceous laminites confused common specimens of *Rhaphidograptus toernquisti* with *Normalograptus normalis* which is probably missing in the upper Rhuddanian of the Prague Synform.

The graptolite assemblage of the lower Aeronian *Demirastrites triangulatus* Biozone (Fig. 2, assemblage 5) can be readily distinguished by abundant specimens of the earliest triangulate monograptid *Demirastrites triangulatus* (Harkness) associated with the first petalolithid *Petalolithus ovatoelongatus* (Kurck) and also *Glyptograptus perneri* sp. nov., *Pernerograptus chrysalis* (Zalasiewicz) and the first rastritid *Rastrites longispinus* Perner. Other typical, though uncommon elements of this assemblage are *Pseudorthograptus inopinatus* (Bouček) and *Pseudorthograptus finneyi* Štorch & Kraft. Long-ranging taxa are represented by common *Rh. toernquisti* and *C. gregarius*.

A few rocks yielded a graptolite association (Fig. 2, assemblage 6) comprising *Demirastrites major* (Elles & Wood), small fragments of *Demirastrites pectinatus* (Richter) not described in this paper, and other taxa consistent with assignment to the *Demirastrites pectinatus* Biozone.

Other rocks preserved graptolites typical of the *Lituigraptus convolutus* Biozone. However, the *convolutus* Biozone fauna, as described by Štorch (1998) from Tmaň, is beyond the scope of this paper.

Systematic palaeontology

New taxa and species new to the Silurian beds of central Bohemia are described whereas material which does not provide a major contribution to understanding of species morphology and classification is only briefly discussed. The generic assignment of biserial taxa follows the classification introduced by Mitchell (1987) and elaborated by Melchin (1998) and Melchin *et al.* (2011). Characters measured on graptolite rhabdosomes correspond with those employed by Štorch & Serpagli (1993, text-fig. 3) and Štorch *et al*. (2011, fig. 13).

Family Normalograptidae Štorch & Serpagli, 1993

Genus *Normalograptus* Legrand, 1987

Type species. – *Climacograptus scalaris* var. *normalis* Lapworth; by original designation; from the Llandovery of County Down, Ireland.

***Normalograptus parvus* sp. nov.**
Figures 3A, C, 4B, I, J

Holotype. – Specimen No. PŠ3427 (Figs 3A, 4I) from the upper *vesiculosus* Biozone of Všeradice, Želkovice Formation, Prague Synform, Czech Republic.

Derivation of name. – From the minute dimensions of the rhabdosome.

Material. – 13 rhabdosomes.

Diagnosis. – Minute septate normalograptid with rounded proximal end and maximum width of 0.7–0.9 mm at third to fourth thecal pair. Thecae densely spaced (6.5–7.5 in 5 mm), sharply geniculate without thickened genicular rims, supragenicular walls parallel-sided, apertural excavations shallow, asymmetrically semicircular.

Description. – Rhabdosome septate, up to 8 mm long, widening from 0.6–0.75 mm at first thecal pair to maximum width 0.7–0.9 mm attained by the third to fourth thecal pair. Proximal end of the rhabdosome rounded, sicula covered except for max. 0.1 mm-long dorsal wall exposed below th1^2. Sicula 0.1–0.15 mm wide at aperture furnished with short and stout virgella.

The downward growing part of th1^1 turns upward only 0.05–0.1 mm below the sicular aperture; the upward growing part is 0.6–0.75 mm long. Thecae are sharply geniculate with straight, parallel-sided supragenicular walls, asymmetrical semicircular apertural excavations and short, almost parallel-sided interthecal septa. Thecal apertures occupy *ca* one-quarter the rhabdosome width. Thecae densely spaced (6.5–7.5 in 5 mm) with 2TRD 1.3–1.45 mm at th2 and 1.45–1.55 at th5.

Remarks. – *Normalograptus parvus* sp. nov. is one of seve-

ral similar normalograptids described from lower–middle Rhuddanian strata. It is considerably narrower with thecae more strongly geniculated and more densely spaced than *Normalograptus angustus* (Perner, 1895). *Normalograptus mirnyensis* (Obut & Sobolevskaya, 1967) has similar thecal spacing but a wider and proximally tapering rhabdosome. *Normalograptus jideliensis* (Koren' & Mikhaylova, 1980) and *N. acceptus* (Koren' & Mikhaylova, 1980) can be distinguished by the presence of genicular flanges. *Normalograptus legrandi* Koren' & Rickards, 2004 is closely similar except for its extremely densely spaced thecae (19–24 in 10 mm) and slightly outwardly inclined supragenicular walls. The inclination described in the three-dimensionally preserved isolated specimens of *N. legrandi* by Koren' & Rickards (2004) would be further enhanced by flattening. *Normalograptus skeliphrus* (Koren' & Melchin, 2000) is narrower than *N. parvus* and more tapering proximally. *Normalograptus melchini* (Koren' & Rickards, 2004) is very narrow, attaining a maximum width of 0.46 mm. *Normalograptus parvus* is confined to the upper *vesiculosus* and lower *cyphus* biozones according to the present material.

***Normalograptus frydai* sp. nov.**
Figures 3F, I, O, P, 4L–N, U, 9M

Holotype. – Specimen No. PŠ3644 (Fig. 9M) from the lower part of the *Coronograptus cyphus* Biozone of Běleč, Želkovice Formation, Prague Synform, Czech Republic.

Derivation of name. – After Jiří Frýda, Czech palaeontologist and geochemist.

Material. – 16 complete rhabdosomes, both immature and mature specimens. Additional material, including the holotype, was collected from the Hlásná Třebaň and Běleč sections.

Diagnosis. – A moderately sized, 1.6–1.95 mm wide normalograptid with a rounded proximal end, sharp genicula, straight to slightly concave and markedly outwardly inclined supragenicular thecal walls and straight apertures perpendicular to the rhabdosome opening into small subtriangular excavations.

Description. – The rhabdosome is up to 20 mm long, probably septate and circular in cross-section, with a rounded proximal end. It widens from 0.85–1.22 mm at the first thecal pair, through 1.2–1.5 mm at the third thecal pair and 1.4–1.75 mm at the fifth thecal pair to the maximum 1.6–1.95 mm attained by the ninth or tenth thecal pair. The sicula is short and completely covered; the sicular aperture is 0.15–0.2 mm wide, straight in juvenile specimens and concave and somewhat depressed in the rounded outline of the proximal end in mature rhabdosomes. $Th1^1$ turns upwards 0.15 mm below the sicular aperture which, in some juvenile specimens, is furnished with a short virgella. The upwards growing part of $th1^1$ is 0.7–0.9 mm long. The proximal end becomes more symmetrical, almost semicircular, in rhabdosomes over 4 mm long, probably due to secondary thickening of the fusellum. The virgella is missing in mature rhabdosomes. Supragenicular thecal walls are inclined at 5–10° to the rhabdosome axis and may be slightly concave in the subapertural part in distal thecae. Straight apertures are either normal to the rhabdosome axis or slightly introverted, but always tightly appressed to the minute geniculum of the suceeding theca, leaving no or just a shallow, asymmetrical, subtriangular apertural excavation in the rhabdosome outline. The thecae overlap for about half their length. Thecae are densely spaced proximally, with 2TRD 1.25–1.45 mm at th2, and 1.4–1.6 mm at th5. Distal thecae number 10 in 10 mm (2TRD is 1.7–2.1 mm at th10).

Remarks. – *Normalograptus frydai* sp. nov. occurs in the lower *cyphus* Biozone in association with *Pernerograptus austerus* (Hutt). Immature specimens exhibit common features of many *Normalograptus* species except for having markedly outwardly inclined supragenicular walls and a rounded proximal end with $th1^2$ crossing the sicula almost at the level of the sicular aperture. Extensive thickening of the cortical layer makes the proximal part more robust and blunt in mature rhabdosomes with the sicular aperture no longer protruding from the proximal rhabdosome outline. Late astogenetic morphology modified by thickened cortical tissue in a similar manner was described by Loydell & Maletz (2009) in *Normalograptus scalaris* (Hisinger, 1837). The subapertural thecal walls become concave and the apertures slightly flaring although still horizontal (perpendicular to the rhabdosome axis) in the distal thecae of mature specimens which, along with the circular or sub-circular cross section of the rhabdosome, mean that *N. frydai* may resemble *Pseudoglyptograptus* Bulman & Rickards, 1968 in some respects. Both *Pseudoglyptograptus vas* Bulman & Rickards and *Pseudoglyptograptus barriei* Zalasiewicz & Tunnicliff, 1994 are readily distingushed by their sigmoidally curved thecae with sharp genicula, everted apertures in the former and apertural lappets in the latter species. The blunt proximal end of mature *N. frydai* is reminiscent of that of *Cystograptus* species which can be readily distinguished, however, by their long sicula, nematularium and long thecae with double sigmoidal curvature. *Neodiplograptus* species differ from *N. frydai* in having a sub-triangular, rapidly widening proximal end and thecal geniculation decreasing in the mesial and distal part of the rhabdosome along with increasing thecal inclination.

***Normalograptus*? sp.**
Figures 3G, J, 4P, CC

Material. – Five specimens.

Description. – Rhabdosome parallel-sided, 10–16 mm long, slightly widening proximally from initial width of 0.95–1.0 mm at first thecal pair, through 1.2–1.35 mm at the third thecal pair to the maximum width of 1.6–1.7 mm attained by the seventh to ninth thecal pair. The proximal end is rounded with the sicula covered in reverse view except for its 0.2 mm wide aperture which is furnished with a short spine-like virgella. The downward grown part of th1[1] turns upwards immediately below the sicular aperture, its upward growing part is 0.85–0.9 mm long. A median septum is barely recognizable. The thecae are sharply geniculate with a thickened genicular rim. Supragenicular thecal walls are straight and parallel-sided. Thecal apertures are horizontal or slightly introverted, facing narrow apertural excavations which occupy almost one-third the rhabdosome width. The 2TRD is 1.35–1.55 mm at th2, 1.5–1.55 mm at th5 and 1.6–1.7 mm at th10.

Remarks. – This form from the upper *vesiculosus* Biozone graptolite assemblage is tentatively assigned to *Normalograptus* although its rounded proximal end without significant exposure of the subapertural dorsal wall of the sicula, deep and narrow apertural excavations and sharp genicula with thickened rims suggests *Metaclimacograptus*. The nature of the median septum has not been recognized in the limited material available but there is some suggestion that it may be wavy. Regardless of generic assignment, the rhabdosomes with deep and narrow apertural excavations, sharp genicula, parallel-sided supragenicular thecal walls, 11.5–12.5 thecae in 10 mm and maximum rhabdosome width of 1.6–1.7 mm are readily distinguishable from all Rhuddanian normalograptids and metaclimacograptids known to date.

Genus *Korenograptus* Melchin, Mitchell, Naczk-Cameron, Fan & Loxton, 2011

Type species. – By original designation: *Glyptograptus gnomus* Churkin & Carter, 1970, from the Llandovery of SE Alaska.

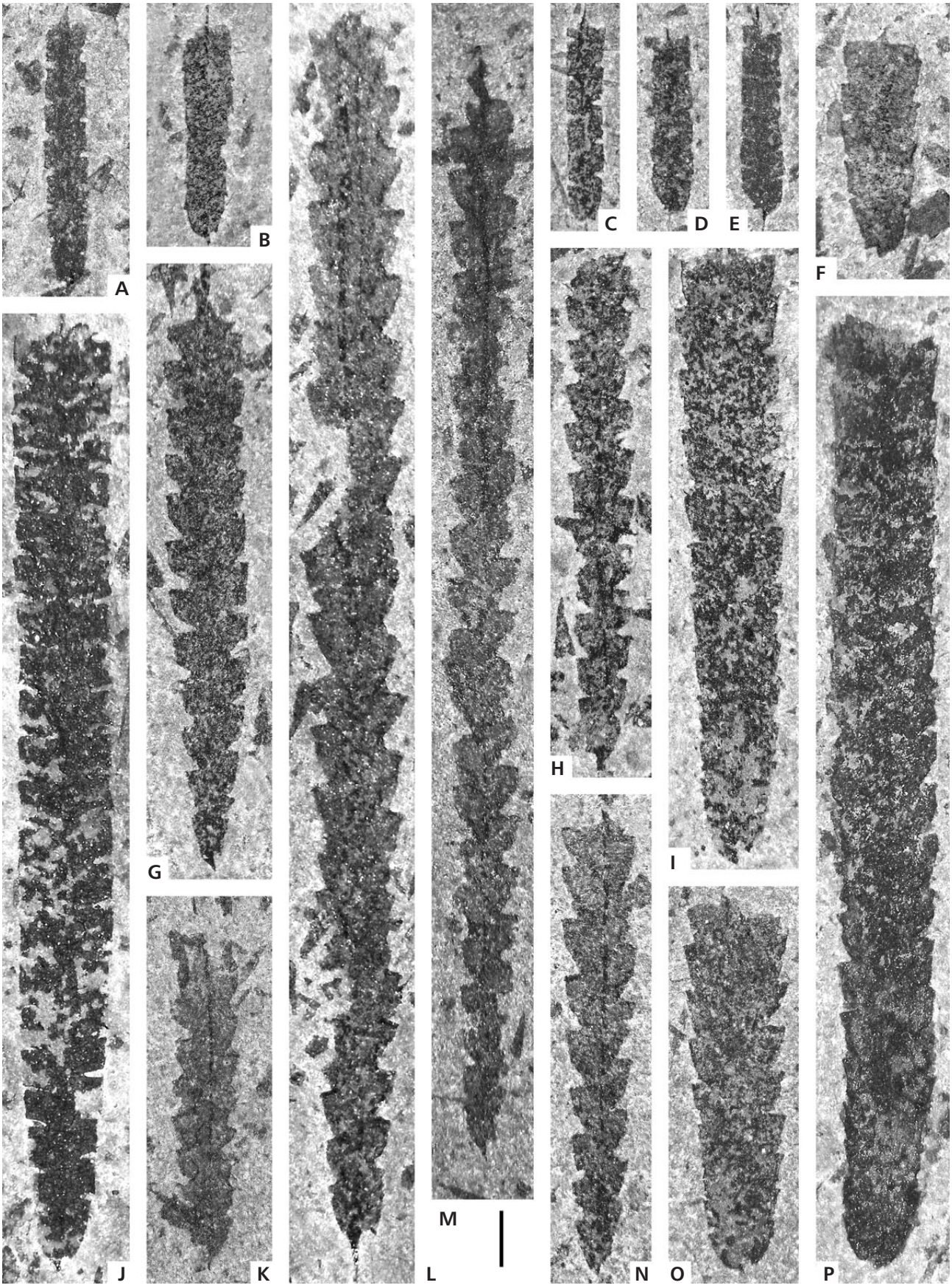
***Korenograptus nikolayevi* (Obut, 1965)**
Figures 3K, L, 4DD, EE, 9L

1965 *Glyptograptus nikolayevi* n. sp.; Obut, p. 36, pl. 1, fig. 5.
1996 *Glyptograptus tamariscus nikolayevi* Obut. – Koren' & Rickards, pp. 29–30, pl. 3, fig. 2; text-fig. 5o, p (see for further synonymy).
1998 *Normalograptus*? *nikolayevi* (Obut). – Štorch, pp. 214, 216; pl. 2, fig. 5; pl. 3, figs 5, 6; text-fig. 4, figs 5A–D.
non 1998 *Normalograptus nikolayevi* (Obut). – Melchin, pl. 1, figs 4–9.
2009 *Normalograptus nikolayevi* (Obut). – Loydell & Maletz, pp. 278–279; text-fig. 3a–e.

Material. – Seven rhabdosomes from Všeradice along with several specimens from Hlásná Třebaň and Běleč and the material figured by Štorch (1998).

Description. – Medium sized septate rhabdosome commonly attaining a length of about 20 mm and with a maximum width of 1.8 mm. One mature specimen, 49 mm long and 2 mm wide (Fig. 9L) exhibits a particularly robust nema projecting well beyond the thecate part of the rhabdosome. The sicula is *ca* 1.7 mm long and 0.26–0.33 mm wide at the aperture which is furnished with a stout virgella which is 3.4 mm long and possibly broken in the specimen figured on Fig. 9L and apparently broken in the other specimens available from Všeradice. Th1[1] grows downwards and slightly (< 0.2 mm) below the sicular aperture it bends sharply. Its upward growing part is 0.9–1.1 mm long. Th1[2] typically crosses the dorsal wall of the sicula immediately above the sicular aperture. The rhabdosome width increases gradually from 0.85–1.05 mm at the first thecal pair to 1.1–1.35 mm at the third thecal pair and 1.4–1.65 mm at th5. The maximum width, 1.6–1.95 mm, is attained by the seventh to tenth thecal pair. The thecae are weakly geniculate, without any genicular thickening, becoming almost straight distally, overlapping for about one-third their length. Ventral walls are inclined at 20–30° to the rhabdosome axis. Thecal apertures are broad, concave in profile, perpendicular to the ventral thecal wall or slightly everted. 2TRD is 1.4–1.8 mm at th2, 1.7–1.95 mm at th5 and 2.0–2.3 mm distally. Distal thecae number 9–10 in 10 mm in mature rhabdosomes.

Figure 3. A, C – *Normalograptus parvus* sp. nov.: A – PŠ 3427, holotype; C – PŠ 3573. • B – *Metaclimacograptus* cf. *hughesi* (Nicholson): PŠ 3612. • D, E – *Metaclimacograptus* aff. *slalom* Zalasiewicz, 1996: D – PŠ 3521; E – PŠ 3473. • F, I, O, P – *Normalograptus frydai* sp. nov.: F – PŠ 3563, juvenile specimen showing proximal rhabdosome structures without secondary thickening of the periderm; I – PŠ 3535; O – PŠ 3536 exhibits typical rounded proximal end; P – PŠ 3531, mature specimen showing median septum and proximal structures obscured by secondary thickening of the peridem. • G, J – *Normalograptus*? sp.: G – PŠ 3558, J – PŠ 3572. • H – *Glyptograptus* sp. A, PŠ 3440. • K, L – *Korenograptus nikolayevi* (Obut, 1965): K – PŠ 3426, L – PŠ 3575b. • M, N – *Glyptograptus perneri* sp. nov.: M – PŠ 3508, N – PŠ 3624, holotype. A, E, G, J from the upper *vesiculosus* Biozone; B–D, F, H, I, O, P from the lower *cyphus* Biozone; K, M, N from the lower *triangulatus* Biozone and L from the upper *cyphus* Biozone. All figures × 10; scale bar represents 1 mm.


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

Remarks. – The material studied matches the original description of *Glyptograptus nikolayevi* (Obut, 1965) from the *triangulatus* Biozone of the Kolyma region in rhabdosome width, thecal spacing and shape and also in the morphology of the proximal end. It can be distinguished from *Glyptograptus tamariscus* (Nicholson) and related species in having Pattern H astogeny, full median septum and flowing, if any, thecal geniculation. The large rhabdosome found in the *cyphus* Biozone at Všeradice matches the late mature specimen of *Korenograptus nikolayevi* from the *leptotheca* Biozone of Tmaň, figured by Štorch (1998, pl. 2, fig. 5; text-fig. 5A), in having a thick nema which gave rise to a narrow nematularium at about the middle of the rhabdosome's length. Material described by Koren' & Rickards (1996) from the *cyphus* Biozone of the southern Urals and by Loydell & Maletz (2009) from the *convolutus* Biozone of Dalarna, Sweden, suggests a long stratigraphical range of this uncommon species, indicated also by the present specimens from the upper *vesiculosus*, *cyphus* and *triangulatus* biozones of Všeradice and supplementary material from the upper *vesiculosus* and *cyphus* biozones of the Běleč section (Štorch 1986) and the *pectinatus* Biozone of the Hlásná Třebaň section.

Genus *Metaclimacograptus* Bulman & Rickards, 1968, emend. Melchin *et al*., 2011

Type species. – *Diplograpsus Hughesi* Nicholson, 1869; by original designation; from the Llandovery of the Lake District, England.

Metaclimacograptus aff. *slalom* Zalasiewicz, 1996
Figures 3D, E, 4A

aff. 1968 *P.* (*Metaclimacograptus*) *hughesi* (Nicholson). – Bulman & Rickards, pp. 3, 5–6; text-fig. 1a–c.
aff. 1996 *Metaclimacograptus slalom* n. sp.; Zalasiewicz, p. 11, text-fig. 2f.

Material. – Three, probably immature rhabdosomes.

Description. – Minute, 4 mm-long rhabdosome attaining its maximum width of 0.75 mm at the first thecal pair. Proximal end rounded, sicula covered except for *ca* 0.15 mm wide aperture with tiny virgella. Th1[1] turns upward immediately below the sicular aperture; its upward growing part is 0.6–0.7 mm long. Strongly geniculated thecae with parallel-sided supragenicular walls and slightly introverted apertures open into deep, slit-like apertural excavations. Septum undulating but poorly seen. Thecae densely spaced with 2TRD 1.1 mm at th2 and 1.2 mm at th5.

Remarks. – Rare minute rhabdosomes associated with the graptolite fauna of the upper *vesiculosus* and lower *cyphus* biozones are similar to specimens assigned to *Metaclimacograptus hughesi* (Nicholson) by Bulman & Rickards (1968) and subsequently recognized as a new species, *Met. slalom*, by Zalasiewicz (1996). Thecal shape and spacing, apertural excavations, and rhabdosome width of the present specimens are identical to those of *Met. slalom.* In contrast to *Met. slalom*, however, the maximum width is attained at the first thecal pair and is succeeded by distal diminution of the rhabdosome width. The present form can be readily differentiated from *Met. hughesi* by having a considerably narrower rhabdosome and a wavy median septum. *Metaclimacograptus undulatus* (Kurck, 1882) exhibits a strongly undulating – angulate median septum and convex supragenicular thecal walls which, however, appear to be transformed to almost straight by flattening. *Metaclimacograptus orientalis* (Obut & Sobolevskaya, 1966) differs from the present specimens in having more introverted thecal apertures. *Metaclimacograptus minimus* (Paškevičius, 1976), *Met. khabakovi* Koren' & Rickards, 1996 and *Met. khvorovi* Koren' & Rickards, 1996 can be distingushed by their inward sloping supragenicular thecal walls and genicular hoods.

The limited material, represented by immature flattened rhabdosomes with a barely recognizable median septum, does not allow for reliable taxonomic assignment of this form. The black shales of the *vesiculosus* and *cyphus* biozones of the Hlásná Třebaň section also yielded some metaclimacograptid rhabdosomes of equal dimensions but again without recognizable morphological details.

Metaclimacograptus cf. *hughesi* (Nicholson, 1869)
Figures 3B, 4K, S, 6J, 8D

cf. 1869 *Diplograpsus Hughesi* Nich.; Nicholson, p. 235, pl. 11, figs 9, 10.
cf. 1906 *Climacograptus Hughesi* (Nicholson). – Elles & Wood (*partim*), pp. 208–210, pl. 27, fig. 11a, c, e (*non* text-fig. 140; pl. 27, fig. 11b, d).
cf. 1996 *Metaclimacograptus hughesi* (Nicholson). – Zalasiewicz, pp. 2–3, text-fig. 2a–c.

Material. – Four rhabdosomes.

Description. – Rhabdosome less than 10 mm long, widening from 0.65–0.8 mm at the first thecal pair, through 0.85–1.0 mm at the third thecal pair to a maximum width of 1.0–1.1 mm attained by about the fifth thecal pair. The proximal end is rounded; the upward-growing part of th1[1] is 0.6–0.75 mm long. Thecae are sharply geniculate with slightly developed genicular flanges. Supragenicular ventral walls are slightly inward sloping or parallel to the rhabdosome axis, terminated by a markedly introverted thecal

aperture. The slit-like apertural excavation occupies *ca* one-third of the rhabdosome width. Median septum not seen. The 2TRD at th2 is 1.1–1.2 mm, at th5 1.25–1.4 mm and distally 1.45 mm.

Remarks. – No specimen of certain identity has been found. The present rhabdosomes differ from *Metaclimacograptus slalom* in having a greater dorso-ventral width, slightly inward sloping supragenicular thecal walls and deep apertural excavations. *Metaclimacograptus hughesi* (Nicholson), as refigured and redefined by Zalasiewicz (1996) according to the lectotype selected by Přibyl (1948), exhibits a similar rhabdosome width, thecal geniculation and introversion of the apertural excavations but its thecae are less densely spaced. Further comparison is unavailable since the median septum is barely traceable in the Všeradice specimens, as in the majority of other flattened metaclimacograptids recorded in the Prague Synform. The Všeradice specimens are from the *cyphus* Biozone as opposed to the type specimen of *Met. hughesi* which is from middle Aeronian *Pribylograptus leptotheca* or *Lituigraptus convolutus* Biozone. *Met. hughesi* has a very long stratigraphical range having been recorded from the Rhuddanian *Cystograptus vesiculosus* Biozone (Koren' & Rickards 1996, Loydell 2007) through to the upper Aeronian *Stimulograptus halli* Biozone (Loydell *et al*. 2015). Slender, *ca* 0.8 mm wide rhabdosomes of *Metaclimacograptus hughesi* as discussed by Bulman and Rickards (1968) and figured also by Loydell (1991) a.o. should be assigned to *Metaclimacograptus slalom* Zalasiewicz, 1996.

Genus *Rhaphidograptus* Bulman, 1936

Type species. – *Climacograptus toernquisti* (Elles & Wood, 1906); by original designation; from the Llandovery of Dob's Linn, Scotland.

Rhaphidograptus toernquisti (Elles & Wood, 1906)

Figures 4T, FF, GG, 6E, K

1906 *Climacograptus Törnquisti* sp. nov.; Elles & Wood, p. 190, pl. 26, figs 6a–f; text-fig. 123a, b.
1970 *Rhaphidograptus toernquisti* (Elles & Wood). – Rickards, p. 54, text-fig. 13, figs 1–3 (see for further synonymy).
1974a *Rhaphidograptus toernquisti* (Elles & Wood). – Hutt, p. 53, pl. 9, figs 1, 2; text-fig. 13, figs 7–9.
1975 *Rhaphidograptus toernquisti* (Elles & Wood). – Bjerreskov, p. 43, pl. 6, figs c, d.
1979 *Rhaphidograptus toernquisti* (Elles & Wood). – Paškevičius, p. 150, pl. 8, figs 1, 2, 3a, b; pl. 23, figs 5a, b, 6.
1996 *Rhaphidograptus toernquisti* (Elles & Wood). – Koren' & Rickards, pp. 93–94, pl. 13, figs 4, 5; text-figs 21d, e, 22l, n–p.

Material. – About 50 complete rhabdosomes, both juvenile and mature specimens.

Remarks. – The majority of rhabdosomes from the *vesiculosus*, *cyphus* and *triangulatus* biozones of Všeradice represent juvenile or immature specimens, commonly without a long, robust and twisted virgella as developed in many mature rhabdosomes. A maximum rhabdosome width of 1.9 mm was attained in one 23 mm long specimen, whereas other specimens are 1.8 mm wide at most. Proximal astogeny matches well the descriptions provided by Elles & Wood (1906), Hutt (1974a) and Bjerreskov (1975). $Th1^2$ is missing, $th2^2$ emerged from the free dorsal wall of the *ca* 1.7 mm long sicula 0.95–1.25 mm above the sicular aperture, at the level of the $th1^1$ aperture. However, the $th2^2$ aperture is regularly situated above $th2^1$ aperture. Narrow genicular flanges have been observed on distal to the deep apertural excavations in some mature rhabdosomes.

Rhaphidograptus sp.

Figures 4O, 6B

Remarks. – A single immature, 5.5 mm long rhabdosome with uni-biserial development and strongly geniculated thecae differs from juvenile specimens of *Rhaphidograptus toernquisti* preserved on the same bedding plane in having three uniserial thecae. The first theca of the second series (probably $th4^2$) emerges from the dorsal wall of the slightly dorsally curved uniserial part above the aperture of $th3^1$. The conical 1.5 mm long sicula is 0.3 mm wide at the aperture and its apex attains a level below the aperture of $th2^1$. The specimen may represent either an early, short-living offshoot of the *Rhaphidograptus toernquisti* stem or just an aberrant specimen with a delayed origin of the second thecal series as some variation in number of uniserial thecae is known in several species of *Dimorphograptus* (Rickards 1970, Hutt 1974a, Štorch & Feist 2008, this paper a.o.). Thus, a decision is pending until more material of this form is available.

Family Neodiplograptidae Melchin, Mitchell, Naczk-Cameron, Fan & Loxton, 2011

Genus *Paraclimacograptus* Přibyl, 1947, emend. Melchin *et al*., 2011

Type species. – *Climacograptus innotatus* Nicholson, 1869; by original designation; from the Llandovery of Dob's Linn, Scotland.

***Paraclimacograptus innotatus* (Nicholson, 1869)**
Figures 4C–F, 6A, 13A, B

1869 *Climacograptus innotatus*; Nicholson, p. 238, pl. 11, figs 16, 17.
partim 1906 *Climacograptus innotatus* Nicholson. – Elles & Wood, pp. 212–213, pl. 27, fig. 10a–e; text-fig. 143b (*non* text-fig. 143a).
1974a *Climacograptus innotatus innotatus* Nicholson. – Hutt, p. 21, pl. 1, figs 6, 7, 12; text-fig. 8, fig. 7 (see for further synonymy).
1977 *Paraclimacograptus innotatus* (Nicholson). – Crowther & Rickards, p. 19, pl. 4, fig. 3.
1996 *Paraclimacograptus innotatus* (Nicholson). – Koren' & Rickards, pp. 49–50, pl. 8, figs 2, 3.
2000 *Paraclimacograptus innotatus* (Nicholson). – Russel *et al*., pp. 85, 87–90; figs 1.3, 6, 7, 10; 2.2–4, 3, 4.
2008 *Paraclimacograptus innotatus* (Nicholson). – Štorch & Feist, p. 947, figs 5.11, 7.1, 2, ?14; 8.1.

Material. – 14 rhabdosomes, mostly juvenile specimens with 4–6 thecal pairs.

Description. – Minute rhabdosome with gently tapering proximal end, then parallel-sided. Rhabdosomes were up to 5.5 mm long, having up to eight thecal pairs. Width of the rhabdosome is 0.65–0.75 mm at the first thecal pair (excluding genicular hoods) and 0.9–1.1 mm at the third thecal pair. A maximum width of 0.9–1.2 mm is attained by the third or fourth thecal pair. $Th1^1$ grows downwards before it turns sharply upwards 0.1 mm below the *ca* 0.15 mm wide sicular aperture. The virgella is 0.3–0.4 mm long, commonly slightly deflexed across the sicular aperture. The upward growing part of $th1^1$ is 0.6–0.73 mm long. $Th1^2$ crosses the sicula, grows upwards and outwards and left a 0.1–0.15 mm length of sicular dorsal wall free. The median septum is barely seen in flattened specimens. All thecae except for the first pair are strongly geniculated and overlap for *ca* two-fifths their length. Genicula are typically furnished by prominent although short (max. 0.1–0.2 mm) genicular flanges succeeded by a concave supragenicular wall. Slightly everted thecal apertures open into deep, sub-triangular apertural excavations which occupy almost one third of the rhabdosome width. The 2TRD is 1.1–1.4 (commonly 1.2) mm at th2 and 1.2–1.4 mm at th5.

Remarks. – Russel *et al*. (2000) redescribed *P. innotatus* (Nicholson) based on flattened, relief, and chemically isolated specimens, discussed the closely related *Paraclimacograptus exquisitus* Rickards, 1970 and *Paraclimacograptus obesus* Churkin & Carter, 1970, and selected a neotype from the specimens figured by Elles & Wood (1906). The present specimens from the upper *vesiculosus* Biozone and, rarely, the *cyphus* Biozone at Všeradice match the biometric data given by Russel *et al*. (2000) for *P. innotatus* and correspond well also with those of the neotype figured by Elles & Wood (1906, pl. 37, fig. 10a) and refigured by Russel *et al*. (2000, fig. 2.2). *P. obesus* is a robust species with greater rhabdosome width (1.5–2.0 mm) and more widely spaced proximal thecae (2TRD prox. is 1.5–1.7 mm). *P. exquisitus* is narrower (0.5–0.6 mm at th1, 0.65–1.0 mm max. width), having densely spaced thecae (2TRD prox. is 0.75–0.81 mm, 2TRD dist. is 0.66–0.94 mm).

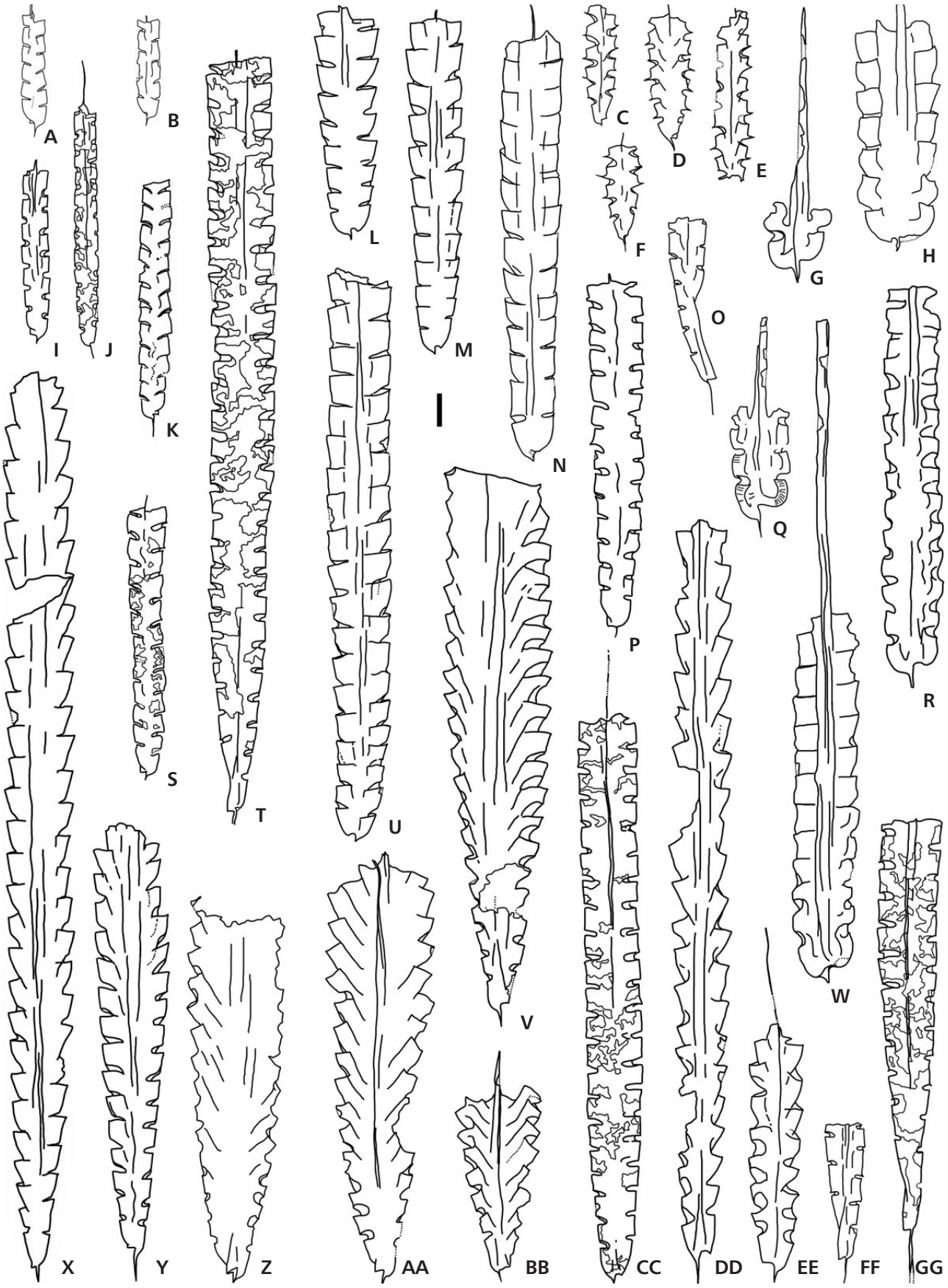
Genus *Neodiplograptus* Legrand, 1987

Type species. – *Diplograptus magnus* H. Lapworth, 1900; by original designation; from the Llandovery of central Wales.

***Neodiplograptus fezzanensis* (Desio, 1940)**
Figures 4V, Z–BB, 5A, B, G, H

1940 *Diplograptus modestus* var. *fezzanensis* nf.; Desio, pp. 26–27, pl. 2, figs 2, 3, 7–9, 11.
1970 *Diplograptus fezzanensis* A. Desio. – Legrand, pp. 27–40, text-fig. 2, figs 031–034.
1983 *Diplograptus fezzanensis* Desio. – Štorch,

Figure 4. A – *Metaclimacograptus* aff. *slalom* Zalasiewicz, 1996: PŠ 3473. • B, I, J – *Normalograptus parvus* sp. nov.: B – PŠ 3573, I – PŠ 3427, holotype; J – PŠ 3633. • C–F – *Paraclimacograptus innotatus* (Nicholson, 1869): C – PŠ 3474, D – PŠ 3477, E – PŠ 3503, F – PŠ 3584. • ?G, H – *Cystograptus vesiculosus* (Nicholson, 1868a): ?G – PŠ 3603, sicula with two thecal pairs; H – PŠ 3559. • K, S – *Metaclimacograptus* cf. *hughesi* (Nicholson): K – PŠ 3633, S – PŠ 3642. • L–N, U – *Normalograptus frydai* sp. nov.: L – PŠ 3536, exhibits typical rounded proximal end and inclined supragenicular thecal walls; M – PŠ 3535, N – PŠ 3445, U – PŠ 3531, mature specimen showing median septum. • O – *Rhaphidograptus* sp., PŠ 3481. • P, CC – *Normalograptus*? sp., P – PŠ 3558, CC – PŠ 3572. • Q, R, W – *Cystograptus penna* (Hopkinson, 1869): Q – PŠ 3543, showing typical, asymmetrically sub-rectangular proximal end; R – PŠ 3502; W – PŠ 3485, mature specimen with nematularium. • T, FF, GG – *Rhaphidograptus toernquisti* (Elles & Wood, 1906): T – PŠ 3430, FF – PŠ 3542, GG – PŠ 3538, exhibits tiny genicular flanges. • V, Z–BB – *Neodiplograptus fezzanensis* (Desio, 1940): V – PŠ 3522, box flattened specimen exhibiting thecal geniculation and rather short supragenicular walls; Z – PŠ 3471, AA – PŠ 3526, BB – PŠ 3618, immature specimen showing long interthecal septa. • X, Y – *Rickardsograptus lautus* (Štorch & Feist, 2008): X – PŠ 3544, Y – PŠ 3529. • DD, EE – *Korenograptus nikolayevi* (Obut, 1965): DD – PŠ 3575b, EE – PŠ 3426. A, C–E, H, I, O–Q, X, Y, CC, FF, GG from the upper *vesiculosus* Biozone; B, J, S, V, Z–BB from the *cyphus* Biozone; F,G, L–N, R, U, W from the lower part of the *cyphus* Biozone; K, DD from the upper part of the *cyphus* Biozone; T, EE from the lower *triangulatus* Biozone. All figures × 6; scale bar represents 1 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
AA
BB
CC
DD
EE
FF
GG

pp. 164–165, pl. 1, fig. 4; pl. 2, figs 1, 3–5; text-fig 2j, l–n.

1993 *Neodiplograptus* aff. *africanus* (Legrand). – Legrand, pp. 416–419, fig. 4a–e.

2002 *Neodiplograptus fezzanensis* (Desio). – Legrand, pl. 12, figs 5, 6; text-fig 5k.

2012 *Neodiplograptus fezzanensis* (Desio, 1940). – Loydell, fig. 3t–v, table 6.

Material. – 26 rhabdosomes from Všeradice, including both juvenile and mature specimens. Other examined specimens came from the Hlásná Třebaň, Zadní Třebaň, Běleč and Karlík sections.

Description. – Robust septate rhabdosome, attaining well over 40 mm in length, widens from 0.85–1.2 mm at the first thecal pair, to 1.5–1.8 mm at the third thecal pair, 1.9–2.4 mm at the fifth thecal pair and 2.4–3.3 mm at the tenth thecal pair. Maximum width of 2.5–3.7 mm is attained by the eighth to fifteenth thecal pair. Rhabdosome width varies considerably, in part due to intraspecific variability and in part due to different effects of flattening. Distal narrowing of the rhabdosome after the ninth to 17th thecal pair to values ranging between 3.15 and 2.0 mm is common, giving a sub-fusiform appearance to many mature specimens.

The proximal end is rounded sub-triangular in profile, having the subapertural walls of th1^1 and th1^2 inclined at 8–23°. Th1^1 grows downwards before it turns abruptly upwards *ca* 0.2 mm below the sicular aperture. The upward growing part of th1^1 is 0.75–1.0 mm long. The sicula is covered for the most part and appears to be max. 1.5 mm long when pressed through. The sicular aperture is 0.2–0.3 mm wide and furnished with a short virgella. Both proximal and distal thecae are geniculated, overlapping for two-thirds their length and terminate in everted apertures facing asymmetrical, broadly sub-triangular excavations. The supragenicular thecal wall is short (0.6–0.8 mm). Thecae are densely spaced with 2TRD 2 1.2–1.6 mm, 2TRD 5 1.25–1.6 mm and 2TRD 10 1.35–1.8 mm. Distal thecae number 10–12.5 thecae in 10 mm (2TRD dist. is 1.55–2.0 mm).

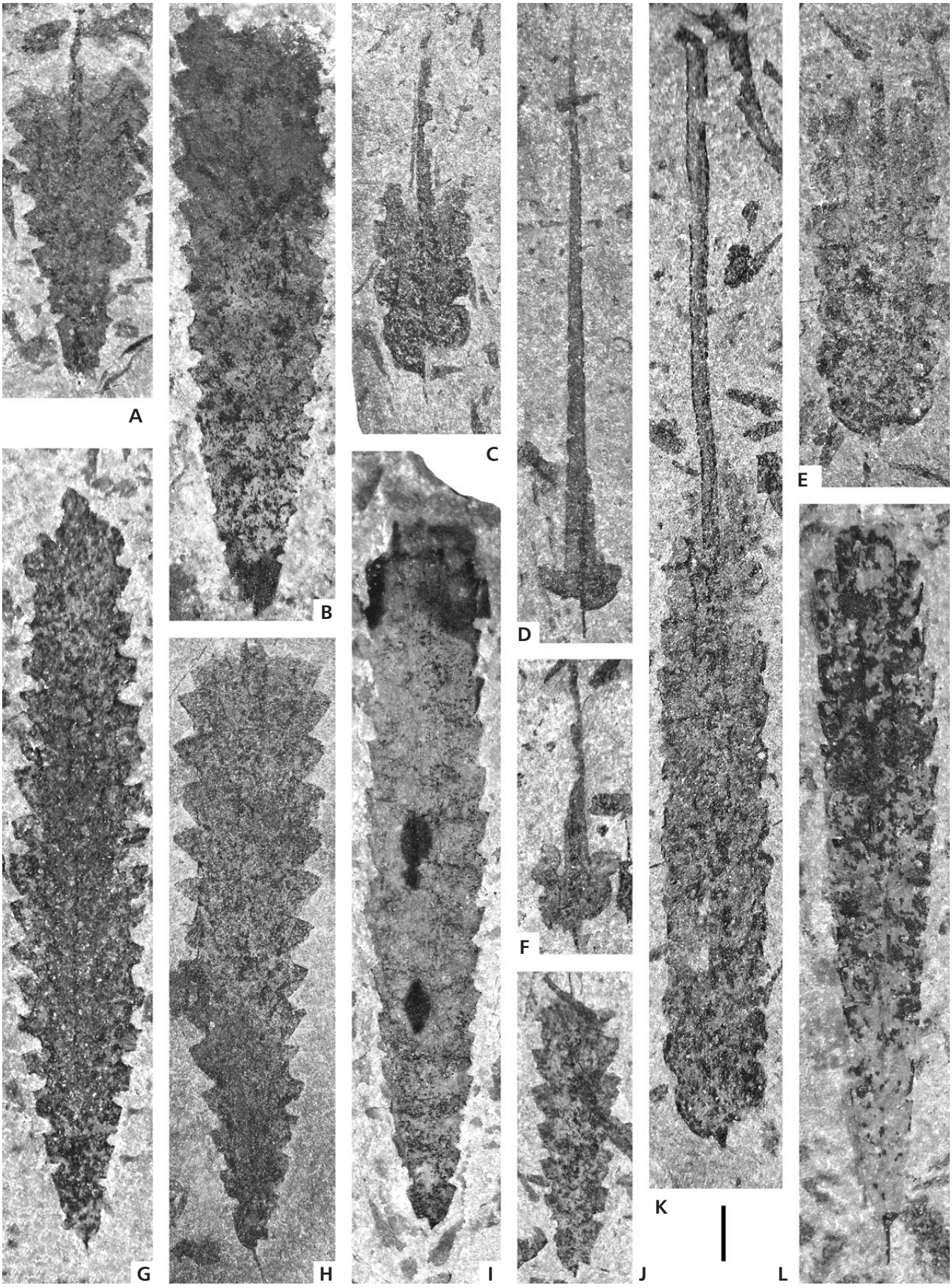
Remarks. – This form is closely related to *Neodiplograptus magnus* (H. Lapworth, 1900), in particular with respect to the revised description and diagnosis by Zalasiewicz & Tunnicliff (1994). *Nd. magnus* can be differentiated by having a slightly narrower proximal end, less rapidly widening rhabdosome and less biform and generally less geniculated thecae with generally shorter supragenicular walls. Whilst *Nd. magnus* gives its name to a biozone above the *triangulatus* Biozone in the British scheme (Rickards 1976b, Zalasiewicz *et al*. 2009), *Nd. fezzanensis* is a prominent constituent of the *cyphus* Biozone assemblages at all relevant sections of the Prague Synform. It is extremely variable species (see Legrand 1970 and his formes α, β, γ, δ). Variability in the rate of rhabdosome widening and maximum width is further enhanced by various mode of flattening and preservation of its robust rhabdosome, which was probably a flat oval in cross-section. Only Legrand's *Nd. fezzanensis* form δ with its extremely wide and rapidly widening rhabdosome and very long, considerably overlapping thecae has never been found in the Prague Synform.

***Neodiplograptus* sp.**
Figure 5I, J

Material. – Three rhabdosomes from Všeradice and several specimens from the Hlásná Třebaň section.

Remarks. – Several specimens found in the upper *cyphus* Biozone assemblage at Všeradice and in the *cyphus* and *triangulatus* biozones at Hlásná Třebaň can be distinguished from *Nd. magnus* and *Nd. fezzanensis* by their smaller rhabdosomes attaining a maximum width of 2.2–2.4 mm at the level of 7th–9th thecal pair. The rhabdosome is 0.9–1.1 mm wide at first thecal pair, 1.3–1.4 mm wide at the third thecal pair and 1.6–1.8 mm wide at the fifth thecal pair. Thecal spacing (2TRD 2: 1.25–1.45 mm, 2TRD 5: 1.45–1.8 mm and 2TRD 10: 1.6–1.8 mm) is less dense, and the thecae overlap less (for half their length) in *Neodiplograptus* sp. *Nd. fezzanensis*, *Neodiplograptus africanus* (Legrand, 1970) and *Nd. posterior* (Legrand, 1970) differ from *Nd*. sp. in having more strongly geniculated thecae and greater thecal overlap although rhabdosome width and rate of proximal widening of the last species are closely similar to those of the present material. Considering the large intraspecific variation observed in neodiplograptids (see also Loydell 2006, p. 12), the present specimens from Všeradice and Hlásná Třebaň have been retained in open nomenclature until more and better preserved rhabdosomes with better preserved siculae are available.

Figure 5. A, B, G, H – *Neodiplograptus fezzanensis* (Desio, 1940): A – PŠ 3618, immature specimen showing interthecal septa and median septum; B – PŠ 3471; G – PŠ 3582; H – PŠ 3447. • C, F, K – *Cystograptus penna* (Hopkinson, 1869): C – PŠ 3543; F – PŠ 3603; K – PŠ 3485, typical mature specimen with nematularium. • ?D, E – *Cystograptus vesiculosus* (Nicholson, 1868a): ?D – PŠ 3480, sicula with thl^1 and partly developed th1^2; E – PŠ 3559. • I, J – *Neodiplograptus* sp.: I – PŠ 3438, box-flattened specimen showing median septum; J – PŠ 3612. • L – *Rickardsograptus lautus* (Štorch & Feist, 2008): PŠ 3529, slightly box-flattened specimen showing median septum. A, B, F–K from the *cyphus* Biozone; C–E, L from the upper *vesiculosus* Biozone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E
F
G
H
I
J
K
L

Genus *Cystograptus* Hundt, 1942, emend. Rickards, 1970

Type species. – *Diplograptus vesiculosus* Nicholson, 1868a; subsequently designated by Jones & Rickards (1967).

Cystograptus vesiculosus (Nicholson, 1868a)

Figures 4?G, H; 5?D, E, ?F; 9G

1868a *Diplograpsus vesiculosus*; Nicholson, pl. 3, fig. 11.
1907 *Diplograptus* (*Orthograptus*) *vesiculosus* Nicholson. – Elles & Wood, p. 229, pl. 28, fig. 8a–f, text-fig. 151a–f.
1970 *Cystograptus vesiculosus* (Nicholson). – Rickards, p. 44, pl. 1, fig. 11; pl. 2, figs 12, 14.
1974a *Cystograptus vesiculosus* (Nicholson). – Hutt, p. 45, pl. 4, fig. 15; text-fig. 9, figs 4, 5 (see for further synonymy).
1975 *Cystograptus vesiculosus* (Nicholson). – Bjerreskov, p. 29, fig. 10e.
partim 1985 *Cystograptus vesiculosus* (Nicholson). – Štorch, pp. 96, 97, pl. 2, figs 5, 7 (*non* 1); pl. 4, figs 7, 8 (*non* 2); text-fig. 3e, f (*non* g, h).
1996 *Cystograptus vesiculosus* (Nicholson). – Koren' & Rickards, pp. 32–33, pl. 3, figs 4–10.
non 2004 *Cystograptus vesiculosus* (Nicholson) s.l. – Koren' & Rickards, p. 885, text-figs 12, 13.
2007 *Cystograptus vesiculosus* (Nicholson). – Loydell, pp. 51–52, text-fig. 20b (see for further synonymy).
2008 *Cystograptus vesiculosus* (Nicholson). – Štorch & Feist, p. 948, figs 6.4, 12; 7.12, 20; 10.9, 10.

Material. – Eight rhabdosomes, including both mature and juvenile specimens, and several siculae with the first thecal pair. Material seen also from the Běleč, Hlásná Třebaň and Karlík sections.

Description. – Large, *ca* 30 mm long rhabdosome, up to 3.8 mm wide when box-flattened, having a prominent, distally projected nematularium which is more or less developed in specimens of roughly equal maturity. The sicula is 8–11.2 mm long and 0.35–0.4 mm wide at its aperture. The proximal end of the rhabdosome is broadly rounded and 1.8–2.0 mm wide at the level of the first thecal pair. $Th1^1$ originates *ca* 2.5 mm above the sicular aperture and grows downwards 0.35–0.45 mm below the sicular aperture before it turns upwards for another 1.2–1.3 mm of its length. $Th1^2$ crossed the dorsal wall of the sicula at the sicular aperture which looks slightly concave and somewhat hidden in the rather asymmetrical outline of the proximal end of the rhabdosome. Further proximal thecae are characterized by their double sigmoidal curvature. Thecal apertures are more or less everted but largely distally facing. Distal thecae are straightened, commonly box-flattened to form two parallel-sided ladder-like rows of subalternate to almost opposite rectangular cells which is the typical appearance of flattened rhabdosomes of *C. vesiculosus*. A nematularium of various width (generally narrow in Bohemian specimens) originated early as it overlaps with the apical part of the sicula.

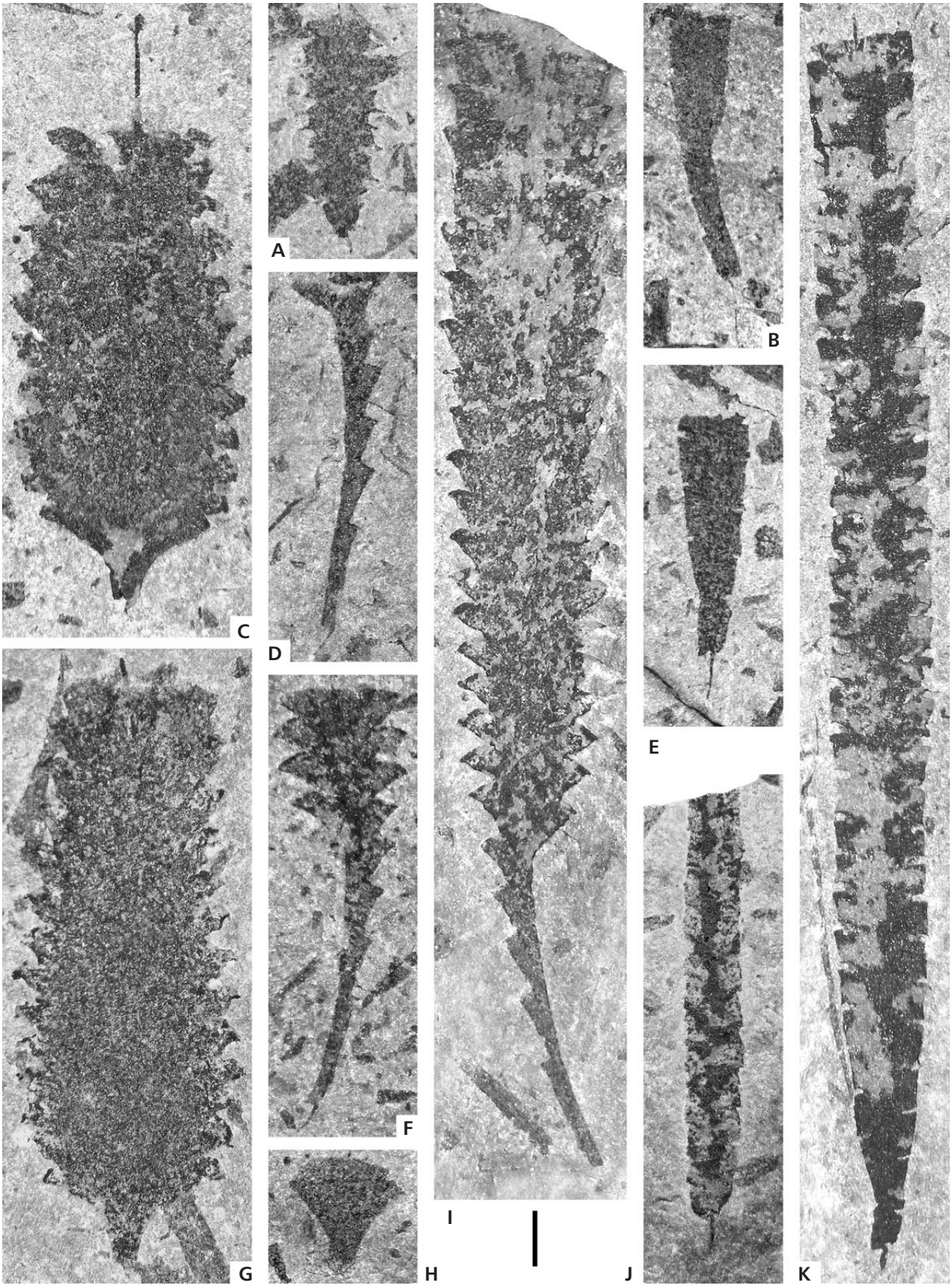
Remarks. – Robust specimens widening from a broadly rounded proximal end to at least 2.4 mm at the third thecal pair and reaching a distal maximum width of up to 3.8 mm have been assigned to *Cystograptus vesiculosus*. Such mature rhabdosomes, exceeding 10 mm in the length of thecate part, however, are markedly rare compared to abundant siculae and juvenile specimens with 1^{st}–3^{rd} thecal pairs. These juvenile specimens can be distinguished from the closely similar *Cystograptus penna* solely by having only slightly everted, dorsally or dorso-ventrally facing thecal apertures.

Cystograptus penna (Hopkinson, 1869)

Figures 4Q, R, W, 5C, K

1869 *Diplograpsus penna*; Hopkinson, p. 159, pl. 8, fig. 12.
1907 *Diplograptus* (*Orthograptus*) *vesiculosus* var. *penna* Hopkinson. – Elles & Wood, p. 231, pl. 28, figs 9a–c.
1967 *Diplograptus penna* Hopkinson. – Jones & Rickards, p. 173, text-figs 1, 2, 3a–c, e; 4, 5b.
1979 *Cystograptus vesiculosus* (Nicholson). – Paškevičius, pp. 128–129, pl. 4, figs 1–6; pl. 19, figs 18–20.
partim 1985 *Cystograptus vesiculosus* (Nicholson). – Štorch, pp. 96–97, pl. 2, fig. 1 (*non* 5, 7), text-fig. 3g (*non* e, f, h), *non* pl. 4, figs 2, 7, 8.
2004 *Cystograptus vesiculosus* (Nicholson) s.l. – Koren' & Rickards, p. 885, text-figs 12, 13.

Figure 6. A – *Paraclimacograptus innotatus* (Nicholson, 1869): PŠ 3477. • B – *Rhaphidograptus* sp., PŠ 3481. • C, G, H – *Petalolithus ovatoelongatus* (Kurck, 1882): C – PŠ 3514; G – PŠ 3429; H – PŠ 3602, juvenile specimen with tiny ancora structure and partly developed thecae of 1^{st} and 2^{nd} pair. • D, F, I – *Dimorphograptus confertus* (Nicholson, 1868b): D – PŠ 3476, juvenile specimen with partly developed initial theca of the second thecal series and flexed virgella; F – PŠ 3600; I – PŠ 3482, incomplete mature specimen. • E, K – *Rhaphidograptus toernquisti* (Elles & Wood, 1906): E – PŠ 3542; K – PŠ 3430. • J – *Metaclimacograptus* cf. *hughesi* (Nicholson): PŠ 3633. A, B, D, F, I from the upper *vesiculosus* Biozone; C, E, G, H, K from the lower *triangulatus* Biozone; J from the upper *cyphus* Biozone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E
F
G
H
I
J
K

Material. – 24 rhabdosomes, mostly immature specimens. Siculae with a single thecal pair are difficult to discriminate from *Cyst. vesiculosus*.

Remarks. – Rhabdosomes 1.6–1.8 mm wide at the first thecal pair and reaching maximum width of 1.9–2.2 mm at the level of the third to fifth thecal pair have been assigned to *Cystograptus penna* (Hopkinson). Their proximal end is rounded and similarly asymmetrical to that of *C. vesiculosus* but th1[1] turns upwards at a lesser distance below the sicular aperture if compared with *C. vesiculosus.* The markedly lesser dorso-ventral width of these rhabdosomes combined with their everted, ventrally facing thecal apertures justified their assignment to *C. penna*. The latter species can be further discriminated by having a narrower, max. 0.4 mm wide ribbon-like, although three-vaned nematularium. The nematularium has been detected as early in astogeny as in 8–12 mm long rhabdosomes where its initial part overlaps significantly with the apical part of the long sicula. While both closely related cystograptids occur in the upper *vesiculosus* Biozone, only narrow specimens with ventrally facing thecal apertures, assigned to *Cystograptus penna* occur in the graptolite assemblage of the lower *cyphus* Biozone in the Všeradice material. The rather narrow rhabdosomes from the *cyphus* Biozone of Lithuania referred to *Cyst. vesiculosus* by Paškevičius (1979) exhibit thecae with double curvature and strongly everted apertures typical of *Cyst. penna*.

Genus *Rickardsograptus* Melchin, Mitchell, Naczk-Cameron, Fan & Loxton, 2011

Type species. – *Diplograptus*(*?*) *tcherskyi* Obut & Sobolevskaya *in* Obut *et al*., 1967; by original designation; from the Yana River Basin, W Kolyma Massif, NE Siberia.

Remarks. – Melchin *et al*. (2011) distinguished *Rickardsograptus* from *Metabolograptus* Melchin *et al*., 2011 and *Neodiplograptus* Legrand, 1987 by the relatively narrow proximal end of its rhabdosome which rapidly widens mesially in the same region where there is a relatively rapid change from strongly geniculated, generally parallel-sided proximal thecae to smoothly glyptograptid to almost orthograptid distal thecae. Most species of *Rickardsograptus* also exhibit heavily sclerotized fuselli, a strong median septum and a robust nema.

Rickardsograptus lautus (Štorch & Feist, 2008)
Figures 4X, Y, 5L

1974a *Diplograptus* aff. *elongatus* Churkin & Carter. – Hutt, pp. 31–32, pl. 5, figs 1, 2; text-fig. 9, fig. 12; text-fig. 10, fig. 3.

1983 *Diplograptus elongatus* Churkin & Carter. – Štorch, p. 168, pl. 3, fig. 6; pl. 4, fig. 5; text-fig. 3C, D.

1996 *Neodiplograptus* cf. *elongatus* (Churkin & Carter). – Štorch, text-fig. 4, fig. 4b.

2008 *Neodiplograptus lautus* sp. nov.; Štorch & Feist, p. 948, figs 6.3, 6, 8, 9; 10.12, 13.

Material. – Two mature and two immature specimens.

Remarks. – Robust septate rhabdosomes widening from 0.85–0.9 mm at the first thecal pair to 1.1–1.25 mm at the third thecal pair, and 1.5–1.65 mm at the fifth thecal pair. The maximum width of 2.05–2.25 mm is attained at 10^{th}–12^{th} thecal pair. Further widening is possible but the present specimens from Všeradice are few and less mature than the type material from Montagne Noire and material described by Štorch (1983) from other Bohemian localities (Vočkov, Běchovice, Hlásná Třebaň, Zadní Třebaň). The virgella is relatively short (0.8–1.7 mm) as is typical in this species. Proximal thecae are sharply geniculated whereas distal thecae become sigmoidal with outward sloping suprageniculare walls. The geniculum is hidden for the most part in the thecal aperture of the preceding theca. 2TRD values increase from 1.5–1.6 mm at th2, through 1.5–1.8 mm at th5, to 1.8–2.05 mm measured in the distal part of the present rhabdosomes. The associated Všeradice graptolite assemblage indicates the upper *vesiculosus* Biozone. *Rickardsograptus lautus* is closely similar to *R. elongatus* (Churkin & Carter) from which can be differentiated by its generally more pronounced thecal geniculation, more prominent and more rapid transition from strongly geniculated proximal thecae to smoothly geniculated distal thecae, and more rapidly widening rhabdosome.

Family Retiolitidae Lapworth, 1873, emend. Melchin *et al*., 2011
Subfamily Petalolithinae Bulman, 1955, emend. Melchin *et al*., 2011

Genus *Glyptograptus* Lapworth, 1873, emend. Melchin *et al.*, 2011

Type species. – *Diplograpsus tamariscus* Nicholson, 1868b; by original designation; from the Llandovery of Duffkinnel, Scotland.

Glyptograptus perneri sp. nov.
Figures 3M, N, 7Y, HH

partim 1907 *Diplograptus* (*Glyptograptus*) *tamariscus* Nicholson. – Elles & Wood, p. 247, pl. 30, fig. 8c (*non* text-fig. 167a–d, pl. 30, fig. 8a, b, d).

1962 *Glyptograptus tamariscus linearis* Perner. – Pack-

ham, p. 506, pl. 72, fig. 8; text-fig. 1v (see for further synonymy).

1996 *Glyptograptus tamariscus linearis* (Perner). – Koren' & Rickards, pp. 26, 29; pl. 3, fig. 1; text-fig. 5m, n.

partim 1996 *Glyptograptus* aff. *elegans* Packham. – Koren' & Rickards, p. 23, pl. 1, figs 3, 4 (*non* 5); text-fig. 4c, d.

Holotype. – Specimen No. PŠ 3624 (Figs 3N, 7Y) from the *Demirastrites triangulatus* Biozone at Všeradice, Želkovice Formation, Prague Synform, Czech Republic.

Derivation of name. – After Jaroslav Perner, a Czech palaeontologist who worked on graptolites and other groups of lower Palaeozoic invertebrates.

Material. – 15 complete and some incomplete rhabdosomes from Všeradice and about 30 specimens from the Hlásná Třebaň and Karlík sections.

Diagnosis. – Medium-sized glyptograptid widening from 0.7–0.85 mm at the first thecal pair to a maximum of 1.4–1.6 mm attained at the seventh to eleventh thecal pair. Thecae with flowing geniculum, convex supragenicular wall and an apertural excavation sub-triangular in profile; 10–12 thecae in 10 mm throughout the rhabdosome length.

Description. – Rhabdosome of moderate size with maximum length *ca* 30 mm widens from 0.7–0.85 mm at the asymmetrical first thecal pair, through 1.0–1.1 mm at the third thecal pair and 1.2–1.25 mm (exceptionally 1.45 mm) at the fifth thecal pair, to a maximum of 1.4–1.6 mm attained between the 7^{th}–11^{th} thecal pair. The distal part is parallel-sided. The sicula is *ca* 1.5 mm long, partly exposed in reverse view. $Th1^1$ turns upwards and outwards immediately below the 0.15–0.2 mm wide sicular aperture which is furnished with minute virgella. The upward growing $th1^1$ is 0.75–0.95 mm long. $Th1^2$ crosses the sicula 0.2–0.3 mm above the sicular aperture. The proximal end of the rhabdosome is somewhat protracted with outward inclined ventral walls of the first thecal pair. Flattening patterns with common sub-scalariform preservation are consistent with an oval or subcircular rhabdosome cross section. A thin nema is attached to obverse side of the rhabdosome, rarely projecting far beyond the distal end. Thecae alternating, with flowing geniculum, slightly everted aperture and straight or slightly convex supragenicular wall inclined at about 5°. Thecae overlap for one-quarter their length. Open, broadly sub-triangular apertural excavations occupy *ca* one-quarter the rhabdosome width. Thecae number 10–12 in 10 mm (2TRD 2: 1.45–1.65 mm, 2TRD 5: 1.7–1.9 mm, 2TRD dist: 1.95 mm).

Remarks. – The present specimens match the widely adopted picture of *Glyptograptus tamariscus linearis* Perner, 1897 distinguished from *G. tamariscus tamariscus* (Nicholson, 1868b) solely by its markedly tapering rhabdosome attaining a greater maximum width. However, the original description of *Gl. tamariscus linearis* by Perner (1897) referred only to a maximum width of 1.2 mm, parallel-sided supragenicular thecal walls and concave (probably everted) thecal apertures. The specimen from the *convolutus* Biozone of Litohlavy, figured by Perner (1897, text-fig. 2) and selected as lectotype by Přibyl (1948), is missing and the type locality is no longer exposed and its location is unknown. The only paratype, a distal rhabdosome fragment figured by Perner (1897, pl. 9, fig. 23) from the *convolutus* Biozone of Velká Chuchle ("Barrande's colony Haidinger") and rich collections from the *convolutus* Biozone of Tmaň described by Štorch (1998) match well *Gl. tamariscus tamariscus* (Nicholson) revised by Packham (1962). No rhabdosome corresponding with the morphology "described" and figured by Perner (1897) is available in the extensive collections from the *convolutus* Biozone of the Prague Synform. The present uppermost Rhuddanian and lower Aeronian specimens, however, differ from *Gl. tamariscus* in having a generally more robust rhabdosome, 0.7–0.85 mm wide at the first thecal pair and 1.4–1.6 mm at about the tenth thecal pair and in having thecae with a rather low, sub-triangular apertural excavation limited by flowing geniculum. Although this material matches the widely adopted concept of *Gl. linearis*, a new species must be established herein to name this form.

***Glyptograptus* sp. A**
Figures 3H, 7W, X

Material. – Four mature rhabdosomes and one juvenile specimen.

Description. – The narrow and for the most part parallel-sided rhabdosome widens from 0.75 mm at the first thecal pair through 0.9–1.05 mm at the third thecal pair and 1.05–1.2 mm at the fifth thecal pair to the maximum of 1.2–1.25 mm attained at the level of the fifth to tenth thecal pair. The sicula is partly exposed in reverse view; its apex attains a level above the aperture of $th1^2$. $Th1^1$ bends upward 0.1–0.15 mm below the 0.2 mm-wide sicular aperture; its upward growing part is 0.75–1.0 mm long. $Th1^2$ crosses the sicula 0.25–0.5 mm above the aperture. Thecae alternating, with a slightly outwardly inclined supragenicular wall, prominent but rounded geniculum, horizontal to slightly everted aperture and sub-triangular apertural excavation which occupies almost one-third the rhabdosome width. 2TRD increases a little from 1.6–2.0 mm at th2 to 1.7–2.0 mm at th5 and th10.

Remarks. – This relatively slender and strongly geniculated representative of the *Gl. tamariscus* group found in the *cyphus* and lower *triangulatus* biozones in Všeradice is differentiated by its small, for the most part parallel-sided rhabdosome, strong genicula and deep apertural excavations which together occupy two-thirds of the rhabdosome width. This form is the most similar to specimens from the British *convolutus* Biozone assigned by some authors (*e.g.* Hutt 1974a) to *Glyptograptus incertus* (Elles & Wood, 1907; see Loydell 1992 for description of *G. incertus sensu stricto*).

***Glyptograptus* sp. B**
Figure 7U, V

Material. – Four rhabdosomes.

Remarks. – Up to 10 mm long, probably immature rhabdosomes widen from 0.75–1.0 mm at the first thecal pair to a supposed maximum width of 1.45 mm at the seventh thecal pair. This form occurs with an upper *vesiculosus* Biozone assemblage and can be differentiated from other glyptograptids by its strongly sigmoidal, moderately geniculated thecae with supragenicular walls parallel to ventral margin of the rhabdosome and its stout nema which extends beyond the distal end of the rhabdosome.

Genus *Pseudorthograptus* Legrand, 1987, emend. herein

Type species. – *Diplograpsus insectiformis* Nicholson, 1869; by original designation; from the Llandovery of the Lake District, England.

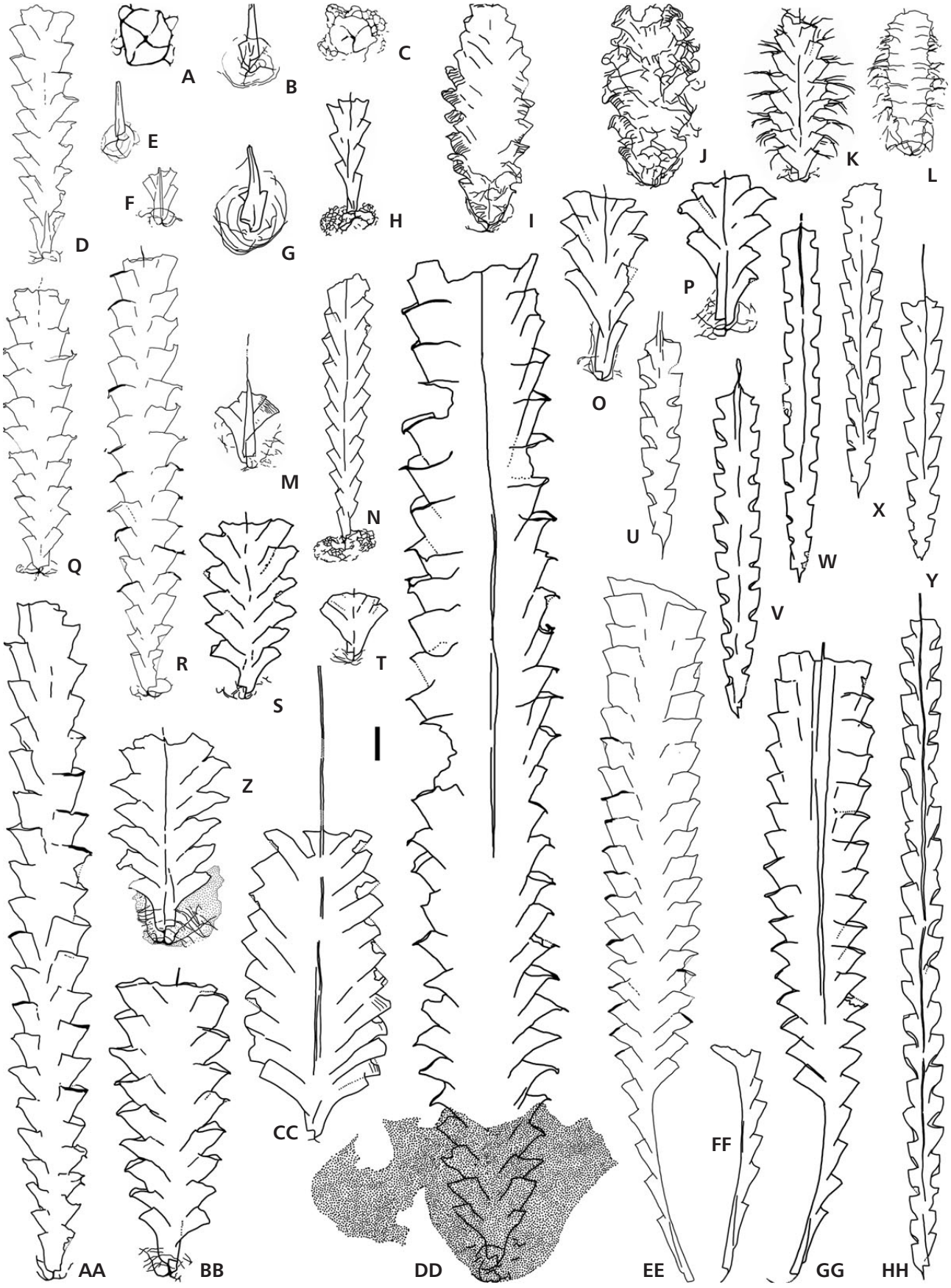
Diagnosis. – Pattern I rhabdosome with partial median septum, flat-ovate cross-section, straight to slightly concave first thecal pair and ancora with four prongs more or less densely connected by concentric and/or spiral loops of additional lists forming a disc-, bowl- or basket-shaped ancora umbrella commonly with a membrane. Distal thecae straight, with normal or slightly everted apertures, ventro-lateral apertural processes, gentle lateral cusps, or spines which are paired or further bifurcated.

Species included. – *Diplograpsus insectiformis* Nicholson, 1869; *Orthograptus mutabilis* Elles & Wood, 1907; *Orthograptus* (?) *inopinatus* Bouček, 1944; *Orthograptus insectiformis minutus* Churkin & Carter, 1970; *Orthograptus obuti* Rickards & Koren', 1974; *Pseudorthograptus finneyi* Štorch & Kraft, 2009 and *Pseudorthograptus mitchelli* sp. nov. Also the ancorate species with a short uniserial part comprising th1[1], *Diplograptus physophora* Nicholson, 1868a and *Dimorphograptus physophora alaskensis* Churkin & Carter, 1970, both refered to the subgenus *Dimorphograptoides* by Koren' & Rickards (1996), are provisionally retained in *Pseudorthograptus*.

***Pseudorthograptus obuti* (Rickards & Koren', 1974)**
Figures 7B, G, M, S, Z, BB, DD, 8A, B, F, I, M, 9C, E

1971 *Dimorphograptus physophora* (Nicholson). – Schauer, p. 52, pl. 17, fig. 10; pl. 18, figs 19, 20.

Figure 7. A, D–F, Q, R, AA – *Pseudorthograptus mitchelli* sp. nov.: A – PŠ 3491, top view of "steering-wheel" type juvenile ancora; D – PŠ 3422, E – PŠ 3507, sicula with ancora umbrella; F – PŠ 3481, juvenile specimen showing first thecal pair with even apertures and ancora in lateral view; Q – PŠ 3497, specimen with lateral view of the ancora and bifurcated ventral apertural processes; R – PŠ 3450, holotype exhibits blunt bifurcated apertural processes; AA – PŠ 3439, mature specimen with bowl-shaped ancora. • B, G, M, S, Z, BB, DD – *Pseudorthograptus obuti* (Rickards & Koren', 1974): B – PŠ 3518, sicula with incomplete thl[1] and large delicate ancora; G – PŠ 3635, sicula with incomplete th1[1], budding th1[2] and basket-like ancora structure dominated by spiralling concentric lists; M – PŠ 3450, juvenile specimen showing complete sicula and partly preserved ancora; S – PŠ 3492; Z – PŠ 3492, ancora exhibits four radial branches connected by slender connecting rods; BB – PŠ 3448; DD – PŠ 3501, mature specimen with ancora membrane and thecal apertures with ventral processes. • C, H, N – *Pseudorthograptus finneyi* Štorch & Kraft, 2009: F – PŠ 3513, top view of juvenile ancora with dense mesh of loops on perimeter of the primary "steering-wheel" structure; H – PŠ 3641, immature specimen with protracted proximal end and dense peripheral mesh of its discoidal ancora in oblique view; N – PŠ 3598, specimen showing dense, disc-shaped ancora in sub-lateral view. • I, J – *Hercograptus* cf. *introversus* Melchin, 1999: I – PŠ 3443, specimen showing delicate ancora and reduced thecal fusellum; J – PŠ 3629, complete specimen with ancora, partly preserved reticulum and reduced fusellum in sub-apertural parts of the thecae. • K, L – *Pseudorthograptus inopinatus* (Bouček, 1944): K – PŠ 3632b, complete specimen showing irregularly bifurcated paired apertural spines; L – PŠ 3431, biscalariform preservation of immature specimen with large bowl-shaped ancora umbrella. • O, P – *Pseudorthograptus* cf. *physophora* (Nicholson, 1868a): O – PŠ 3595b, juvenile specimen with partly preserved ancora; P – PŠ 3627, four branched ancora umbrella exhibits delicate concentric (spiralling) connecting lists. • T, CC – *Petalolithus ovatoelongatus* (Kurck, 1882): T – PŠ 3602, juvenile specimen with tiny ancora and incompletely developed thecae of 1st and 2nd pair; CC – PŠ 3514. • U, V – *Glyptograptus* sp. B: U – PŠ 3496, V – PŠ 3533. • W, X – *Glyptograptus* sp. A: W – PŠ 3445, aseptate specimen with protracted proximal end and strongly geniculate thecae; X – PŠ 3440. • Y, HH – *Glyptograptus perneri* sp. nov.: Y – PŠ 3624, holotype; HH – PŠ 3508. • EE–GG – *Dimorphograptus confertus* (Nicholson, 1868b): EE – PŠ 3482, incomplete mature specimen; FF – PŠ 3476, juvenile specimen with partly developed initial theca of the second thecal series and flexed virgella; GG – PŠ 3577, specimen showing ?partial septum in the distal part. A, B, D–G, I, J, M, Q–S, Z–BB, DD from the *cyphus* Biozone; C, H, K, L, N, T, Y, CC, HH from the lower *triangulatus* Biozone; O, P, W, X from the lower part of the *cyphus* Biozone; U, V, EE–GG from the upper *vesiculosus* Biozone. All figures × 6; scale bar represents 1 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
AA
BB
CC
DD
EE
FF
GG
HH

1974 *Orthograptus obuti* sp. nov.; Rickards & Koren', p. 199, pl. 1, figs a–c; text-figs 6–9, *non* 10–12.
1982 *Orthograptus obuti* Rickards & Koren'. – Howe, pl. 1, figs d, e.
1985 *Orthograptus obuti* Rickards & Koren'. – Štorch, pp. 92–93, pl. 3, figs 1, 2, 4, 5; pl. 4, fig. 6; text-fig. 2h–j.
1987 *Orthograptus obuti* (?) Rickards & Koren'. – Bates & Kirk, p. 92, fig. 6c.
1996 *Pseudorthograptus* (*Pseudorthograptus*) *obuti* (Rickards & Koren'). – Koren' & Rickards, pp. 72, 75; pl. 11, figs 3–9; text-fig. 15a–j.

Material. – 38 rhabdosomes ranging from juvenile specimens with a single thecal pair to large mature specimens plus several siculae with early growth stages of the ancora structures.

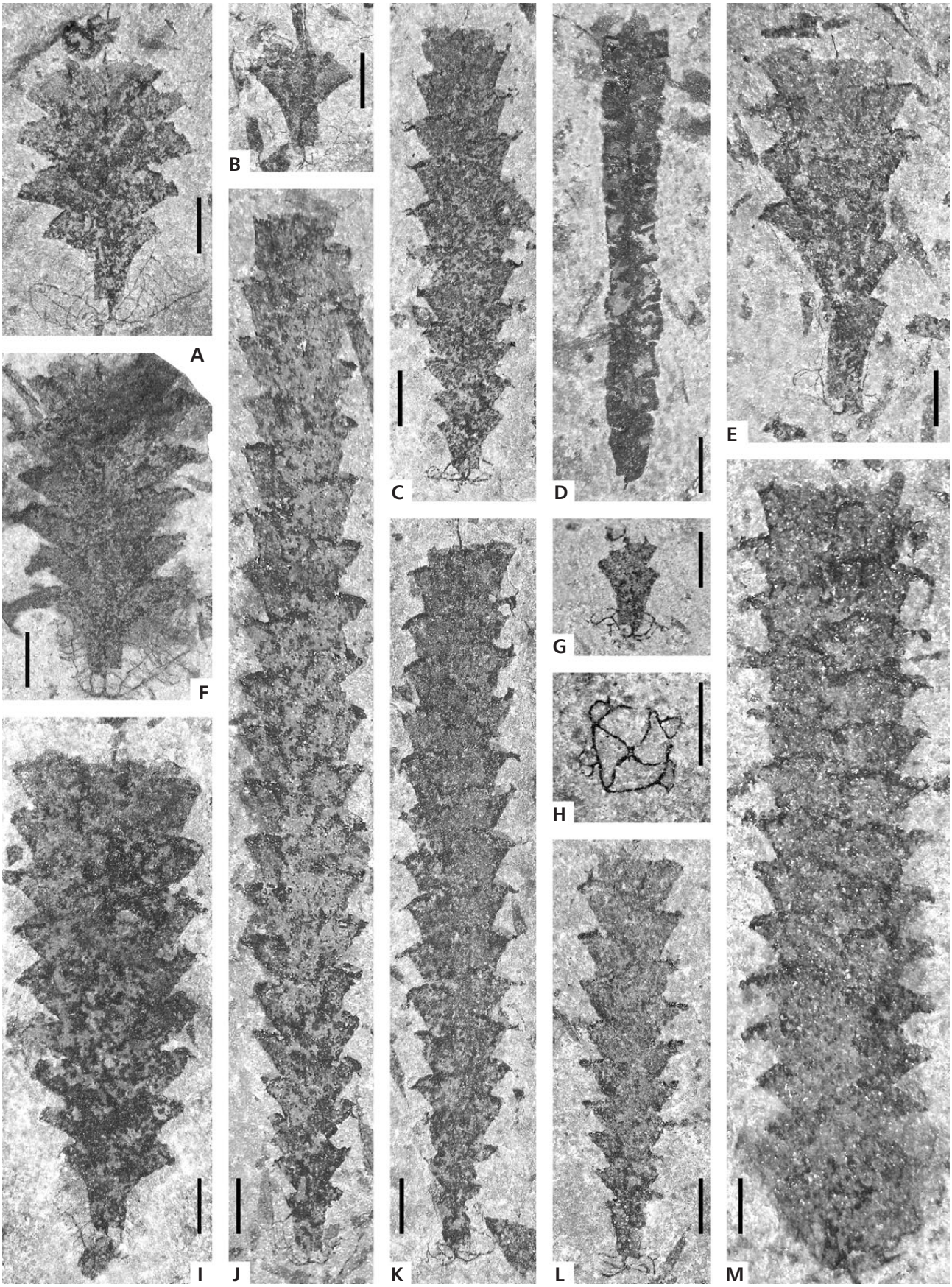
Description. – Large, up to 4.25 mm wide and about 80 mm long rhabdosome furnished with an ancora and complex ancora umbrella with membrane. The sicula is 2.0–2.2 mm long, 0.26–0.3 mm wide at the aperture, with its apex attaining the level of the apertures of th2^1–2^2. Virgella forked 0.2–0.45 mm below the sicula aperture into four radial lists of ancora. Bowl-shaped ancora umbrella is formed by the four, long principal radial lists interconnected by rather irregular and delicate, seemingly concentric lists (flat-spiral according to Bates & Kirk 1992) which are roughly horizontal in profile view. The initial ancora umbrella, 1.7–1.8 mm in diameter, is developed early in astogeny on a metasicula without any thecae. Th1^1 grows down the sicular aperture before turning and growing upwards and outwards for 1.45–1.9 mm. Th1^2 buds from th1^1 before its turning point and crosses the sicula at an angle of 35° leaving a 0.4–0.7 mm length of sicular dorsal wall exposed. Th1^1 and 1^2 are both ventrally curved. The ancora umbrella includes a large, 6-12 mm wide, probably broadly funnel-shaped membrane which enclosed the proximal part of mature, at least 13 mm long rhabdosomes. Conversely some rhabdosomes, up to 18 mm long, possess just an ancora umbrella, without any membrane. The membrane of mature rhabdosomes extends to the level of the third to sixth thecal pair and attains still higher level laterally.

The thecae are relatively broad straight tubes overlapping for less than half their length in the proximal part of the rhabdosome and for more than half distally. Thecal apertures are everted and typically ventrally flaring with slight lateral cusps. The thickened apertural lip extends in a short, blunt forked process (Figs 7DD, 8M) developed and/or seen only in some mature specimens. The rhabdosome width varies with respect to profile or subscalariform flattening and degree of ventral apertural extension. If measured without apertural processes the rhabdosome widens from 1.8–2.6 mm at th1^1–1^2 apertures, through 2.5–3.4 mm at 3rd thecal pair and 3.0–3.7 mm at the fifth thecal pair, to the maximum of 3.4–4.25 mm which is attained by the eighth to fourteenth thecal pair and maintained in distal parts of long rhabdosomes. Proximal thecae number 10–10.5 in 10 mm; distal thecae are widely spaced, numbering 7–8 in 10 mm. The 2TRD increases gradually from 1.4–1.8 mm at th2 to 1.8–2.0 mm at th5, 2.0–2.2 mm at th10, and 2.4–2.7 mm distally in long, 3.7–4.25 mm wide rhabdosomes.

Remarks. – The present specimens match the type material of *Ps. obuti* illustrated by Rickards & Koren' (1974) as well as subsequent collections studied by Koren' & Rickards (1996) except for having a greater dorso-ventral width. This difference can be ascribed to different preservation combined with the presence of long, late mature specimens in the Czech material. The flaring thecal apertures with apertural processes make the width measurements difficult and rather subjective. Other details such as sicula, ancora umbrella, thecal apertures and spacing match well the type material from the Urals. *Pseudorthograptus mutabilis* (Elles & Wood, 1907) differs from the closely similar *Ps. obuti* in having rapid widening of its generally fusiform rhabdosome, longer, more greatly overlapping and steeply inclined thecae and in the lack of divided blunt apertural processes. Also the ancora and proximal membrane, not found by Elles & Wood (1907) and described for the first time by Koren' & Rickards (1996), may be less developed in *Ps. mutabilis*.

Pseudorthograptus obuti with its long, ventrally curved thecae, flaring and slightly cuspate thecal apertures and a deep, bowl-shaped ancora umbrella with prominent

Figure 8. A, B, F, I, M – *Pseudorthograptus obuti* (Rickards & Koren', 1974): A – PŠ 3585a, specimen with laterally flattened umbrella-shaped immature ancora and sicula pressed through; B – PŠ 3492, ancora exhibits four radial branches connected by slender connecting rods; F – PŠ 3450, juvenile specimen showing complete sicula and early ancora development; I – PŠ 3448; M – PŠ 3619, relatively mature specimen with ancora membrane and thecal apertures with bifurcated ventral processes. • C, G, H, J–L – *Pseudorthograptus mitchelli* sp. nov.: C – PŠ 3497, specimen showing lateral view of "steering-wheel" structure of the ancora and bifurcated ventral apertural processes; G – PŠ 3481, juvenile rhabdosome showing first thecal pair with even aperures and ancora in lateral view; H – PŠ 3491, top view of juvenile ancora; J – PŠ 3439, mature specimen with bowl-shaped ancora; K – PŠ 3450, holotype, specimen exhibits thecal apertures with bifurcated processes. • D – *Metaclimacograptus* cf. *hughesi* (Nicholson): PŠ 3642. • E – *Pseudorthograptus* cf. *physophora* (Nicholson, 1868a): PŠ 3595b, juvenile specimen with partly preserved ancora. All specimens from the *cyphus* Biozone. All figures × 10, except for H × 15; scale bars represent 1 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M

primary radial lists and subordinate but dense irregular concentric (?spiralled) secondary lists qualifies as a prime candidate as precursor of the earliest *Petalolithus*. Also the stratigraphical superposition of the lowest occurrence of *Petalolithus ovetoelongatus* (Kurck) immediately above the highest *Ps. obuti* in the lowermost *triangulatus* Biozone in the Hlásná Třebaň section suggests this ancestry which apparently lies in pseudorthograptids with long, greatly overlapping, ventrally curved proximal thecae, and ancora having long primary radial lists and subordinate connecting lists.

***Pseudorthograptus mitchelli* sp. nov.**
Figures 7A, D–F, Q, R, AA, 8C, G, H, J–L, 9B

Holotype. – Specimen No. PŠ3450 (Figs 7R, 8K); from the *Coronograptus cyphus* Biozone at Všeradice, Želkovice Formation, Prague Synform, Czech Republic.

Derivation of name. – After Charles E. Mitchell, American palaeontologist – founder of the modern systematic approach to biserial graptolites.

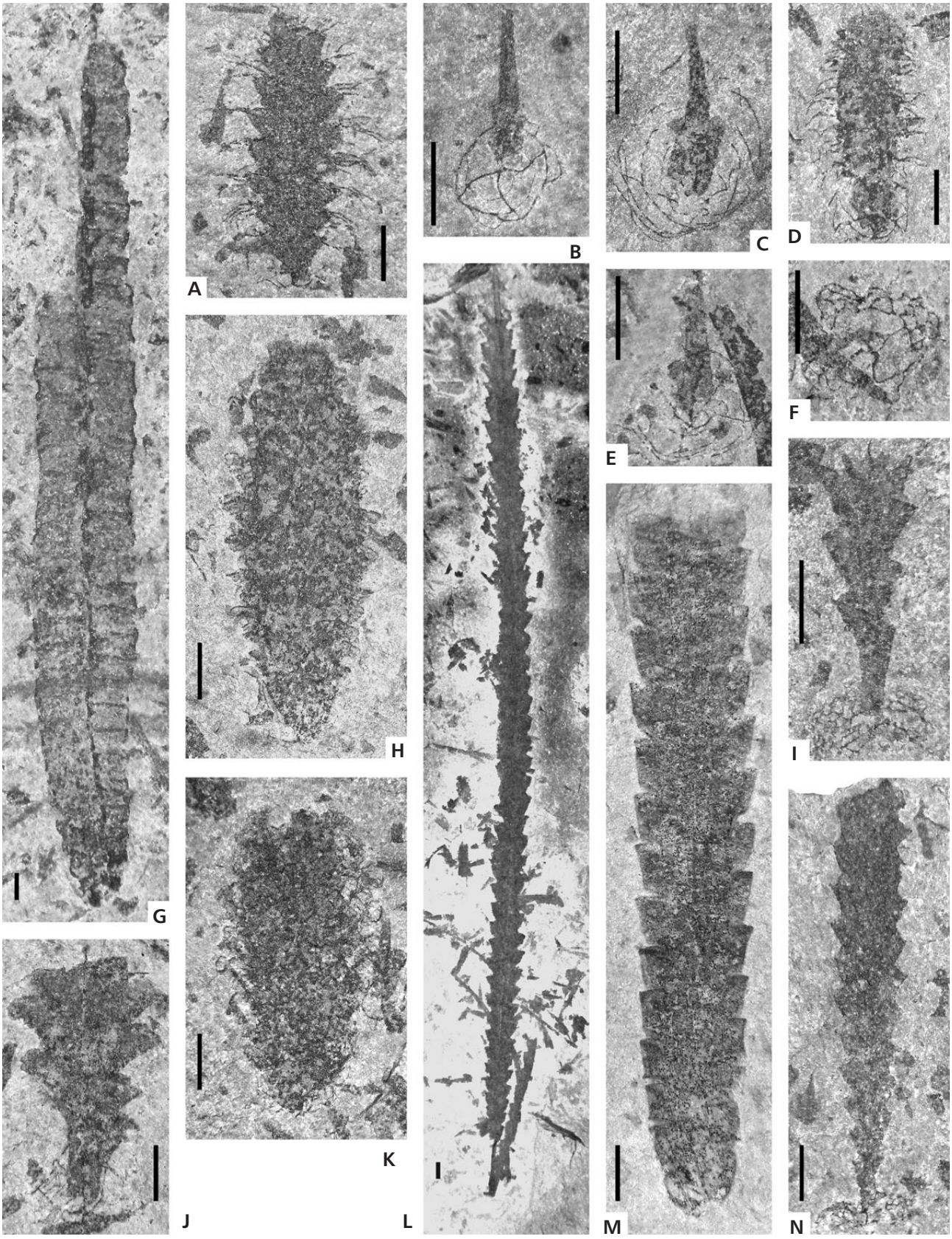
Material. – About 50 mature rhabdosomes along with many juvenile specimens and siculae with typical ancorae.

Diagnosis. – Medium-sized pseudorthograpid with maximum width of 1.9–2.4 mm. Moderately outwardly inclined thecae with slightly everted apertures, weakly cuspate and flaring outwards in profile view. Thickened thecal apertural lips with short and blunt ventral processes developed beginning at the second thecal pair. Horizontal disc-shaped ancora umbrella composed of four radial branches interconnected by concentric circular list with additional loops on its perimeter.

Description. – Aseptate rhabdosome with maximum length of about 20 mm widens from 1.0–1.2 mm at the apertures of the first thecal pair, through 1.4–1.75 mm at the third thecal pair and 1.7–2.0 mm at the fifth thecal pair to the maximum width of 1.9–2.4 mm attained by the fifth to tenth (commonly eighth) thecal pair. The apex of the 1.7–1.8 mm-long sicula attains about the level of the aperture of th2^2. The sicula is exposed for 0.5 mm on the dorsal side and is furnished with a short virgella which bifurcated twice giving origin to the four primary radial branches of the ancora. The simple ancora umbrella composed of four radial branches interconnected by a concentric circular thread (umbrella rim *sensu* Bates & Kirk 1992) is already present in siculae, before the origin of th1^1. The ancora umbrella closely resembles a tiny steering wheel *ca* 1.0 mm in diameter in top view. Further ancora growth resulted in loops originating from the main circular list. The horizontal, disc- or bowl-shaped ancora umbrella is slightly more complex in mature rhabdosomes, attaining 1.2–1.3 mm in diameter. Th1^1 grows downwards, 0.1 mm below the sicular aperture before it turns upwards and outwards; the ascending part is 0.9–1.1 mm long. Thecae are relatively short, overlapping for half their length; they are inclined at 21–36° to the rhabdosome axis. The apertures of th1^1 and th1^2 are approximately perpendicular to the ventral thecal walls. The apertures of the succeeding thecae become somewhat everted in appearance, slightly cuspate and flaring outwards in profile view. Short ventral apertural processes can be observed beginning at the second thecal pair. 2TRD increases from 1.25–1.5 at th2, through 1.45–1.7 mm at th5 to 1.6–2.2 mm measured in the distal parts of mature rhabdosomes.

Remarks. – *Pseudorthograptus mitchelli* sp. nov. is common in the lower and middle part of the *cyphus* Biozone. The species has been found, although rarely, as high as in the lower(?most) *triangulatus* Biozone. The specimens are very distinctive. The maximum width of 1.9–2.4 mm is about mid-way between the wide rhabdosomes of *Ps. mutabilis* (Elles & Wood, 1907) and *Ps. obuti*, and the minute rhabdosomes of the wedge-shaped *Ps. finneyi* Štorch & Kraft, 2009 and spinose *Ps. insectiformis* (Nicholson, 1869) and *Ps. inopinatus* (Bouček, 1944), both with densely set

Figure 9. A, D – *Pseudorthograptus inopinatus* (Bouček, 1944): A – PŠ 3632b; D – PŠ 3431, biscalariform preservation of immature specimen with large bowl-shaped ancora. • B – *Pseudorthograptus mitchelli* sp. nov.: PŠ 3507, sicula with ring-like ancora umbrella with loops on perimeter and secondary concentric lists. • C, E – *Pseudorthograptus obuti* (Rickards & Koren', 1974): C – PŠ 3635, sicula with incomplete th1^1, budding th1^2 and basket-like ancora structure dominated by spiralling concentric lists; E – PŠ 3518, sicula with incomplete th1^1 and large delicate ancora. • F, I, N – *Pseudorthograptus finneyi* Štorch & Kraft, 2009: F – PŠ 3513, top view of juvenile ancora with dense mesh of loops on perimeter of the primary "steering-wheel" structure; I – PŠ 3641, juvenile specimen with protracted proximal end and dense peripheral mesh of its discoidal ancora in oblique view; N – PŠ 3598, specimen showing dense, disc-shaped ancora in lateral view. • G – *Cystograptus vesiculosus* (Nicholson, 1868a): PŠ 3621b. • H, K – *Hercograptus* cf. *introversus* Melchin, 1999: H – PŠ 3443, complete specimen with delicate ancora and reduced thecal fusellum; K – PŠ 3629, complete specimen with ancora, partly preserved reticulum and reduced fusellum in sub-apertural parts of the thecae. • J – *Pseudorthograptus* cf. *physophora* (Nicholson, 1868a): PŠ 3627, juvenile specimen with partly preserved ancora umbrella. • L – *Korenograptus nikolayevi* (Obut, 1965): PŠ 3588a, large specimen with robust virgella and extended nema. • M – *Normalograptus frydai* sp. nov.: PŠ 3644. A, D, F, I, N from the lower *triangulatus* Biozone; B, C, E, H, J–M from the *cyphus* Biozone; G from the upper *vesiculosus* Biozone; M from the lower *cyphus* Biozone of the Běleč section. Figures A, D, H, J, K, M, N × 10; B, C, E, F, I × 15; G × 5; L × 3; scale bars represent 1 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M
N

thecae. The thecal apertures of *Ps. mitchelli* exhibit thickened lips and short processes closely resembling the blunt, bifurcated ventral apertural processes of *Ps. obuti*.

Ps. mitchelli can be distinguished from other pseudorthograptids even in its early growth stages. The ancora developed in siculae with budding th1[1] forms four, relatively robust radial branches connected by an equally robust circular list to make an ancora umbrella structure similar to a steering wheel, later in early astogeny supplemented by peripheral loops. The similar ancora was developed in the spinose *Ps. insectiformis* (see Bates & Kirk 1984, 1992, figs 1–28 for detail) and *Ps. inopinatus*. *Ps. obuti*, and probably also *Ps. mutabilis* and *Ps.*? *physophora* (Nicholson, 1868a), developed a basket-shaped ancora umbrella with long radial lists and relatively slender and multiple ?spiral connecting rods. All of the structure is covered by a membrane, in later astogeny enveloping the entire proximal end of the rhabdosome to the level of several proximal thecae. Conversely, no membranous tissue has been seen covering the ancora umbrella and proximal end of the rhabdosome developed in the present rich material of *Ps. mitchelli*. *Ps. finneyi* possesses a similar, flat, disc-shaped ancora umbrella with a dense mesh of loops at the periphery of the "steering-wheel" structure, but all is covered by a membrane in mature specimens.

***Pseudorthograptus inopinatus* (Bouček, 1944)**
Figures 7K, L, 9A, D

1944 *Orthograptus* (?) *inopinatus* n. sp.; Bouček, p. 2, pl. 1, fig. 8; text-fig. 1b, c.
1971 *Orthograptus* (?) *inopinatus* Bouček. – Schauer, p. 37, pl. 7, fig. 14.
1985 *Orthograptus inopinatus* Bouček. – Štorch, p. 91, pl. 1, figs 6–9; pl. 2, fig. 3; text-fig. 2a–e, k.
1996 *Pseudorthograptus inopinatus* (Bouček). – Koren' & Rickards, pp. 69, 71; pl. 11, fig. 10; text-figs 16b–f, 17.
non 2000 *Pseudorthograptus* (*P.*) *inopinatus* (Bouček). – Rickards *et al*., p. 113, text-figs 4k, l, 5a, b.

Material. – Four flattened specimens, including one in nearly scalariform view; further material examined from the Hlásná Třebaň section.

Remarks. – The few rhabdosomes of *Pseudorthograptus inopinatus* from the *triangulatus* Biozone of Všeradice are well supplemented by rich collections made in the *triangulatus* and *pectinatus* biozones of the Hlásná Třebaň section. The small aseptate rhabdosome is characterized by its short, closely set, simply tubular thecae furnished with paired and bifurcating apertural spines. Both the latero-ventral position and proximally directed curvature of the spines are illustrated by an immature specimen preserved in sub-scalariform view (Figs 7L, 9D). The upward growing part of th1[1] is 0.95 mm long. The *ca* 0.2 mm wide sicular aperture possesses a short virgella divided most probably into four principal radial branches of the ancora interconnected by several threads. The bowl-shaped ancora umbrella is structurally similar to that of *Pseudorthograptus obuti* but much smaller, only 1 mm in diameter. The rhabdosome is 1.0–1.25 mm wide at the apertures of the first thecal pair and 1.7 mm wide distally (without spines). The 2TRD of 1.25 mm corresponds with 8 thecae in the first 5 mm of the rhabdosome. The present material, although very limited, supplements well the description of topotypical material by Štorch (1988). New observations by Koren' & Rickards (1996) based, in part, on a chemically isolated specimen from Arctic Canada confirmed also the presence of rare spines on the lateral wall of the rhabdosome. The Iranian specimens described by Rickards *et al*. (2000) match *Ps. insectiformis* (Nicholson) in all respects except for the reported bifurcation of the apertural spines which, unfortunately, is not well demonstrated by the figured specimens.

***Pseudorthograptus finneyi* Štorch & Kraft, 2009**
Figures 7C, H, N, 9F, I, N

1985 *Orthograptus cyperoides* Törnquist. – Štorch, p. 90, pl. 1, figs 1–4; text-fig. 2f, g.
2009 *Pseudorthograptus finneyi* sp. nov.; Štorch & Kraft, figs 6n, o, 12a, b.

Material. – Four mature rhabdosomes with preserved ancorae and two juvenile specimens. Rich supplementary material is available from the Hlásná Třebaň and Karlík sections.

Remarks. – The present specimens match well the type material described by Štorch & Kraft (2009). *Ps. finneyi* occurs only in the lower *triangulatus* Biozone in both the Prague Synform and Hlinsko area of the Bohemian Massif. The species can be differentiated from other pseudorthograptids by its minute, wedge-shaped rhabdosome widening from *ca* 0.6 mm at the first thecal pair to the maximum of 1.4–1.5 mm attained by the 6th or 7th thecal pair. Thecae are short, straight tubes, inclined at a markedly low angle (25°), and ending in perpendicular or slightly everted apertures without any spines or processes. The 2TRD is 1.2–1.35 mm at th2, 1.35–1.4 mm at th5 and 1.45–1.5 mm distally which corresponds with 13–14 thecae in 10 mm. The small disc-like ancora umbrella is formed by a four-pronged ancora and circular connecting list (umbrella rim) that comprise a "steering-wheel" structure surrounded

by a rather irregular meshwork of multiple peripheral loops (Figs 7C, 9F). Membranous tissue covering the ancora umbrella, observed in many specimens from Karlík and Hlásná Třebaň, is barely seen in the single relatively mature specimen from Všeradice.

***Pseudorthograptus* cf. *physophora* (Nicholson, 1868a)**
Figures 7O, P, 8E, 9J

cf. 1868a *Diplograptus physophora* n. sp.; Nicholson, pp. 56, 61, pl. 3, fig. 7.
cf. 1908 *Dimorphograptus physophora* (Nicholson). – Elles & Wood, pp. 353–354, pl. 35, fig. 7a–d; text-fig. 231a, b.
? 1982 *Dimorphograptus* cf. *physophora* (Nicholson). – Lenz, p. 28, figs 3k, n; 15d, e.
cf. 1996 *Pseudorthograptus* (*Dimorphograptoides*) *physophora* (Nicholson). – Koren' & Rickards, pp. 85–86, pl. 12, figs 6, 7; text-fig. 19a–e (see for further synonymy).
cf. 2008 *Dimorphograptus*? *physophora* (Nicholson). – Štorch & Feist, p. 954, figs 7.18, 10.7.
2009 *Dimorphograptoides* aff. *physophora* (Nicholson). – Štorch & Kraft, p. 66, figs 6p, 8h.

Material. – Two juvenile rhabdosomes.

Remarks. – The rhabdosomes preserved in obverse view are composed of a short uniserial part comprising th1[1] and a rapidly widening biserial part with five thecal pairs. The prominent sicula is 0.35 mm wide at the aperture; the dorsal wall of the sicula is free for 1.25–1.55 mm of its length. The virgella divides 0.22 mm below the sicular aperture, with both branches bifurcating again into delicate, ventrally and upward directed threads interconnected by tiny connecting rods. This structure can be interpreted as the early development of a disc- or bowl-shaped ancora umbrella which would be subsequently covered by a membrane as recorded in mature specimens by Hutt (1974a), Koren' & Rickards (1996) and Štorch & Feist (2008). The thecae are simply tubular with the aperture slightly everted and extended ventrally in a similar fashion to the thecae of *Dimorphograptus confertus* (Nicholson) or *Pseudorthograptus obuti* (Rickards & Koren'). The uniserial th1[1] is 1.25–1.35 mm long. The much longer th1[2] (2.55 mm) probably buds from th2[1] (as suggested by Elles & Wood 1908), 0.95 mm above the sicular aperture. The aperture of th1[2] reaches almost to the level of the aperture of th3[1]. Thecal overlap increases from one-third at th2[1] to two-thirds at th5[1]. Rhabdosome widens from 0.95–1.1 mm at th1[1], through 2.0–2.65 mm at the apertures of the first paired thecae, to 2.55–3.25 mm at the third thecal pair. 2TRD is 1.7–2.1 mm at th2 and decreases to about 1.8 mm in subsequent thecae. A median septum has not been detected in the present juvenile specimens. The two rhabdosomes are closely similar to *Pseudorthograptus physophora* (Nicholson) from which they can be differentiated solely by their markedly more robust, at least 2.55–3.25 mm wide rhabdosome which is diagenetically flattened but not affected by tectonic strain. This rare form occurs together with typical graptolites of the lower *cyphus* Biozone in Všeradice whereas the single specimen from the Mrákotín Formation of the Hlinsko area (Štorch & Kraft 2009) came probably from the *vesiculosus* Biozone level.

Genus *Hercograptus* Melchin, 1999

Type species. – *Hercograptus introversus* Melchin, 1999; by original designation; from NE Cornwallis Island, Arctic Canada.

***Hercograptus* cf. *introversus* Melchin, 1999**
Figures 7I, J, 9H, K

cf. 1999 *Hercograptus introversus* n. sp.; Melchin, pp. 265–267, figs 1a–e, 2a–h, 3a–e.

Material. – Two complete rhabdosomes with ancora and partly preserved primitive ancora sleeve.

Description. – The rhabdosome is generally ellipsoidal in outline and is up to 6.8 mm long. The proximal end is sub-rounded triangular and slightly asymmetrical. The sicula is covered except for its aperture. The virgella divides only 0.1–0.15 mm below the upward bend of th1[1] into delicate branches growing upwards along the ventral walls of the first thecal pair. The upward growing portion of th1[1] is 1.3–1.35 mm long. The rhabdosome is aseptate, probably flat oval in cross section, 1.8–1.9 mm wide at the apertures of the first thecal pair. Thereafter it widens rapidly to 2.15–2.4 mm at the second thecal pair and 2.6–2.7 mm at the third thecal pair. The maximum width of 2.9 mm is attained at the 5th thecal pair and the rhabdosome then narrows towards the distal end. Thecae are relatively broad, steeply inclined and densely spaced, with 2TRD 2 1.45–1.55 mm and 2TRD 5 1.35–1.4 mm. Thecal apertures are broad and probably slightly introverted. Thecal geniculation has not been observed. The fusellum is reduced, in particular near thecal apertures, leaving prominent thickenings of fusellar outlines similar to those observed in some petalolithids. The dense framework of sub-apertural lateral lists is connected by a thick ventral list. The laterally projecting apertural lists of the thecae are incorporated into a rather irregular meshwork, probably homologous with the retiolitid ancora sleeve (see also Melchin 1999) connecting the basket-like ancora with the thecal apertures. In on

specimen the meshwork is confined to two proximal thecal pairs (Figs 7I, 9H) whereas in the other specimen it extends farther onto the distal part of the rhabdosome (Figs 7J, 9K).

Discussion. – The two complete specimens from the *cyphus* Biozone of Všeradice exhibit most of the features diagnostic of *Hercograptus* Melchin, 1999, in particular the sub-rounded triangular asymmetrical proximal end, largely covered sicula, relatively broad thecae with reduced fusellum and thickened fusellar outlines in their laterally extended sub-apertural part, the ancora enveloping the proximal end and primitive ancora sleeve that connected the ancora with the thecal apertures. The flat cross-section can be inferred from the mode of flattening. The limited material found in Všeradice is only tentatively assigned to *Hercograptus introversus* Melchin, 1899, a bizarre form from the *cyphus* Biozone of Arctic Canada that shows a possible path to the early retiolitids, although the rhabdosome and thecal form are both still shared with petalolithids. Preservation of the Czech specimens does not allow for recognition of some details of lateral apertural lappets and construction of the ancora and ancora sleeve observed in the chemically isolated type material of *He. introversus*. The thecae of the two specimens from Všeradice are closely similar to those of *Corbograptus enigmatica* Koren' & Rickards, 1996 except for not having the thecal geniculation claimed for the latter species. To date knowledge of the early astogeny and general morphology of the monospecific genus *Corbograptus*, based upon a single small and incomplete specimen (Koren' & Rickards 1996, pl. 12, fig. 8 and text-fig 20I) is very limited and does not allow for confident assessment of the relationship between *Hercograptus* and *Corbograptus*. It is notable from an evolutionary point of view, that all the three possible morphological transients to the Retiolitinae Lapworth, 1873: the Czech material, *Cb. enigmatica* and *He. introversus* appeared in the late Rhuddanian *cyphus* Zone when they could have been derived from *Pseudorthograptus* shortly before *Petalolithus* derived from the same ancestral group in the earliest *triangulatus* Zone.

Genus *Petalolithus* Suess, 1851

Type species. – *Prionotus folium* Hisinger, 1837; subsequently designated by Lapworth (1873); from the Llandovery of Sweden.

Petalolithus ovatoelongatus (Kurck, 1882)

Figures 6C, G, H, 7T, CC

1882 *Cephalograptus ovato-elongatus* n. sp.; Kurck, p. 303, pl. 14, fig. 10.

partim 1908 *Petalograptus palmeus* var. *ovato-elongatus* (Kurck). – Elles & Wood, p. 277, pl. 32, fig. 4a (*non* b–d), ?text-fig. 191a–c.

1942 *Petalolithus ovato-elongatus* (Kurck). – Bouček & Přibyl, p. 2, pl. 1, figs 1, 2, text-fig. 1a–e.

1970 *Petalograptus ovatoelongatus* (Kurck). – Rickards, p. 47, pl. 3, fig. 6.

1971 *Petalolithus* (*Pet*.) *ovatoelongatus* (Kurck). – Schauer, pp. 40–41, pl. 8, figs 2–4; pl. 11, figs 2, 3.

1974a *Petalograptus ovatoelongatus* (Kurck). – Hutt, pp. 39–40, pl. 10, figs 2, 7–10.

1975 *Petalograptus ovatoelongatus* (Kurck). – Bjerreskov, pp. 32–33, pl. 4, fig. h.

1979 *Petalograptus ovatoelongatus* (Kurck). – Paškevičius, pp. 138–139, pl. 5, figs 12, 13; pl. 21, figs 16, 17.

1979 *Petalograptus parallelus* sp. n.; Paškevičius, pp. 139–141, pl. 5, fig. 15; pl. 22, figs 1, 2.

non 1996 *Petalolithus ovatoelongatus* (Kurck). – Koren' & Rickards, pp. 54, 56; pl. 9, figs 2, 4; text-figs 10i, j, 11d.

Material. – Four complete mature rhabdosomes, several incomplete rhabdosomes and one juvenile specimen. Additional material came from all other stratigraphically relevant localities in the Prague Synform.

Remarks. – The rhabdosome of this well-known *Petalolithus* is characterized by its elongated ovato-rectangular outline with a somewhat protracted proximal end and ventrally curved proximal thecae. The apical angle between the thecae of the first pair is about 85° in mature rhabdosomes. Th 1^1 is 2.1–2.2 mm long. The short virgella splits into lateral branches 0.2–0.25 mm below the sicular aperture to form a delicate ancora umbrella structure composed of four upward directed rods interconnected by barely recognizable ?subhorizontal lists. The width of mature, *ca* 10 mm long rhabdosomes increases from 3.0–3.5 mm at the apertures of the first thecal pair to 3.65–4.35 mm at the third thecal pair. The maximum width of 4.0–4.6 mm is attained at about the fifth thecal pair. Thereafter the rhabdosome width is either maintained or decreases towards the distal end. Distal narrowing is due to lesser thecal inclination rather than decrease in thecal length. Proximal thecae (except for the ventrally curved thl^1 and l^2 are inclined at about 50° to the rhabdosome axis; distal thecae are inclined at 35–45°).

Family Dimorphograptidae Elles & Wood, 1908

Genus *Dimorphograptus* Lapworth, 1876

Type species. – *Dimorphograptus elongatus* Lapworth, 1876; subsequently designated by Bassler (1915); from the Llandovery of Scotland.

***Dimorphograptus confertus* (Nicholson, 1868b)**
Figures 6D, F, I, 7EE–GG

1868b *Diplograpsus confertus*; Nicholson, p. 526, pl. 19, figs 14, 15.
1908 *Dimorphograptus confertus* (Nicholson). – Elles & Wood, p. 349, pl. 35, fig. 3a–d, text-fig. 227a, b.
1970 *Dimorphograptus confertus confertus* (Nicholson). – Rickards, p. 50, pl. 3, fig. 11.
1974a *Dimorphograptus confertus confertus* (Nicholson). – Hutt, pp. 50–51, pl. 8, figs 4, 7, 8; pl. 9, fig. 7; text-fig. 13, fig. 3.
1975 *Dimorphograptus confertus confertus* (Nicholson). – Bjerreskov, pp. 41–42, pl. 6, fig. a; text-fig. 13c.
2008 *Dimorphograptus confertus* (Nicholson). – Štorch & Feist, p. 953, figure 6.2.

Material. – 18 rhabdosomes, comprising both juvenile (uniserial) and mature specimens. Rich material has been collected also from Hlásná Třebaň, Zadní Třebaň, Běleč, Vočkov and Karlík.

Description. – The development of the robust, up to 35 mm long biserial rhabdosome commences with a dorsally curved uniserial part comprising 3–5 thecae. The sicula is 1.9–2.1 mm long, with its apex reaching just below or above the level of the aperture of th1. The sicula is 0.2–0.25 mm wide at the aperture which is furnished with an up to 0.8 mm long virgella, typically deflected obliquely across the sicula aperture. The thecae of the uniserial part are simple tubes, overlapping for one-quarter to one-third their length, with apertures perpendicular to the ventral thecal wall. Proximal thecae vary in both length, width and spacing. Th1 is 1.45–1.9 mm long. 2TRD generally decreases from 2.0–2.4 mm at th2 to 1.45–2.0 mm at th5. Uniserial part of the rhabdosome is 0.42–0.5 mm wide at th1 and 0.55–0.6 mm wide at th3. The biserial part is 1.8–2.2 mm wide at the level of the first thecal pair, and widens further through 2.2–2.6 mm at the 3rd thecal pair to the maximum of 3.0–3.3 mm attained by the 10th–12th thecal pair. Thecal spacing is the most dense at about th10 (2TRD 1.35–1.7 mm). Thecae are distinctly alternating in the biserial part but no median septum has been observed or mentioned in earlier descriptions of the species. Distal thecae numbering 10–12 in 10 mm (2TRD 1.6–2.1 mm) are inclined at 38–58° to the rhabdosome axis and overlap for just over half their length. Thecal apertures become slightly ventrally extended, everted (flaring) near the ventral margin, and are either horizontal as a whole or weakly cuspate. Apertural lips are thickened.

Remarks. – The uniserial part of the rhabdosome varies in length, thecal spacing and number of thecae involved. This variation does not exhibit any step allowing for recognition between typical *Dimorphograptus confertus* with 3 or 4 uniserial thecae and its supposed close relative *Dimorphograptus swanstoni* (Lapworth, 1876) which was differentiated for the most part by having 5 uniserial thecae. In the Všeradice material a specimen with 4 uniserial thecae was found on the same slab as one having 5 uniserial thecae. *D. swanstoni* can be differentiated from *D. confertus* primarily by its narrower biserial part and less overlapping thecae. All rhabdosomes from Všeradice and other localities of the Prague Synform can be assigned to *Dimorphograptus confertus* although Bouček (1953) reported also *Dimorphograptus swanstoni*, albeit without any description or illustration. His material came from localities and stratigraphic levels which yield specimens with 3, 4 and 5 proximal thecae according to present observations.

Family Monograptidae Lapworth, 1873

Genus *Atavograptus* Rickards, 1974

Type species. – *Monograptus atavus* Jones, 1909; by original designation; from the Llandovery of the Rheidol Gorge, Mid-Wales.

***Atavograptus atavus* (Jones, 1909)**
Figures 10M, N, 11D, G

1909 *Monograptus atavus* sp. nov.; Jones, p. 531, text-fig. 18a–d.
1911 *Monograptus atavus* Jones. – Elles & Wood (*pars*), p. 403, pl. 39, fig. 1a–d; text-fig. 270b–e (*non* a).
1975 *Atavograptus atavus* (Jones). – Hutt, pp. 62–63, pl. 11, fig. 1; pl. 12, figs 5, 9, 10.
1994 *Atavograptus atavus* (Jones). – Zalasiewicz & Tunnicliff, text-fig. 10a, b.
1997 *Atavograptus atavus* (Jones). – Koren' & Bjerreskov, figs 5a, b, 6a–f, 7a–d, f.

Material. – 15 immature rhabdosomes with siculae and a dozen incomplete, fragmentary specimens.

Description. – The rhabdosome is generally straight in the distal part and gently dorsally curved in the proximal part which comprises 12–22 thecae. Sicula conical, 1.2–1.8 mm long, 0.25 mm wide at the aperture, the apex attaining a level below the aperture of the 1.2–1.4 mm-long th1. Dorso-ventral width increases gradually from 0.25–0.3 mm at the aperture of th1, through 0.3–0.35 mm at th3, 0.35–0.4 mm at th5, and 0.42–0.45 mm at th10, to 0.45–0.55 mm (exceptionally 0.6 mm) at th20. Distally from this level the rhabdosome widens extremely slowly to 0.6–0.85 mm observed in more than 50 mm long distal

fragments from Všeradice. Thecae of pristiograptid type overlap for one-quarter of their length in the proximal part of the rhabdosome and for about half in the distal part. 2TRD is 2.15–2.4 mm at th2 and decreases to 1.9–2.2 mm at th5 and th10. Distal fragments exhibit 2TRDs of 1.9–2.4 mm. The ventral thecal wall is straight and the geniculum negligible, if recognized at all. Thecal apertures are straight and perpendicular to the thecal axis in proximal thecae, becoming slightly everted in distal thecae. The apertures occupy half the rhabdosome width.

Remarks. – The Všeradice material collected from the upper *vesiculosus* and lower *cyphus* biozones is represented mostly by immature specimens. The rhabdosome form, dimensions, sicula, thecal spacing and shape, except for the flowing, almost negligible geniculation, match *Atavograptus atavus* (Jones). However, considerable variation in thecal geniculation has been discussed previously by Elles & Wood (1911) and Zalasiewicz & Tunnicliff (1994). *Huttagraptus strachani* (Hutt & Rickards, 1970) and *H. praestrachani* Hutt & Rickards (*in* Rickards *et al*., 1977) can be differentiated by having a longer sicula and apertural excavations and genicular rims or flanges which are missing in *Atavograptus*.

***Atavograptus*? *pristinus* (Hutt, 1975)**
Figures 10F, S, T, 13D, E

1975 *Pristiograptus fragilis pristinus* subsp. nov., Hutt, p. 60, text-fig. 14, figs 8, 9.
1997 "*Pristiograptus*" *pristinus* Hutt, 1975. – Koren' & Bjerreskov, pp. 28, 30; figs 5c, 13a–d, 19.

Material. – *Ca* 100 more or less fragmentary rhabdosomes, usually clustered on certain bedding planes.

Description. – Rhabdosome extremely slender, with slight and variable flexure. Sicula and most proximal thecae not found. Maximum length of available fragments does not exceed 30 mm. The thecae are simple tubes with little overlap, widening from prothecal minimum of 0.05 mm to the maximum of 0.18–0.25 mm attained at the level of significantly everted, commonly flaring aperture. Thecal apertures may be sligthtly isolated; some specimens exhibit a structure resembling a thickened ventral apertural lip. The ventral thecal wall is straight, inclined at an angle of *ca* 3° to the rhabdosome axis. The 2TRD varies between 2.7 mm and 3.15 mm (the thecae number 6.5 in 10 mm on average).

Remarks. – This species is abundant in the upper *vesiculosus* Biozone, fragmented and usually densely clustered on bedding planes in association with less abundant *Huttagraptus billegravensis* and juvenile *Cystograptus vesiculosus*. Less common finds are from the lower part of the *cyphus* Biozone. The species does not have the simple, overlapping tubular thecae with even apertures typical of *Pristiograptus*. Its tentative reassignment to *Atavograptus* is prefered herein although better understanding of the distinctive thecal apertures may lead to the future recognition of a new genus.

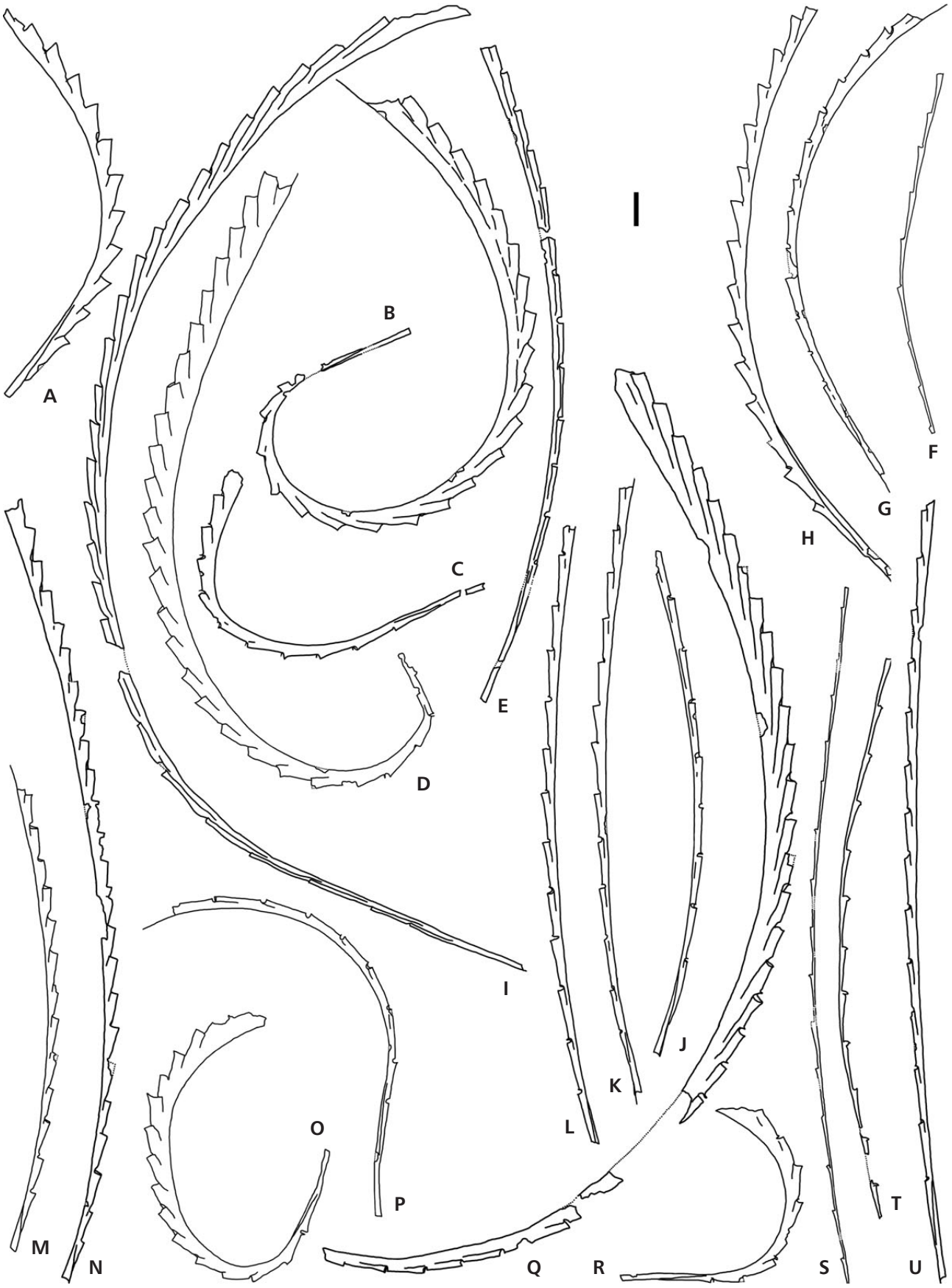
Genus *Huttagraptus* Koren' & Bjerreskov, 1997

Type species. – *Atavograptus praestrachani* Hutt & Rickards *in* Rickards *et al*. (1977); by original designation; from the Llandovery of Keisley, England.

***Huttagraptus acinaces* (Törnquist, 1899)**
Figures 10E, I, Q, 13H, I

1899 *Monograptus acinaces* n. sp.; Törnquist, p. 5, pl. 1, figs 7, 8.
1909 *Monograptus rheidolensis* sp. nov.; Jones, p. 535, text-fig. 19a–c.
1911 *Monograptus acinaces* Törnquist. – Elles & Wood, p. 364, pl. 36, fig. 2a–d; text-fig. 237a–d.

Figure 10. A, H – *Coronograptus gregarius* (Lapworth, 1876): A – PŠ 3516; H – PŠ 3610. • B–D, O, R – *Coronograptus cyphus* (Lapworth, 1876) *sensu* Elles & Wood (1911): B – PŠ 3580, typical specimen with partly damaged straight part of the proximal end; C – PŠ 3637, proximal thecae of the immature specimen exhibit tiny genicular flanges; D – PŠ 3523, O – PŠ 3459, typically curved proximal part with incompletely preserved sicula and thecae furnished with genicular flanges; R – PŠ 3459, another specimen from the same slab exhibits genicular flanges and complete, straight sicula. • E, I, Q – *Huttagraptus acinaces* (Törnquist, 1899): E – PŠ 3576, gently dorsally curved proximal part with greatly overlapping thecae; I – PŠ 3601, typical specimen with slender, greatly overlapping thecae; Q – PŠ 3587, mesial part of the rhabdosome showing transition from strongly geniculated thecae with minute genicular flanges to simple tubular thecae. • F, S, T – *Atavograptus*? *pristinus* (Hutt, 1975): F – PŠ 3553, one of several fragmentary rhabdosomes densely clustered on bedding plane; S – PŠ 3486, extremely slender rhabdosome yet without proximal end; T – PŠ 3613 exhibits extremely short metathecae with tendency to isolation and possible ventro-lateral lobes. • G – *Huttagraptus* cf. *lunata* (Chen & Lin, 1978): PŠ 3608. • J–L, U – *Huttagraptus billegravensis* Koren' & Bjerreskov, 1997: J – PŠ 3539, note large sicula and thecae with sharp geniculum highlighted by genicular flange; K, L – PŠ 3564, specimens showing little thecal overlap and genicular flanges; U – PŠ 3578. • M, N – *Atavograptus atavus* (Jones, 1909): M – PŠ 3521, dorsally curved immature rhabdosome; N – PŠ 3471. • P – *Coronograptus cirrus* Hutt, 1975?: PŠ 3593, note long, gently ventrally curved sicula and sharply geniculated thecae. A, H from the lower *triangulatus* Biozone; B–D, M, N, O, R, T from the *cyphus* Biozone; E, P, Q from the lower *cyphus* Biozone; F, G, I–L, S, U from the upper *vesiculosus* Zone. All figures × 6; scale bar represents 1 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U

1975 *Monograptus acinaces* Törnquist. – Bjerreskov, pp. 45–46, pl. 6, fig. I; text-fig. 14c.
1975 *Lagarograptus acinaces* (Törnquist). – Hutt, p. 69, pl. 13, figs 5, 6; text-fig. 16, figs 1–3 (see for further synonymy).
1997 *Huttagraptus acinaces* (Törnquist). – Koren' & Bjerreskov, pp. 18, 20, figs 5d–f, 11a–t, 12a–i, ?1a–c; 13b, e–g.
2011 *Huttagraptus acinaces* (Törnquist). – Zalasiewicz *et al*., fig. 3a–d.

Material. – 18 more or less complete rhabdosomes and a dozen proximal and distal fragments. Additional material studied is from the Běleč and Hlásná Třebaň sections.

Description. – The rhabdosome is dorsally arcuate throughout its length. The proximal part is long and slender, the mesial part markedly widening, with slightly accentuated dorsal curvature before the less curved, robust distal part. The sicula is straight, 4.6–5.1 mm long, slender (0.15 mm) and apparently fragile, since the apertural part is probably broken off in the few preserved proximal ends. The sicular apex reaches above the aperture of the *ca* 2.5 mm long th1. Proximal thecae are slender, more or less strongly geniculated tubes with straight apertures perpendicular to the ventral thecal wall which is inclined at an angle of 2–3° to the rhabdosome axis. In some specimens the thecal geniculum is accentuated by a small genicular flange. The flange is responsible for the prominent apertural excavation in profile view, which occupies almost half the rhabdosome width. Geniculated thecae with distinct flanges extend well into the mesial part of the rhabdosome. Distal thecae are long, straight tubes without significant genicula, overlapping for two-thirds their length. The straight ventral thecal wall inclined at 10° to the rhabdosome axis terminates at a straight, perpendicular to slightly everted aperture. Thecae number 8.5–9 in 10 mm proximally and 8.5–10 in 10 mm distally (2TRD 10: 2.0–2.3 mm, 2TRD dist.: 1.95–2.3 mm). Rhabdosome widens from 0.25 mm at the level of th1–th2 and *ca* 0.4 mm at th5 to 0.5–0.6 mm at th10. A maximum width of 1.0–1.2 mm was attained in the distal part of the rhabdosome.

Remarks. – Dorsally curved huttagraptid rhabdosomes with a particularly long sicula and greatly overlapping thecae have been assigned to *Huttagraptus acinaces* (Törnquist) despite the considerable variation in thecal spacing recorded for this species. For example, Koren' & Bjerreskov (1997) recorded 4–5 thecae/10 mm proximally and 6–7 thecae/10 mm distally whereas Hutt (1975) recorded 7–8 thecae/10 mm proximally and 10–11 thecae/10 mm distally. Thecal spacing in specimens from the upper *vesiculosus* and lower *cyphus* biozones of the Všeradice locality are similar to the values observed by Hutt (1975). Proximal parts are poorly represented in Czech material; the genicula of mesial thecae are commonly furnished with small flange. The distal part of the rhabdosome can be distinguished from equally wide distal fragments of *Coronograptus cyphus* (Lapworth) and pernerograptids by having less inclined, longer and more slender thecae.

Huttagraptus billegravensis Koren' & Bjerreskov, 1997

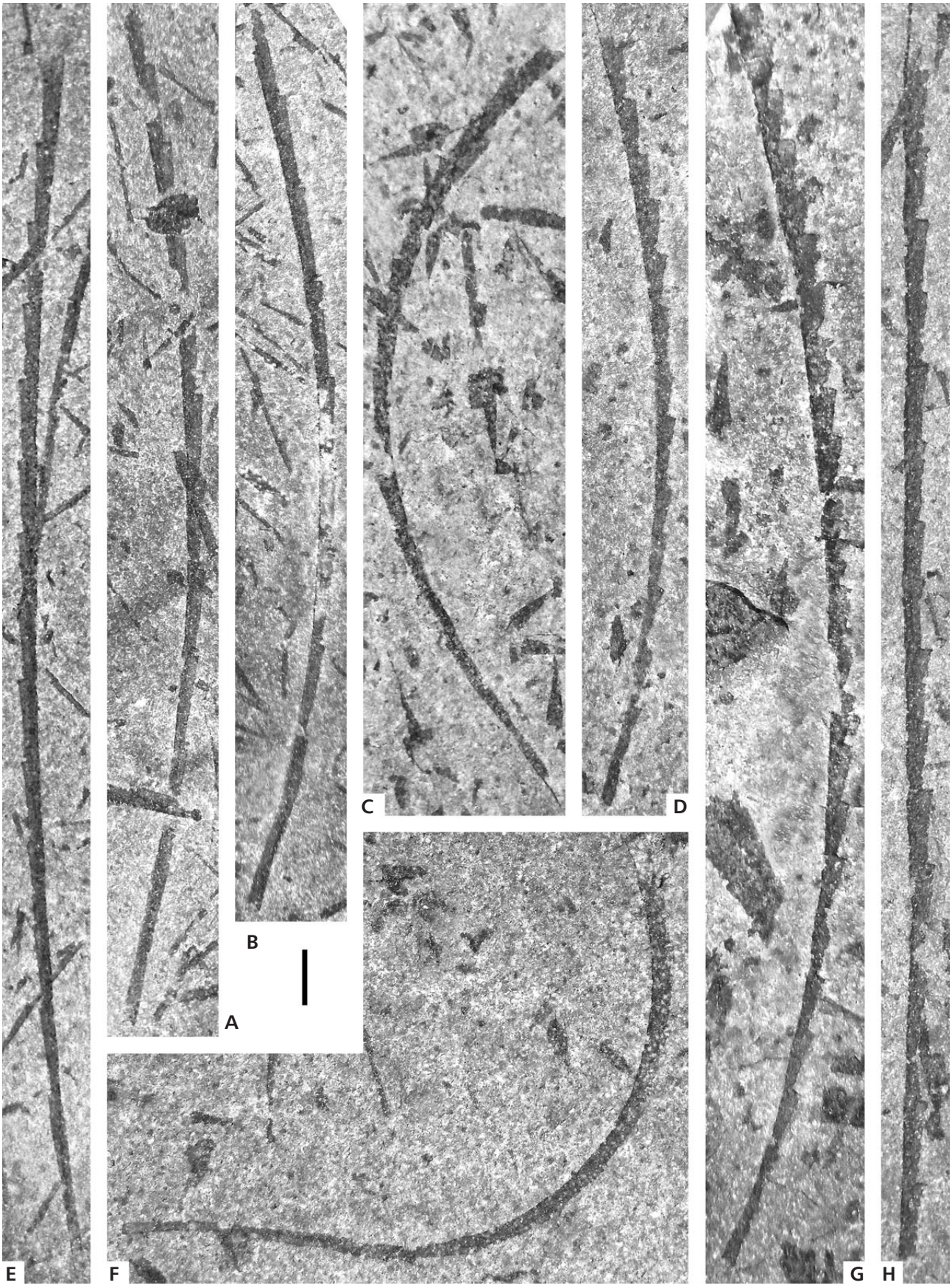
Figures 10J, L, U, 11A, B, E, H

1997 *Huttagraptus billegravensis* sp. nov.; Koren' & Bjerreskov, p. 20, fig. 14a–p.

Material. – About 40 rhabdosomes, mostly immature specimens and/or proximal fragments.

Description. – Most specimens are immature *ca* 20–25 mm-long rhabdosomes and proximal fragments, gently dorsally curved throughout. A maximum length of 36.3 mm was recorded. The rhabdosome is 0.2–0.25 mm wide at th1, widening to 0.28–0.3 mm at th5 and 0.35 mm at th10. A maximum width of 0.45 mm was reached in complete specimens; some distal fragments are up to 0.65 mm wide. The sicula is 2.6–3.15 mm long and *ca* 0.2 mm wide at the aperture. The position of the sicular apex is variable (possibly due to poor preservation), reaching a level from two-thirds up th1 to the aperture of th1. The distance between the sicular aperture and aperture of th1 ranges from 3 mm to 3.6 mm. Th1 is a narrow tube, 2.2–2.4 mm long. Proximal thecae are strongly geniculate with small genicular flanges. The straight, distally facing thecal aperture occupies one-third to half the rhabdosome width. Inclination of the ventral thecal wall is slight to negligible. Beginning with *ca* th5 the thecae become less strongly geniculate with genicular flanges scarcely developed or absent. Geniculation further decreased in distal thecae the ventral thecal walls of which are inclined at 5–7° to the rhabdosome axis and the apertures became slightly everted. Thecae overlap for about one-third their length. Thecae number 6–6.5 in

Figure 11. A, B, E, H – *Huttagraptus billegravensis* Koren' & Bjerreskov, 1997: A, B – PŠ 3539, specimens showing large sicula and thecae with sharp geniculum highlighted by genicular flange; E – PŠ 3578; H – PŠ 3436, straight distal part of mature specimen. • C – *Huttagraptus* cf. *lunata* (Chen & Lin, 1978): PŠ 3608. • D, G – *Atavograptus atavus* (Jones, 1909): D – PŠ 3521, dorsally curved immature rhabdosome; G – PŠ 3471. • F – *Coronograptus cirrus* Hutt, 1975?: PŠ 3593, specimen with long, ventrally curved sicula and sharply geniculated proximal thecae. A–C, E, H from the upper *vesiculosus* Biozone; D, F, G from the lower *cyphus* Biozone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E
F
G
H

the proximal 10 mm of the rhabdosome. The 2TRD decreases from 3.0–3.4 mm at th2 and th5 to 2.9–3.1 mm at th10. Distal fragments exhibit a 2TRD of 2.5–2.7 mm (7.5 thecae in 10 mm).

Remarks. – The present specimens match the original description of *Huttagraptus billegravensis* in having widely spaced biform thecae, strongly geniculate with genicular hoods in the proximal part of the rhabdosome and with flowing geniculum and inclined supragenicular walls distally. The sicula is shorter in the Czech material which is a common difference observed in other huttagraptids and coronograptids, probably due to difficulty in recognition of the sicular apex. The most distal fragments, more than 0.6 mm wide and comprising more outwardly inclined distal thecae with everted apertures, are almost missing in the Czech material. Both *Huttagraptus strachani* (Hutt & Rickards, 1970) and *Huttagraptus praestrachani* Hutt & Rickards, 1977 can be differentiated by their densely spaced and/or more geniculated thecae. *Huttagraptus acinaces* is readily distinguishable by its tighter dorsal curvature and very long, greatly overlapping thecae. *H. billegravensis* is associated with *H. acinaces*, *Cyst. vesiculosus* and abundant *A.*? *pristinus* in the Všeradice collections which indicates its occurrence in both the upper *vesiculosus* and lower *cyphus* biozones.

Huttagraptus cf. *lunata* (Chen & Lin, 1978)

Figures 10G, 11C

cf. 1978 *Monoclimacis lunata* sp. nov.; Chen & Lin, p. 60, pl. 13, figs 1–6; text-fig. 15a, b.

cf. 2002 *Monoclimacis lunata* Chen & Lin. – Mu *et al*., p. 893, pl. 238, figs 4, 5 (see for further references).

Description. – A single, 15 mm-long, dorsally curved rhabdosome with *ca* 2.8 mm long sicula, straight proximal part and strongly geniculated thecae. The sicula is 0.17 mm wide at the aperture, furnished with a 0.6 mm long virgella. The sicular apex reaches almost to the level of the aperture of th2. Th1 is 2.1 mm long. The rhabdosome widens from 0.26 mm at the aperture of th1 through 0.38 mm at th5 to 0.5 mm at th10. All thecae are strongly geniculated, furnished with tiny genicular flanges, and overlapping for up to half their length. Thecae number 9.5–10 in 10 mm throughout the rhabdosome (2TRD 2: 2.2 mm; 2TRD 5: 2.1 mm and 2TRD 10: 2.2 mm).

Remarks. – The present specimen from the upper *vesiculosus* Biozone resembles "*Monoclimacis*" *lunata* Chen & Lin, 1978 from about the same stratigraphical level (*cyphus* Biozone) in China in having an equally open-arcuate rhabdosome with a slender proximal end, long sicula and thecae of monoclimacid appearance with roughly semicircular apertural excavations and small ?genicular hoods. According to the published data, however, "*Monoclimacis*" *lunata* is more robust proximally, with parallel supragenicular walls and hooded apertures throughout its length. The species is reassigned herein to the genus *Huttagraptus* which, in contrast to *Monoclimacis*, possesses a long sicula ("primitive" *sensu* Melchin & Koren' 2001). Another closely similar species, *Huttagraptus ninae* Koren' & Bjerreskov, 1997 has the same rhabdosome width, thecal spacing, overlap and apertures but exhibits prominent genicular flanges and a sicular apex reaching only to the level of the aperture of th1. Similarly, the arcuate *Huttagraptus acinaces* can be readily distinguished by a relatively narrow, more protracted proximal part, longer and relatively slender sicula and greatly overlapping thecae.

Genus *Coronograptus* Obut & Sobolevskaya, 1968, emend. Rickards, 1976a

Type species. – *Monograptus gregarius* Lapworth, 1876; by original designation; from the Llandovery of Dob's Linn, Scotland.

Coronograptus gregarius (Lapworth, 1876)

Figures 10A, H, 12A, B

1876 *Monograptus gregarius* sp. nov.; Lapworth, p. 317, pl. 10, figs 12a–c.

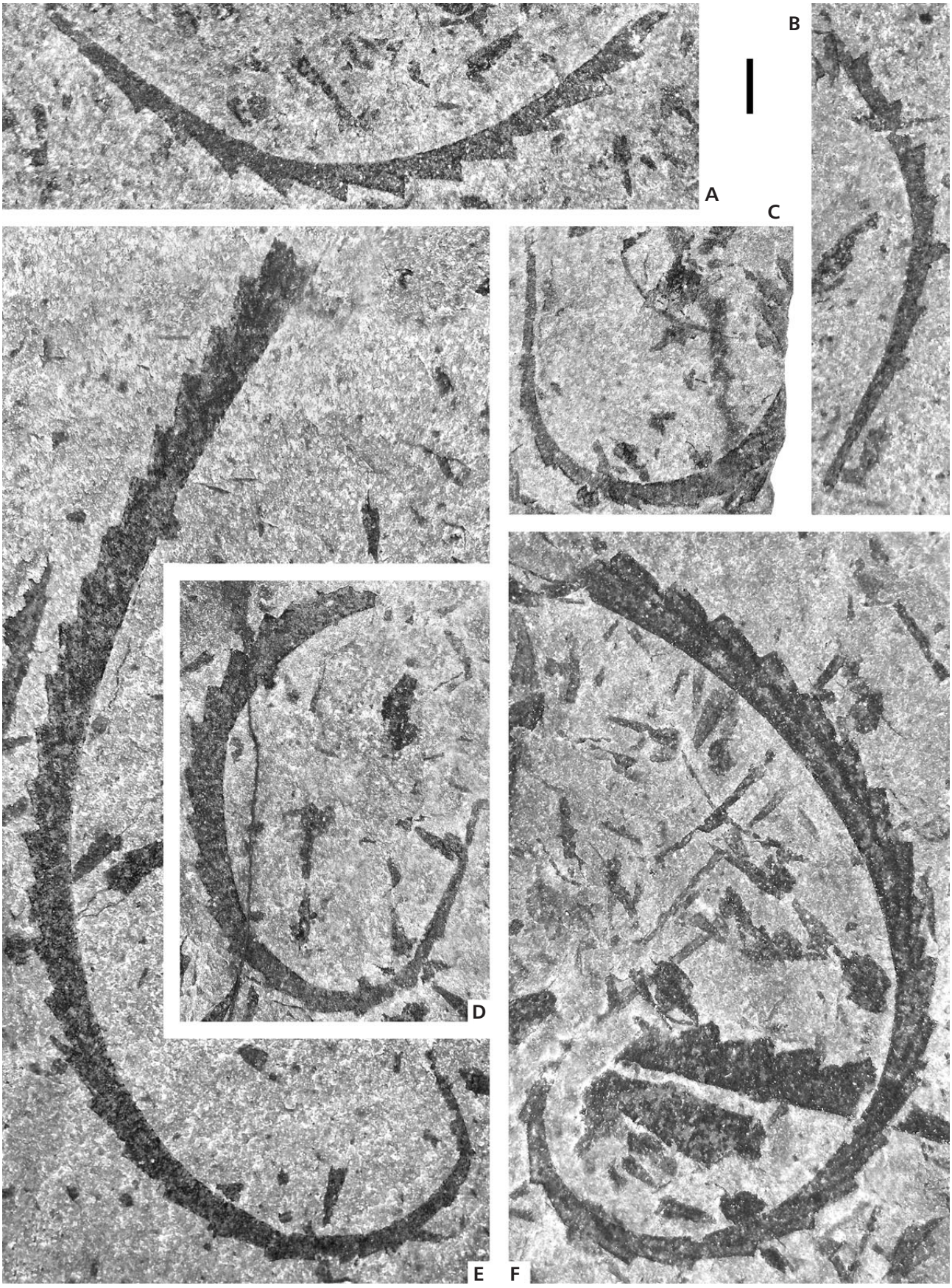
1911 *Monograptus gregarius* Lapworth. – Elles & Wood, p. 365, pl. 36, figs 3a–d; text-fig. 238a, b.

1975 *Monograptus gregarius* Lapworth. – Bjerreskov, p. 46, pl. 6, fig. f; text-fig. 15a.

partim 1975 *Coronograptus gregarius* (Lapworth). – Hutt, pp. 64–67, pl. 13, fig. 2; pl. 14, figs 1, 3 (*non* 2); text-fig. 15, figs 3, 4 (*non* 1, 2) (see for further synonymy).

1988 *Coronograptus gregarius gregarius* (Lapworth). – Štorch, pp. 18–19, pl. 4, figs 1–3; text-fig. 2i, j (see for further synonymy).

Figure 12. A, B – *Coronograptus gregarius* (Lapworth, 1876): A – PŠ 3516; B – PŠ 3590. • C–F – *Coronograptus cyphus* (Lapworth, 1876) *sensu* Elles & Wood (1911): C – PŠ 3459, typically curved proximal part with incompletely preserved sicula and thecae furnished with genicular flanges; D – PŠ 3459, another specimen from the same slab exhibits a complete, almost straight sicula; E – PŠ 3523; F – PŠ 3580, specimen with partly damaged proximal end, arrow points to isolated part of the sicula. A from the lower *triangulatus* Biozone, B–F from the *cyphus* Biozone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E
F

Material. – Twelve complete rhabdosomes from Všeradice along with rich material studied from other lower Aeronian sections of the Prague Synform.

Remarks. – The morphology and dimensions of the present material agree well with those reported for the species by a number of previous authors (see the synonymy above). Specimens from the lower *triangulatus* Biozone of Všeradice exhibit 4.1–6.1 mm-long siculae with the apex reaching the level of the aperture of th3. The rhabdosome is 0.5–0.6 mm wide at the aperture of th1; the maximum width of 0.7–0.75 mm is reached by *ca* th5. Specimens from the *cyphus* Biozone have slightly shorter siculae (4.2–4.4 mm) and less robust rhabdosomes (0.42–0.45 mm wide at th1 and 0.55 mm wide at th3–th5). All specimens can be assigned to *C. gregarius* (Lapworth). Short siculae and strongly curved rhabdosomes typical of *Coronograptus minusculus* Obut & Sobolevskaya, 1968 and, in particular, *Coronograptus hipposideros* (Toghill, 1968a) have not been recorded in the Czech material.

Coronograptus cyphus (Lapworth, 1876) *sensu* Elles & Wood (1911)

Figures 10B–D, O, R, 12C–F

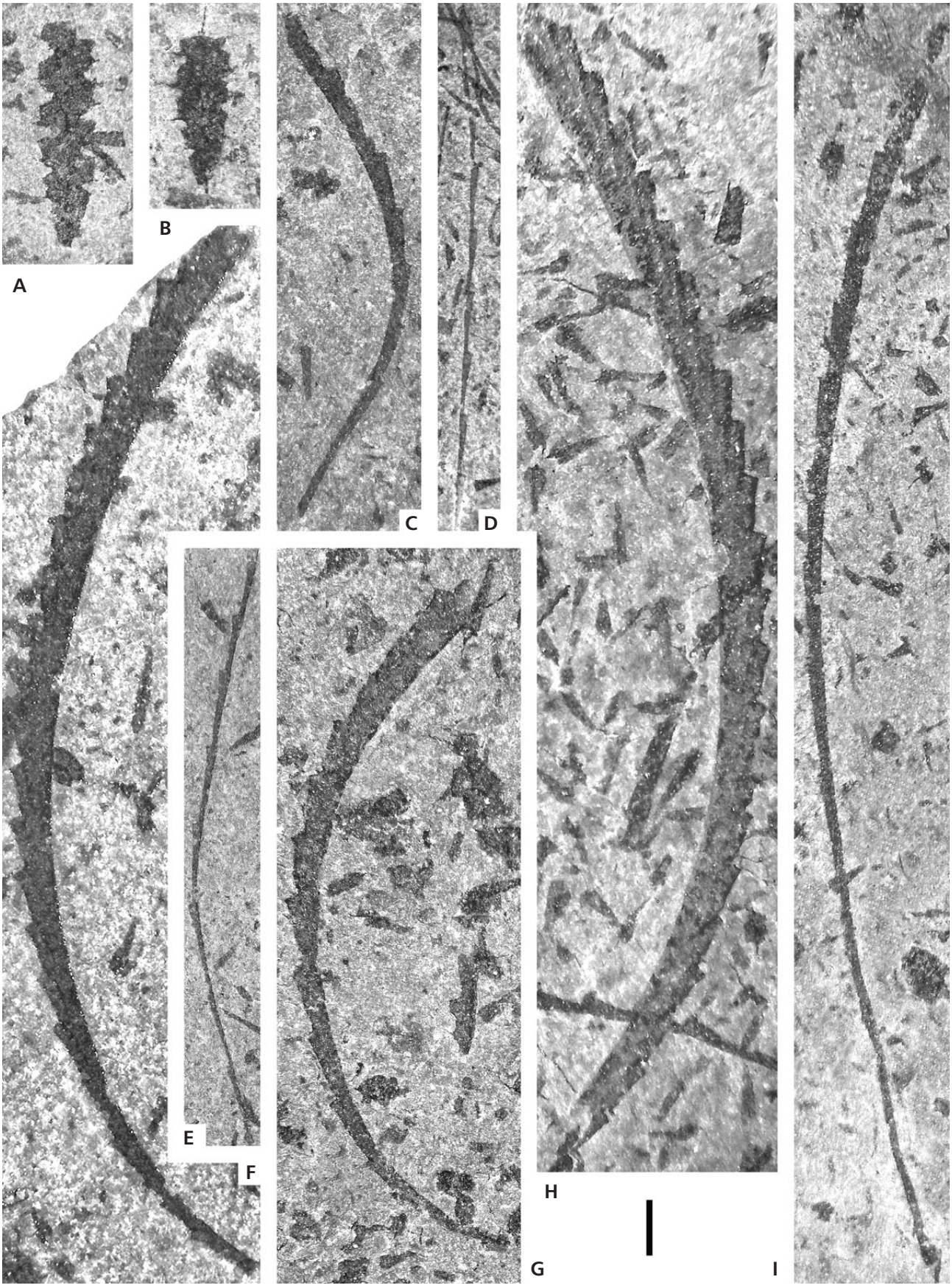
? 1876 *Monograptus cyphus* sp. nov.; Lapworth, p. 352, pl. 12, figs 3a, c (*non* 3b, d).
1911 *Monograptus cyphus* Lapworth. – Elles & Wood, p. 362, pl. 36, figs 1a–e; text-fig. 236a–e.
1970 *Monograptus cyphus* Lapworth. – Rickards, pp. 62–63, pl. 4, fig. 11; pl. 5, figs 1, 2; text-fig. 14, fig. 31.
1975 *Coronograptus cyphus* (Lapworth). – Hutt, pp. 67–68, pl. 12, figs 6, 11; pl. 14, figs 6, 7.
1988 *Coronograptus cyphus* (Lapworth). – Štorch, p. 17, pl. 2, fig. 1; pl. 3, fig. 1; pl. 4, figs 4, 5; text-fig. 2k, l.
2003 *Coronograptus cyphus* (Lapworth) *sensu* Elles & Wood. – Zalasiewicz *et al*., fig. 2a–e.

Material. – 25 complete rhabdosomes comprising both juvenile and mature specimens, along with *ca* 20 fragmentary rhabdosomes. Further specimens were available from the Běleč, Hlásná Třebaň and Karlík sections.

Description. – The rhabdosome is dorsally curved, resembling a swan neck in lateral profile, commonly with characteristic proximal accentuation of the curvature after th2–th3. The slender sicula is 3.0–3.6 mm long, straight, apparently fragile, about 0.17 mm wide at the aperture. The sicular apex attains a level up to half-way between the apertures of th1 and th2. The rhabdosome widens from 0.3–0.35 mm at th1, through 0.4–0.45 mm at th3, 0.5–0.6 mm at th5, and 0.7–0.85 mm at th10, to 0.95–1.05 mm at th20. Mature, 40–60 mm long rhabdosomes are 1.2–1.3 mm wide in the distal part, with some distal fragments reaching 1.5 mm in width. Th1 is a 1.7–2.2 mm-long, extremely slender tube; succeeding proximal thecae are slightly geniculated, overlapping for about half their length. Tiny genicular flanges have been observed in proximal thecae, up to th7 in the majority of specimens. The everted thecal apertures occupy two-fifths of the rhabdosome width in the proximal part of the rhabdosome and one-third distally. 2TRD gradually decreases slightly from 1.9–2.35 mm at th2, to 1.8–2.2 mm at th5 and 1.7–2.1 mm at th10. Distal thecae are straight tubes, overlapping for at least half their length, numbering 9–10 in 10 mm (2TRD is 2.1–2.2 mm) and are inclined at 13–18° to the rhabdosome axis. Apertures are straight, perpendicular to the ventral thecal wall or slightly everted.

Remarks. – The morphology ascribed to *Coronograptus cyphus* (Lapworth, 1876) by Elles & Wood (1911) exhibits a distinctive dorsally curved rhabdosome with a sharp bend proximally, terminated by a long and straight sicula, and having simply tubular thecae with increasing overlap distally. This concept of the species has been followed by Hutt & Rickards (1970), Rickards (1970), Hutt (1975), Bjerreskov (1975) and all subsequent authors including Štorch (1988). Zalasiewicz *et al*. (2003) re-examined the type material of *Coronograptus cyphus* (Lapworth) and revealed that Lapworth primarily had a different morphology of biform monograptid in mind when creating the taxon (see the type material refigured therein). Strachan (1997) noted that the lectotype of *C. cyphus* selected by Obut *et al*. (1965) "did not correspond to any of Lapworth's original illustrations, although it is from his original collection and was subsequently figured by Elles & Wood (1911, pl. 36, fig. 1a)". The present author follows the pragmatic suggestion by

Figure 13. A, B – *Paraclimacograptus innotatus* (Nicholson, 1869): A – PŠ 3474; B – PŠ 3584. • C – *Coronograptus*? sp. A: PŠ 3623. • D, E – *Atavograptus*? *pristinus* (Hutt, 1975): D – PŠ 3573, one of fragmentary rhabdosomes densely clustered on bedding plane; E – PŠ 3553 showing extremely short metathecae with tendency to isolation. • F, G – *Coronograptus*? sp. B: F – PŠ 3599, mesial part of the rhabdosome showing transition from geniculated thecae with genicular flanges to simple tubular thecae; G – PŠ 3423. • H, I – *Huttagraptus acinaces* (Törnquist, 1899): H – PŠ 3587 comprising both geniculated mesial thecae and simply tubular distal thecae; I – PŠ 3473, slender proximal part with long sicula and slender, much elongated proximal thecae. A, D, E, I from upper *vesiculosus* Zone; B, F–H from lower *cyphus* Zone; C from upper *cyphus* Zone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E
F
G
H
I

Zalasiewicz *et al*. (2003) to retain the well-established conception of *Coronograptus cyphus* (Lapworth) *s.l.* based upon the detailed description and illustration provided by Elles & Wood (1911) to avoid serious confusion in taxonomy and biostratigraphy.

Numerous rhabdosomes from Všeradice and other localities in the Prague Basin match *Coronograptus cyphus* (Lapworth) *sensu* Elles & Wood (1911) except for one detail: the possession of distinct genicular hoods developed in up to seven proximal thecae in the majority of specimens studied (see Fig. 10C, D, O, R). No earlier descriptions and illustrations recorded any genicular hoods which could be barely preserved in pyritized or chlorite-coated internal moulds. Zalasiewicz *et al*. (2003) took the absence of genicular hoods in *C. cyphus* as evidence against its possible derivation from *Huttagraptus praematurus* (Toghill, 1968c) as suggested by Toghill (1968b). Although derivation of *C. cyphus* from either *H. praematurus*, *Huttagraptus solidus* Štorch & Feist, 2008 or other related huttagraptids would necessarily incorporate more changes in morphology than just recession of genicular hoods in distal thecae, the ancestry of *C. cyphus* should be reconsidered bearing in mind in particular that Lukasik & Melchin (1997) recorded tiny genicula and small genicular hoods in chemically isolated rhabdosomes of coronograptids, including *Coronograptus gregarius*.

***Coronograptus cirrus* Hutt, 1975?**
Figures 10P, 11F

?1975 *Coronograptus cirrus* sp. nov.: Hutt, p. 68, text-fig. 16, fig. 7.

Material. – One complete immature rhabdosome.

Description. – Rhabdosome dorsally curved with a 3.7 mm long straight sicula, slightly reflexed near the aperture. The sicula is 0.17 mm wide at the aperture; the apex reaches to about the level of th1 aperture. Thecae are slender, geniculated, overlapping for about one-third their length. Thecal apertures are perpendicular to the rhabdosome axis and do not exhibit significant ventral extension. The rhabdosome widens very little, from 0.25 mm at the aperture of th1 to 0.3 mm at th5. A maximum width of 0.4 mm was recorded at th7. 2TRD increased slightly from 2.4 mm at th2 to 2.6 mm at th5.

Remarks. – This form is tentatively assigned to *Coronograptus cirrus* Hutt, 1975 according to its extremely slender, strongly arcuate rhabdosome with long sicula and long, markedly geniculated but only slightly overlapping thecae. The strongly curved rhabdosome and slight thecal overlap on the other hand differentate this specimen from the otherwise closely similar *Huttagraptus acinaces* (Törnquist). Both species are known from about the same stratigraphical level – *acinaces* (upper *vesiculosus* – lower *cyphus*) Biozone of the British biozonal scale (Hutt 1974, Zalasiewicz *et al*. 2009).

***Coronograptus*? sp. A**
Figure 13C

Material. – One immature rhabdosome.

Remarks. – A single slender rhabdosome from the *cyphus* Biozone differs from juvenile specimens of *Coronograptus cyphus* in having less overlapping and narrower thecae. DVW increases from 0.25 mm at th1 through 0.35 mm at th3 to 0.43 mm attained at th5. Thecal geniculation is barely seen; no genicular flanges were detected. The apertural part of the 3.15 mm-long sicula is missing. Th1 is 1.7 mm long; other thecae are 2.1–2.3 mm long, overlapping for one-third their length.

***Coronograptus*? sp. B**
Figures 13F, G, 14I, K, L

Material. – Six incomplete rhabdosomes.

Remarks. – Regularly dorsally arcuate specimens uncommon in the *cyphus* Biozone have been questionably assigned to *Coronograptus* due to the lack of relevant morphological details in the present material. The sicula and most proximal thecae are missing. The rhabdosomes resemble *C. cyphus* in having a robust, 1.0 mm wide distal part with simply tubular thecae overlapping for *ca* one-third to half their length. In contrast to *C. cyphus*, however, *Coronograptus*? sp. B widens more gradually (see Fig. 14I, K), the slender proximal thecae are geniculated and both proximal and mesial thecae are slightly everted with apertures bearing gentle lateral elevations and a dorsal hood. Mesial and distal fragments of *Huttagraptus acinaces* can be readily distinguished from *C*.? sp. B by their longer, much more overlapping thecae.

Genus *Pernerograptus* Přibyl, 1941, emend. herein

Type species. – *Graptolites argenteus* Nicholson, 1869; by original designation; from Skelgill, the Lake District, England.

Diagnosis. – Dorsally curved monograptids with biform thecae. Sicula extremely minute; the apex does not reach up to the first metatheca. Proximal thecae slender, axially

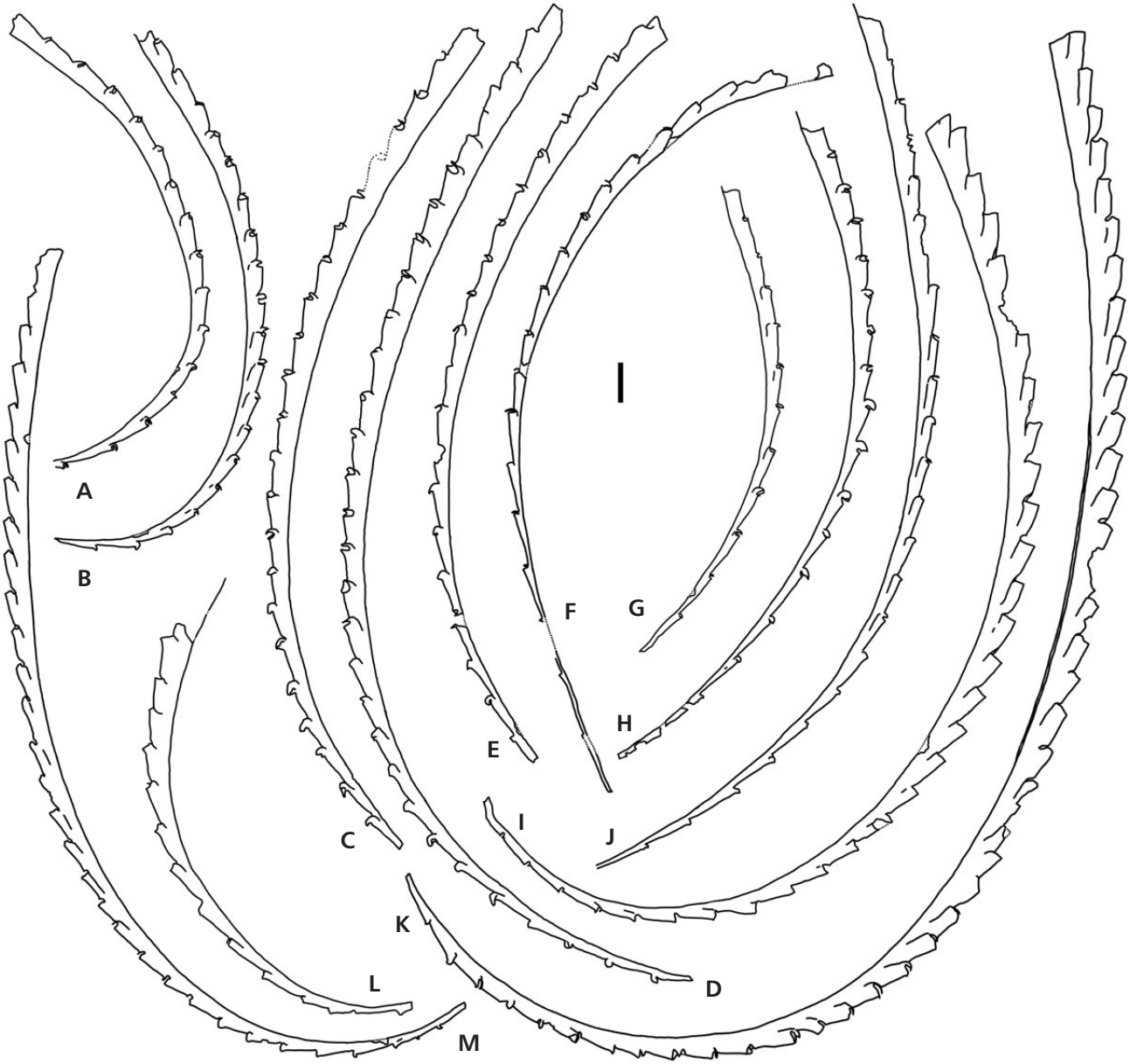


Figure 14. A, B, M – *Pernerograptus chrysalis* (Zalasiewicz, 1992): A – PŠ 3509, B – PŠ 3616, specimen showing transition from hooked proximal thecae to hooded mesial thecae; M – PŠ 3551. • C–H, J – *Pernerograptus pribyli* sp. nov.: C – PŠ 3438, mesial fragment exhibits transition from hooked proximal thecae to thecae with dorsal apertural hood; D – PŠ 3574, holotype; E – PŠ 3494, F – PŠ 3534, proximal part with slender elongated thecae; G – PŠ 3525, H – PŠ 3617, J – PŠ 3519. • I, K, L – *Coronograptus*? sp. B: I – PŠ 3437, specimen showing geniculated proximal thecae with small hoods and simple distal thecae with even apertures; K – PŠ 3450, L – PŠ 3423. A, B, M from the lower *triangulatus* Biozone; C–L from the *cyphus* Biozone. All figures × 6; scale bar represents 1 mm.

elongated without overlap, terminated by apertural hooks which are either simple or transversely expanded. Apertural hooks retreat in mesial thecae leaving only lateral lappets and dorsal apertural hoods which also subsequently retreat resulting in simple cylindrical, greatly overlapping distal thecae.

Remark. – The sicula and proximal end of the type species were described and illustrated by Hutt (1975).

Species included. – In addition to the species included in *Pernerograptus* by Přibyl (1941), the genus as emended herein is expanded to include the whole *revolutus* Group of Hutt (1974b) and other early monograptids with biform thecae that are elongated, isolated and hooked in the proximal part and considerably overlapping with even or lappeted apertures in the distal part: *Monograptus argenteus* Nicholson, 1869; *Monograptus difformis* Törnquist, 1899; *Monograptus revolutus* Kurck, 1882; *Monograptus*

revolutus austerus Törnquist, 1899; *Pernerograptus revolutus praecursor* Obut & Sobolevskaya, 1968; *Pernerograptus tenuipraecursor* Obut & Sobolevskaya, 1968; *Monograptus austerus vulgaris* Hutt, 1974b; *Monograptus austerus sequens* Hutt, 1974b; *Monograptus austerus praecursor* Elles & Wood, 1911; *Monograptus austerus bicornis* Hutt, 1974b; *Monograptus sudburiae* Hutt, 1974b and *Monograptus chrysalis* Zalasiewicz, 1992. In flattened preservation some kind of lateral apertural lobes or elevations have been detected in all of these species. Dorsal apertural hoods are equally widespread although more or less distinctive and developed in a diverse number of thecae. The present data concur with Hutt's (1974b) assumptions of the pribylograptid affinities and ancestry of these biform monograptids.

Species with biform, but largely monoclimacid thecae, confined mostly to Aeronian strata, such as *Monograptus limatulus* Törnquist, 1892, *Monograptus inopinus* Törnquist, 1899, *Monograptus havliceki* Štorch, 1988, and *Monograptus imago* Zalasiewicz, 1992, are provisionally retained in *Monograptus sensu lato*.

***Pernerograptus pribyli* sp. nov.**
Figures 14C–H, J, 15B, E, 16F, 17D

1992 *Monograptus* cf. *sudburiae* Hutt. – Zalasiewicz, text-fig. 2a–f.

Holotype. – Specimen No. PŠ 3574 (Fig. 14D); from the *Coronograptus cyphus* Biozone at Všeradice, Želkovice Formation, Prague Synform, Czech Republic.

Derivation of name. – After the late A. Přibyl, Czech palaeontologist who worked on graptolites.

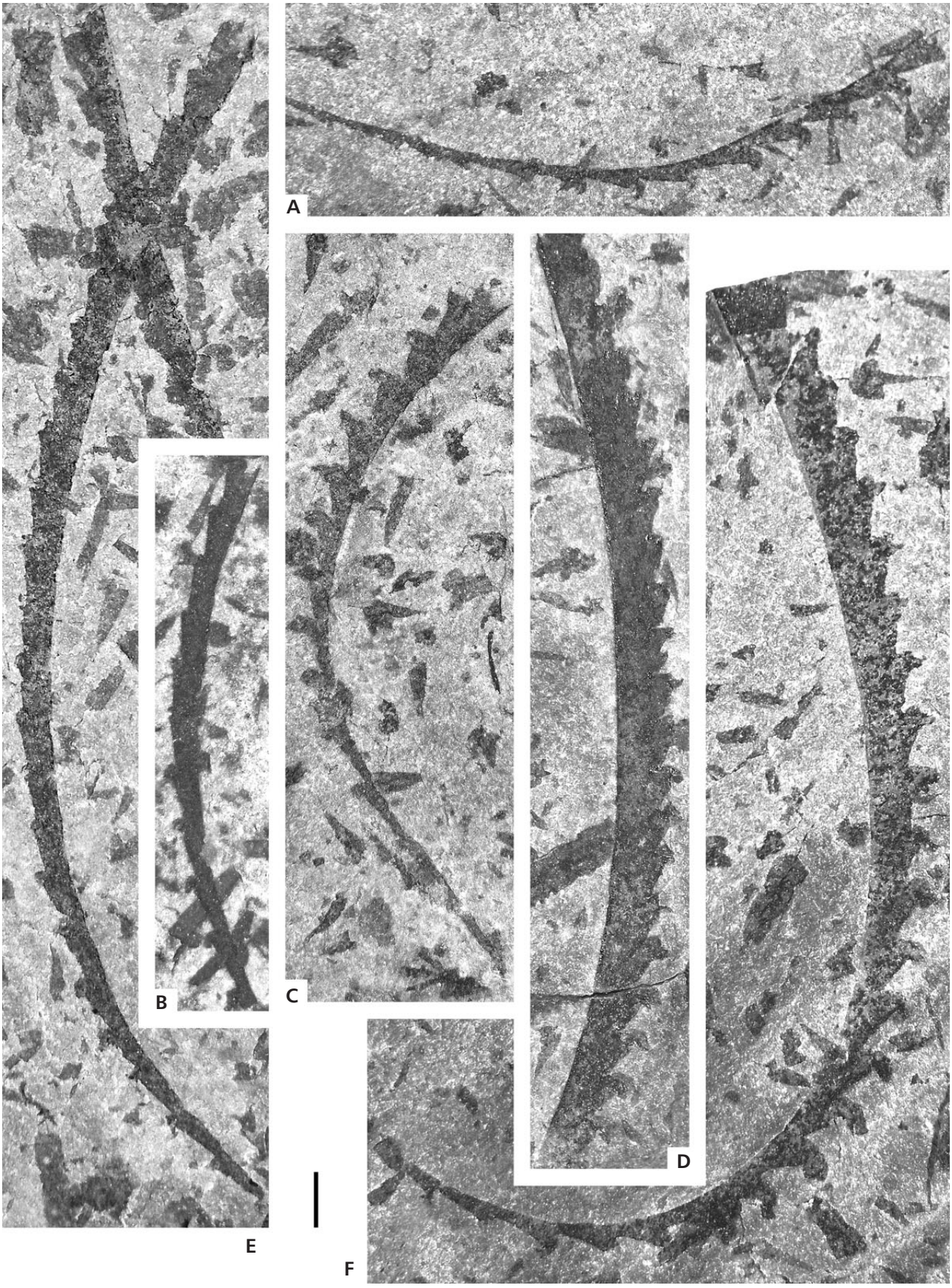
Material. – 18 more or less fragmentary specimens.

Diagnosis. – Rhabdosome regularly dorsally arcuate, widening gradually through the proximal, mesial and early distal part to a maximum distal width of 0.8 mm. Proximal thecae elongated, with small apertural hooks which divide into a pair of small sub-rounded, ventrally directed subtriangular lateral lappets and a dorsal hood in 5–7 mesial thecae. Reduced lateral apertural lappets and minute hoods are retained also in the tubular distal thecae which overlap for one-third to half their length.

Description. – The rhabdosome has open dorsal curvature slightly accentuated in its mesial part whereas the proximal part is relatively straight. The maximum length is more than 30 mm. The rhabdosome widens gradually from 0.15–0.2 mm in the proximal part, through 0.45–0.6 mm in the mesial part to the maximum of 0.8 mm in distal part. The sicula and th1 have not been found. *Ca* 10 proximal thecae preserved in the present incomplete rhabdosomes are much elongated, not overlapping, and terminated by a small apertural hook. In the mesial part of the rhabdosome 5–7 thecae retain a hook-like appearance but the hook is divided into two small sub-rounded and dorso-ventrally extended lateral lappets. The dorsal wall of the apertural hook retreated and appears to be obscured by the lateral lappets. The lateral lappets retreated further in distal thecae and exposed a small dorsal apertural hood which protrudes a little from the rhabdosome outline. Thecal apertures closely resemble those figured by Bjerreskov (1975, text-fig. 16A–C) in her "*Monograptus*" *revolutus* Kurck and Zalasiewicz (1996, fig. 2a–f) in his "*M.*" cf. *sudburiae* Hutt. Mesial thecae overlap for about one-quarter their length, distal thecae for almost half their length but interthecal septa are seldom well seen in the present material. Thecae number 7–8.5 in 10 mm in the proximal part and *ca* 10 in 10 mm in the distal part of the rhabdosome. 2TRD decreases from 2.4–2.9 mm in proximal thecae to 1.9–2.2 mm in mesial and distal thecae.

Remarks. – This slender monograptid with biform thecae is associated with a typical assemblage of the *cyphus* Biozone in the Všeradice collection. This form matches "*Monograptus*" cf. *sudburiae* of Zalasiewicz (1996) in thecal shape, including the lobe-like lateral apertural lappets and sharp genicula in distal thecae and all measured dimensions of the rhabdosome. *Pernerograptus chrysalis* (Zalasiewicz) differs in having a flowing, more open dorsal curvature and a more gradually widening rhabdosome. Also, the transition from slender, axially elongated and hooked proximal thecae to overlapping mesial thecae with lateral lappets and distal thecae with reduced lappets and dorsal apertural hoods is considerably more gradual in *P. pribyli* sp. nov. than observed in *P. chrysalis*. *Pernerograptus sudburiae* (Hutt) can be differentiated by having more hooked proximal thecae, a relatively abrupt change in thecal morphology mesially, and a rapid increase in dorso-ventral width in the strongly curved mesial part of the rhabdosome. The new species differs from the generally similar *Pernerograptus revolutus* (Kurck)

Figure 15. A – *Pernerograptus* cf. *vulgaris* (Hutt, 1974b): PŠ 3498, mesial fragment with elongated hooked thecae. • B, E – *Pernerograptus pribyli* sp. nov.: B – mesial fragment; E – PŠ 3438, incomplete rhabdosome showing transition from hooked proximal thecae, through mesial thecae with apertural hoods to simple, tubular distal thecae. • C, D, F – *Pernerograptus difformis* (Törnquist, 1899): C – PŠ 3555, proximal fragment showing transition from elongated proximal thecae to high-triangular mesial thecae, D – PŠ 3459, fragment showing transition from high-triangular mesial thecae to tubular distal thecae, F – PŠ 3499. A, C, D, F from the upper *cyphus* Biozone; B, E from the lower *cyphus* Biozone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E
F

in having less pronounced apertural hooks in the proximal thecae and lesser thecal overlap in distal thecae which exhibit short but distinctive dorsal apertural hoods.

***Pernerograptus chrysalis* (Zalasiewicz, 1992)**
Figures 14A, B, M, 16E

1988 *Pribylograptus argutus argutus* (Lapworth). – Štorch, pp. 27–28, pl. 5, figs 1–4; text-fig. 3a–d.
1992 *Monograptus chrysalis* sp. nov.; Zalasiewicz, pp. 779, 781–782, text-fig. 1a–n.

Material. – Seven incomplete specimens and several proximal fragments along with supplementary material from the Hlásná Třebaň, Karlík and Černošice sections.

Description. – The rhabdosome is over 50 mm long, with dorsal curvature accentuated in the mesial part which represents an interval of abrupt change from slender, axially elongated proximal thecae with small, not fully developed apertural hooks comprising a ventrally facing slit-like apertural excavation sheltered by a small hood to distal thecae with slightly expanded apertures furnished with broad, perhaps asymmetrical lateral lappets. The rhabdosome is 0.2 mm wide in the *ca* 10 mm long proximal part comprising these slender, extremely low-triangular thecae without any significant overlap. 2TRD ranges from 2.5 mm to 2.6 mm in sub-mesial thecae; the most proximal fragments and sicula are not preserved in the Všeradice material. In the mesial part, the rhabdosome widens to 0.4–0.5 mm within about 4 thecae coinciding with the rapid change from proximal to distal thecal morphology. The 2TRD decreases to 1.8–2.1 mm which is maintained in the distal part of the rhabdosome which attains a maximum dorsoventral width of 0.55–0.7 mm. Distal thecae are straight tubes, inclined at 7–13°, overlapping for almost half their length. Indistinct genicular hoods observed in some distal thecae may actually be a margin of the lateral apertural lappet of the opposite side of the thecal aperture buried in the sediment.

Remarks. – The present specimens match *Monograptus chrysalis* Zalasiewicz, 1992 in thecal morphology, the long and slender, nearly straight proximal part of the rhabdosome, the mesially accentuated dorsal curvature and widening, and the maximum width attained in the distal part. The only difference is the denser thecal spacing although the most proximal thecae are missing in the Všeradice material and better matching 2TRDs (2.7 mm) have been recorded in the proximal parts of rhabdosomes collected from other localities in the Prague Synform. Curvature ranges from gently dorsally arcuate to almost straight in the distal part of the rhabdosome as shown by mature specimens from Hlásná Třebaň. In the Všeradice material late distal parts are missing. *Pernerograptus sudburiae* (Hutt, 1974b) can be distinguished by its proximal thecae having more pronounced apertural hooks and proximally rather than ventrally facing apertures. Specimens assigned to *Pernerograptus chrysalis* are common in the *triangulatus* Biozone assemblage at Všeradice. Further material came from the *triangulatus*, *pectinatus* and *simulans* biozones of the localities listed above (see Štorch's 1988 description and figures of *Pribylograptus argutus*).

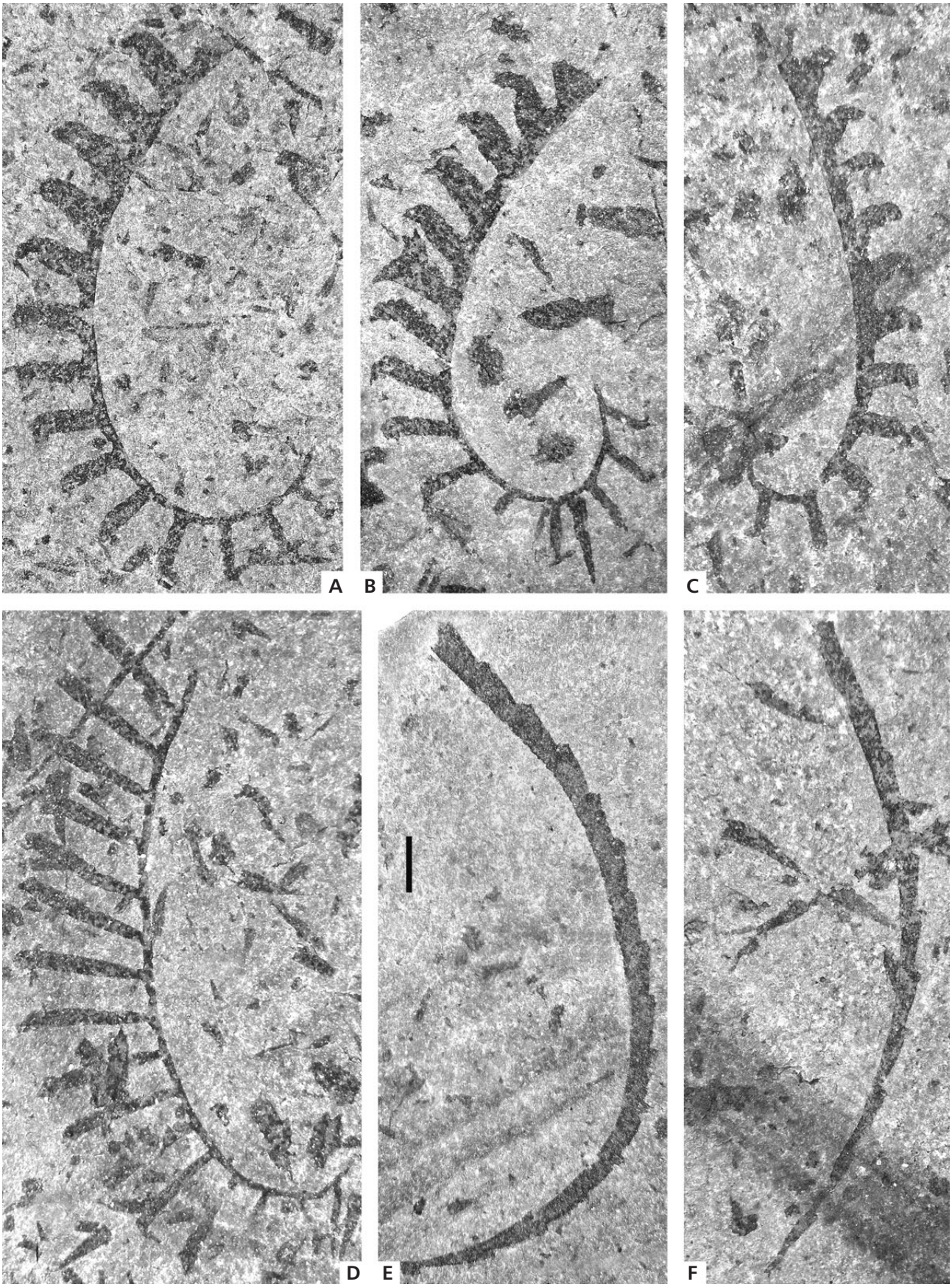
***Pernerograptus difformis* (Törnquist, 1899)**
Figures 15C, D, F, 17C, I, J, O, P

1899 *Monograptus difformis* n. sp.; Törnquist, p. 13, pl. 2, figs 15–17.
1911 *Monograptus difformis* Törnquist. – Elles & Wood, p. 386, pl. 38, figs 4a–c (?*non* fig. 4d); text-fig. 256a (?*non* 256b).
1942 *Pernerograptus* cf. *difformis* (Törnquist). – Přibyl, p. 12, pl. 1, fig. 7; pl. 2, figs 2, 3.
1974b *Monograptus difformis* Törnquist. – Hutt, text-fig. 1c.
1975 *Monograptus difformis* Törnquist. – Hutt, pp. 88–89, pl. 15, fig. 4; text-fig. 17, fig. 4.
1988 *Monograptus* cf. *difformis* Törnquist. – Štorch, pp. 33–34, pl. 8, fig. 3; text-figs 5a, 6e.

Material. – 17 incomplete rhabdosomes and *ca* twenty proximal, mesial or distal fragments. No sicula and th1 detected. Several other specimens from Hlásná Třebaň and Zadní Třebaň.

Description. – The rhabdosome exhibits open dorsal curvature which is typically accentuated in the mesial part. The proximal part apparently straightens although most proximal thecae and sicula are missing in the present material. The maximum length of the incomplete rhabdosome exceeds 60 mm. Up to five proximal thecae preserved are slender, axially elongated, without significant overlap, terminated by small apertural hooks. The rhabdosome is 0.25–0.35 mm wide in this level, with 2TRD ranging from

Figure 16. A, B – *Demirastrites triangulatus* (Harkness, 1851): A – PŠ 3433 showing typical isolated proximal thecae, B – PŠ 3432. • C – *Demirastrites* sp.: PŠ 3597. • D – *Rastrites longispinus* Perner, 1897: PŠ 3615a. • E – *Pernerograptus chrysalis* (Zalasiewicz, 1992): PŠ 3509. • F – *Pernerograptus pribyli* sp. nov.: PŠ 3525. A–E from the *triangulatus* Biozone; F from the upper *cyphus* Biozone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E
F

2.3 mm to 2.9 mm. When dorsal curvature of the rhabdosome tightens mesially, the thecae get shorter and high triangular, with prominent apertural hooks. The maximum dorso-ventral width attained is 1.0–1.2 mm (with extreme values ranging from 0.95 mm to 1.4 mm). Mature rhabdosomes possess more developed apertural hooks which occupy one-third the thecal height and cause the extreme values of the mesial dorso-ventral width. Thecal overlap originated and rapidly increased in the mesial part of the rhabdosome, before the gradual retreat of the apertural hooks. The 2TRD is 1.8–2.1 mm in mesial thecae. Gradual retreat of the apertural hook, which involves 8–12 thecae after the maximum dorsal curvature of the rhabdosome, commenced with the dorsal wall of the hook, subsequently leaving paired, sub-triangular lateral apertural lobes. Distal thecae are straight tubes, overlapping for half or just over half their length. Apertural margins are generally straight but slight dorso-lateral elevations may be retained in some specimens. Distal thecae number about 10 in 10 mm (2TRDdist. is 1.95–2.1 mm); rhabdosome dorso-ventral width ranges between 1.1 mm and 1.4 mm distally.

Remarks. – *Pernerograptus difformis* is a common constituent of the upper *cyphus* Biozone assemblage in the Prague Synform. Its high triangular, isolated mesial thecae make it well recognizable from other biform monograptids of the upper *cyphus* to *pectinatus* Biozone interval. Although the rhabdosome width and/or thecal height varies in the present material, the hooked triangular mesial thecae match well those figured by Hutt (1975, pl. 15, fig. 4). The same mode of gradual retreat of the apertural hook was illustrated by Hutt (1974, text-fig. 1c) in a specimen preserved in relief in pyrite. The thecal shape and strong mesial curvature of the rhabdosome with relatively few axially elongated proximal thecae are typical of *P. difformis* and, if combined with the degree and late beginning of thecal overlap, readily differentiate the species from *Pernerograptus austerus* (Törnquist), *P. vulgaris* (Hutt), and *P. sequens* (Hutt). *P. bicornis* (Hutt) can be differentiated by its greatly overlapping thecae with apertural horns and a regularly widening rhabdosome which becomes markedly robust distally. *Pernerograptus revolutus* (Törnquist) and *Pernerograptus sudburiae* (Hutt) can be readily distinguished from *P. difformis* by their more slender, less curved rhabdosomes with mesial thecae furnished with lateral apertural lappets and dorsal hoods, derived from or mimicking the early pribylograptids, the likely ancestors of all pernerograptids.

Pernerograptus cf. *vulgaris* (Hutt, 1974)

Figures 15A, 17B

Material. – Two incomplete rhabdosomes and several doubtful fragments from Všeradice supplemented by several specimens from Hlásná Třebaň.

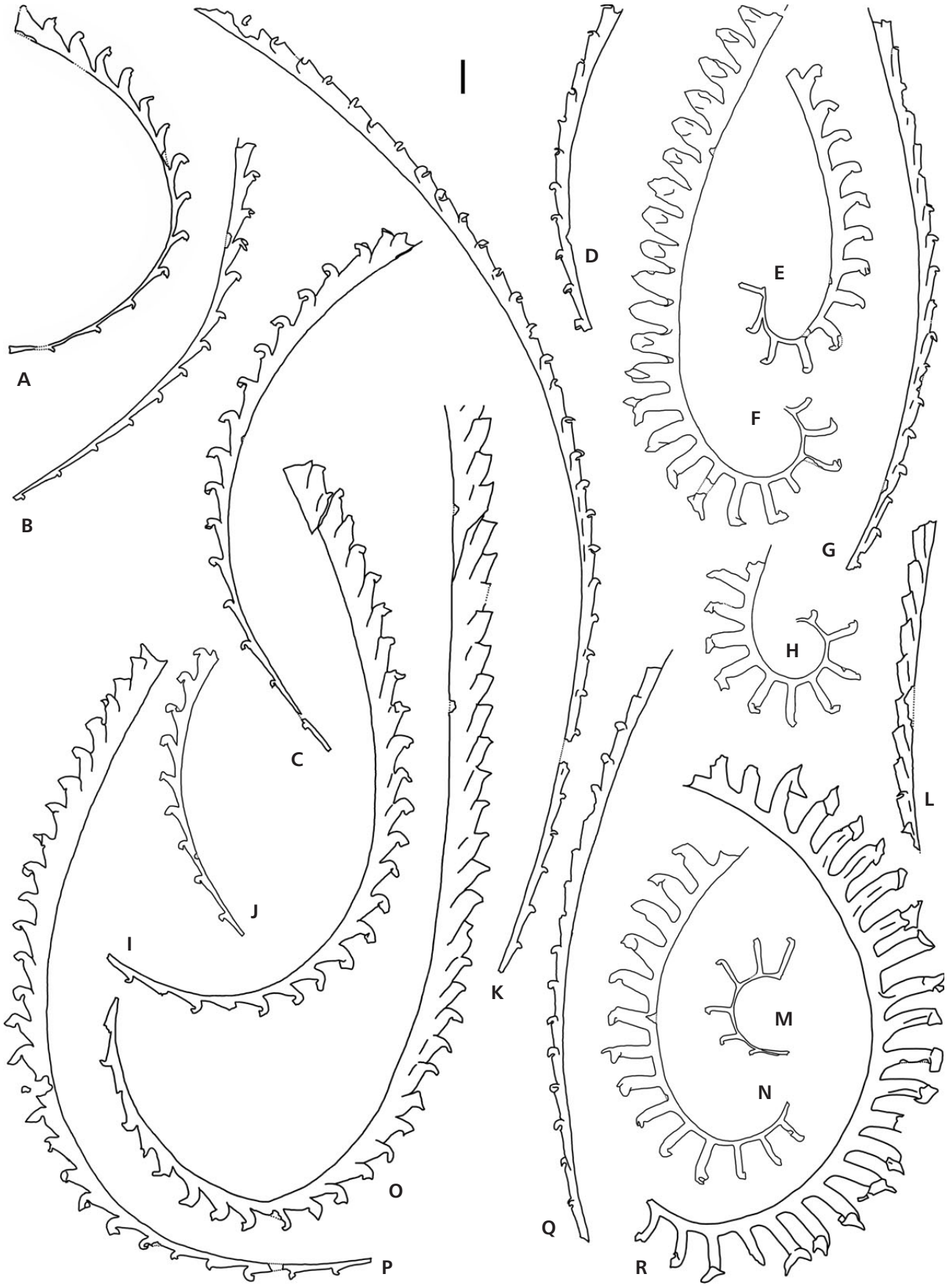
Remarks. – Some incomplete specimens exhibit elongated, low triangular, slightly overlapping early mesial thecae different from the high-triangular, isolated mesial thecae of *Pernerograptus difformis*. These fragments widen from 0.2 mm to *ca* 0.7 mm. The most complete specimens are regularly dorsally arcuate without significant mesial accentuation of the curvature. The maximum width attained in an over 50 mm-long incomplete rhabdosome is 1.2 mm. Simply tubular distal thecae number 9–9.5 in 10 mm (2TRD is 2.0–2.2 mm) and overlap for just over half their length. Simply tubular and overlapping hooked mesial thecae with 2TRD *ca* 2.7 mm, simply tubular distal thecae, and a rhabdosome dorsally arcuate without mesial tightening match the diagnostic features of *Pernerograptus vulgaris* (Hutt, 1974). The present limited material is retained in open nomenclature because the few flattened specimens do not allow for reasonable comparison with the markedly less robust (max 0.85 mm reported by Hutt 1974), but pyritized relief material of *P. vulgaris.*

Pernerograptus austerus (Törnquist, 1899)

Figures 17G, K, L, Q

1899 *Monograptus revolutus* Kurck var. *austerus*. – Törnquist, pp. 12–13, pl. 2, figs 12–14.

Figure 17. A – *Demirastrites*? cf. *toernquisti* (Sudbury, 1958): PŠ 3570. • B – *Pernerograptus* cf. *vulgaris* (Hutt, 1974): PŠ 3498, mesial fragment with elongated hooked thecae. • C, I, J, O, P – *Pernerograptus difformis* (Törnquist, 1899): C – PŠ 3457, mesial fragment showing transition from elongated proximal thecae to high-triangular mesial thecae; I – PŠ 3499, transition from high-triangular hooked mesial thecae to early distal thecae with paired lateral apertural lobes; J – PŠ 3524, O – PŠ 3459, mesial and distal parts of mature rhabdosome, distalmost portion not figured; P – PŠ 3561. • D – *Pernerograptus pribyli* sp. nov.: mesial fragment with rapid transition from hooked proximal thecae to geniculated mesial thecae with dorsal apertural hoods. • E – *Demirastrites* sp.: PŠ 3597, note short and widely separated metathecae. • F, H, M, N – *Demirastrites triangulatus* (Harkness, 1851): F – PŠ 3517, H – PŠ 3513, immature specimen without sicula and thl; M – PŠ 3643, juvenile rhabdosome showing sicula and th1; N – PŠ 3433. • G, K, L, Q – *Pernerograptus austerus* (Törnquist, 1899): G – PŠ 3645, mesial fragment showing hooked, moderately overlapping thecae; K – PŠ 3484b, note large number of hooked thecae and gradual transition to thecae with apertural hoods; L – PŠ 3484b, the same slab, transition from hooded thecae to simply tubular distal thecae; Q – PŠ 3646. • R – *Demirastrites major* (Elles & Wood, 1913): PŠ 3515, twisted thecae exhibit typical lateral horns on apertural hooks. A, E, F, H, M, N from the lower *triangulatus* Biozone; B–D, I, J, O, P from the *cyphus* Biozone; G, K, L, Q from the lower *cyphus* Biozone; R from the lower *pectinatus* Zone. All figures × 6; scale bar represents 1 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R

1911 *Monograptus revolutus* var. *austerus* Törnquist. – Elles & Wood, pp. 385–386, pl. 38, fig. 2a–c, text-fig. 254b (?a).
1941 *Pernerograptus revolutus austerus* (Törnquist). – Přibyl, pp. 4–5, pl. 2, figs 5, 6.
1974 *Monograptus austerus austerus* (Törnquist). – Hutt, p. 199, text-fig. 6a.
1988 *Monograptus austerus austerus* Törnquist. – Štorch, pp. 31–32, pl. 3, figs 2–4, text-fig. 2f, g, m.

Material. – 14 incomplete rhabdosomes and fragments, supplemented by collections from the Běleč section. Proximal end and sicula not found.

Remarks. – The description of the Bohemian specimens based upon material from Běleč (Štorch 1988) is completed and revised by new observations on the Všeradice material. The rhabdosome is dorsally arcuate throughout its length of more than 80 mm. At least 20 hooked thecae are developed in the proximal part, although the most proximal portion and sicula has not yet been found (*cf.* Hutt 1974). The rhabdosome widens very gradually from 0.3 mm to *ca* 0.6 mm in the proximal part; apertural hooks occupy about one-third of the rhabdosome width. In the mesial part of the rhabdosome, the apertural hooks retreated (Fig. 17G, K) leaving a ventrally facing apertural excavation capped by a hood – the remainder of the retreating dorsal wall resembling the homologous genicular flanges of *Huttagraptus* or *Pribylograptus*. This change takes place within 7–10 mesial thecae overlapping for one-third to two-fifths their length. Distal thecae are simply tubular with everted apertures, overlapping for *ca* half (Fig. 17L). The distal part of the rhabdosome is commonly 0.95 mm, exceptionally 1.0 mm wide. 2TRD decreases from 2.9–2.4 mm in the proximal part (7–8 thecae in 10 mm), through 2.3–2.0 mm in the mesial part to 2.1–1.95 mm distally (*ca* 10 thecae in 10 mm).

Pernerograptus austerus is common in the lower *cyphus* Biozone in the Prague Synform and may represent the earliest monograptid with truly hooked proximal thecae. Its potential evolutionary links with early pribylograptids is a matter of speculation until relevant studies on chemically isolated material are undertaken.

Genus *Demirastrites* Eisel, 1912, emend. herein

Type species. – *Rastrites triangulatus* Harkness, 1851; subsequently designated by Přibyl & Münch (1942); from Frenchland Burn near Moffat, Scotland.

Diagnosis. – Rhabdosome with proximally accentuated dorsal curvature. Sicula small, apex reaches about the level of the first metatheca at maximum. Thecae isolated, inclined at a high angle and hooked. Hooks extend transversely into a pair of horns. Mesial and distal thecae are more or less high-triangular in profile. Up to several proximal thecae may have very slender elongated prothecae slightly widening towards the base of widely separated, parallel-sided rastritiform metathecae.

Species included. – *Rastrites triangulatus* Harkness, 1851; *Monograptus pectinatus* Richter, 1853 (= *Graptolites fimbriatus* Nicholson, 1868b); *Monograptus triangulatus major* Elles & Wood, 1913; *Monograptus simulans* Pedersen, 1922; *Monograptus separatus separatus* Sudbury, 1958; *Rastrites orbitus* Churkin & Carter, 1970; *Rastrites guizhouensis* Mu *et al*., 1974; *Rastrites confertus* Chen & Lin, 1978 (= *Rastrites approximatus* Perner *sensu* Lenz 1982); *Rastrites cirratus* Ni, 1978 and probably *Monograptus paradenticulatus* Zalasiewicz, 1996.

Morphologically distinct and separated are species with elongated prothecae and relatively short isolated metathecae in the proximal part of the rhabdosome (*Monograptus nobilis* Törnquist, 1899; *Monograptus toernquisti toernquisti* Sudbury, 1958 and *Monograptus toernquisti brevis* Sudbury, 1958) and these may be only tentatively assigned to *Demirastrites* since their apertural morphology is unknown.

Demirastrites triangulatus (Harkness, 1851)

Figures 16A, B, 17F, H, M, N, 18B, C

partim 1851 *Rastrites triangulatus*; Harkness, p. 59, pl. 1, figs 3a, b (*non* 3c, d).
1912 *Demirastrites triangulatus.* – Eisel, p. 36, pl. 3, figs 8–12 (?6, 7, 13).
1913 *Monograptus triangulatus* Harkness. – Elles & Wood (*pars*), p. 471, pl. 47, figs 4a, c, d, f (*non* b, e); text-fig. 327b (*non* a, c).
1942 *Demirastrites triangulatus* (Harkness). – Přibyl & Münch (*pars*), p. 3, pl. 1, figs 1–5; text-fig. 1, figs 1, 2 (*non* 3).
1958 *Monograptus separatus triangulatus* (Harkness). – Sudbury, pp. 503–506, pl. 20, figs 52–63 (see for further synonymy).
1970 *Monograptus triangulatus triangulatus* (Harkness). – Rickards, pp. 80–81, text-fig. 18, fig. 1.
1975 *Monograptus triangulatus triangulatus* (Harkness). – Hutt, pp. 109–110, pl. 19, figs 1, 2; pl. 20, figs 2, 7.

Material. – 10 incomplete mature rhabdosomes and several proximal fragments, along with large collections from the Hlásná Třebaň and Karlík sections.

Description. – Hook-shaped rhabdosome with tight dorsal curvature proximally. Sicula 0.85–1.0 mm long,

0.15–0.17 mm wide at the aperture; the apex reaches a level just below the isolated th1 metatheca. The th1 metatheca and, in some specimens, also th2 metatheca are short, inclined at *ca* 30–40° to the rhabdosome axis. Subsequent proximal thecae are typically rastriform until th8–9. The thread-like protheca is 0.07–0.09 mm wide in the most proximal thecae, very slightly widening towards the base of metathecal tube which is 0.15–0.17 mm wide at th3, and *ca* 0.2 mm wide at th5. Thecal height rapidly increases from 0.3 mm at th1, through 0.7–0.8 mm at th3 and 1.0–1.1 mm at th4, to about 1.4 mm at th6. The maximum thecal height (width of the rhabdosome), 1.7 mm, is attained by the last purely rastritiform thecae. 2TRD is *ca* 1.6 mm at the level of th2 and 1.4–1.5 mm at th5. From about th9–10 the thecae become highly triangular, with broad bases and a parallel-sided, 0.55–0.6 mm-wide distal portions teminated by an apertural hook expanded laterally into a pair of small horn-like processes. Transverse extension of the apertural hook can be observed rarely, when the hook is axially twisted by sediment compaction. The protheca is 0.33–0.4 mm wide and relatively short in distal thecae which thus appear much less separated despite the greater values of 2TRD (1.9–2.1 mm). Distal thecae number 10 in 10 mm.

Remarks. – This material matches the detailed description of "*Monograptus*" *separatus triangulatus* (= *Demirastrites triangulatus*) provided by Sudbury (1958) in both the number of rastritiform thecae, rate of the rhabdosome widening and the maximum width of the rhabdosome. *Demirastrites separatus* (Sudbury) can be differentiated from *D. triangulatus* by its fewer rastritiform thecae in the proximal part succeeded by high-triangular and subsequently more robust thecae beginning at th6–7, and by the generally lesser thecal height (and rhabdosome width). Specimens morphologically equivalent to the present Všeradice material have been collected in the lower part of the *triangulatus* Biozone in the Hlásná Třebaň and Karlík sections whereas specimens closely resembling *D. separatus* are confined to the upper *triangulatus* and lower *pectinatus* biozones in these two sections. Sudbury (1958) reported "*M*." *separatus* from the Rheidol Gorge succession as ranging from the base of the *triangulatus* Band to the *magnus* Band in which the species accompanied "*M*." *fimbriatus* (= *Demirastrites pectinatus* of this paper). "*M*." *triangulatus* in turn was reported as an abundant component of about the middle–upper part of the *triangulatus* Biozone in the current sense.

***Demirastrites major* (Elles & Wood, 1913)**
Figures 17R, 18E

partim 1913 *Monograptus triangulatus* var. *major,* var. nov.; Elles & Wood, p. 472, pl. 47, fig. 5c (?5d, *non* 5a, b); text-fig. 328b (*non* 328a).
1958 *Monograptus separatus major* (Elles & Wood). – Sudbury, p. 506, text-fig. 10.
1963 *Monograptus triangulatus* var. *major* E. & W. – Willefert, pp. 45–46, ?pl. 2, fig. 2; text-fig. 73.
1970 *Monograptus triangulatus major* Elles & Wood. – Rickards, p. 81, text-fig. 18, fig. 2.
1975 *Monograptus triangulatus major* Elles & Wood. – Hutt, pp. 110–111; pl. 20, fig. 1 (see for further synonymy).

Material. – One incomplete rhabdosome and one fragment. Further material was collected from the Hlásná Třebaň section.

Description. – The rhabdosome is dorsally arcuate; the proximal part is missing. Distal thecae are up to 2.25 mm high, including prominent apertural hooks. Prothecae are 0.2 mm wide in the most proximal part available and 0.35 mm wide near the distal end of the rhabdosome. Metathecal tubes are ventrally curved, 0.35 mm wide in relatively proximal thecae and 0.5 mm wide in the most distal thecae. Apertural hooks are extended laterally into a pair of horn-like winglets, which are clearly demonstrated by thecae axially twisted by rock compaction. The dorsally facing aperture is mostly covered by the central lobe of the hook. Thecae number 11.5 in 10 mm with 2TRD *ca* 1.7 mm.

Remarks. – This species can be distinguished from *Demirastrites triangulatus* (Harkness) and the related forms *D. separatus* (Sudbury) and *D. pectinatus* (R. Richter) by having a greater dorso-ventral width (thecal height is 2.25 mm), markedly ventrally curved metathecae and prominent apertural hooks extended laterally into horn-like winglets. The present specimen, accompanied by a proximal fragment of *Demirastrites pectinatus* is from the stratigraphically highest level preserved in the loose stones from Všeradice. This material, as well as the specimens collected from the upper *triangulatus* and *pectinatus* biozones of the Hlásná Třebaň section match well the descriptions and illustrations of "*Monograptus triangulatus major* Elles & Wood" provided by Elles & Wood (1913), Sudbury (1958) and Hutt (1975).

***Demirastrites* sp.**
Figures 16C, 17E

Material. – Two incomplete rhabdosomes from Všeradice and limited material from Hlásná Třebaň.

Remarks. – This uncommon form differs from the other demirastritids of the *triangulatus* and *pectinatus* biozones by

its considerably shorter metathecae which attain a maximum height of 1.2 mm. The proximal end is missing in the present specimens but up to five rastritiform thecae can be observed. 2TRD ranges from 1.9 mm to 2.1 mm. Apertural hooks match those in *Demirastrites triangulatus* but both the prothecae and metathecae of *Demirastrites* sp. tend to be more gracile than the corresponding thecae of *D. triangulatus*. The species is known also from the middle *triangulatus* Biozone of the Hlasná Třebaň section. It is left in open nomenclature until better preserved and complete material is available.

Demirastrites? cf. *toernquisti* (Sudbury, 1958)

Figures 17A, 18A

cf. 1958 *Monograptus toernquisti* sp. nov.; Sudbury, p. 516, pl. 22, figs 84, ?88–90.

Material. – One immature rhabdosome. Several specimens have been found in the Hlásná Třebaň section.

Description. – The dorsally curved, 14 mm-long rhabdosome exhibits 3 or 4 axially elongated, low-triangulate hooked thecae in the proximal part. Proximal thecae are isolated; slight overlap is developed from about th8. The triangulate distal thecae overlap for max. one-fifth of their length. The rhabdosome widens from *ca* 0.2 mm at th1 through 0.38 mm at th3 and 0.6 mm at th5 to the maximum width of 0.9 mm attained at th10. 2TRD is 2.9 mm at th2, 2.3 mm at th5 and decreases to about 1.9 mm at th10. Apertural hooks may be slightly laterally extended in distal thecae.

Remark. – This rhabdosome and rare specimens from the *triangulatus* Biozone of the Hlásná Třebaň section resemble "*M.*" *toernquisti* in having an open arcuate rhabdosome with several axially elongated proximal thecae and subsequent thecae becoming triangular in shape with small hooked apertures. The present material, however, differs from "*M.*" *toernquisti* in possessing about half its rhabdosome width, although none of the Czech specimens is a mature rhabdosome. The species is assigned tentatively to *Demirastrites* because of the isolated, axially elongated hooked proximal thecae and equally isolated triangular distal thecae. Similar thecae may be expected in the early species of *Campograptus* Obut, 1949.

Genus *Rastrites* Barrande, 1850, emend. Štorch, 1998

Type species. – *Rastrites peregrinus* Barrande, 1850; subsequently designated by Hopkinson (1869); from the Llandovery of Bohemia.

Rastrites longispinus Perner, 1897

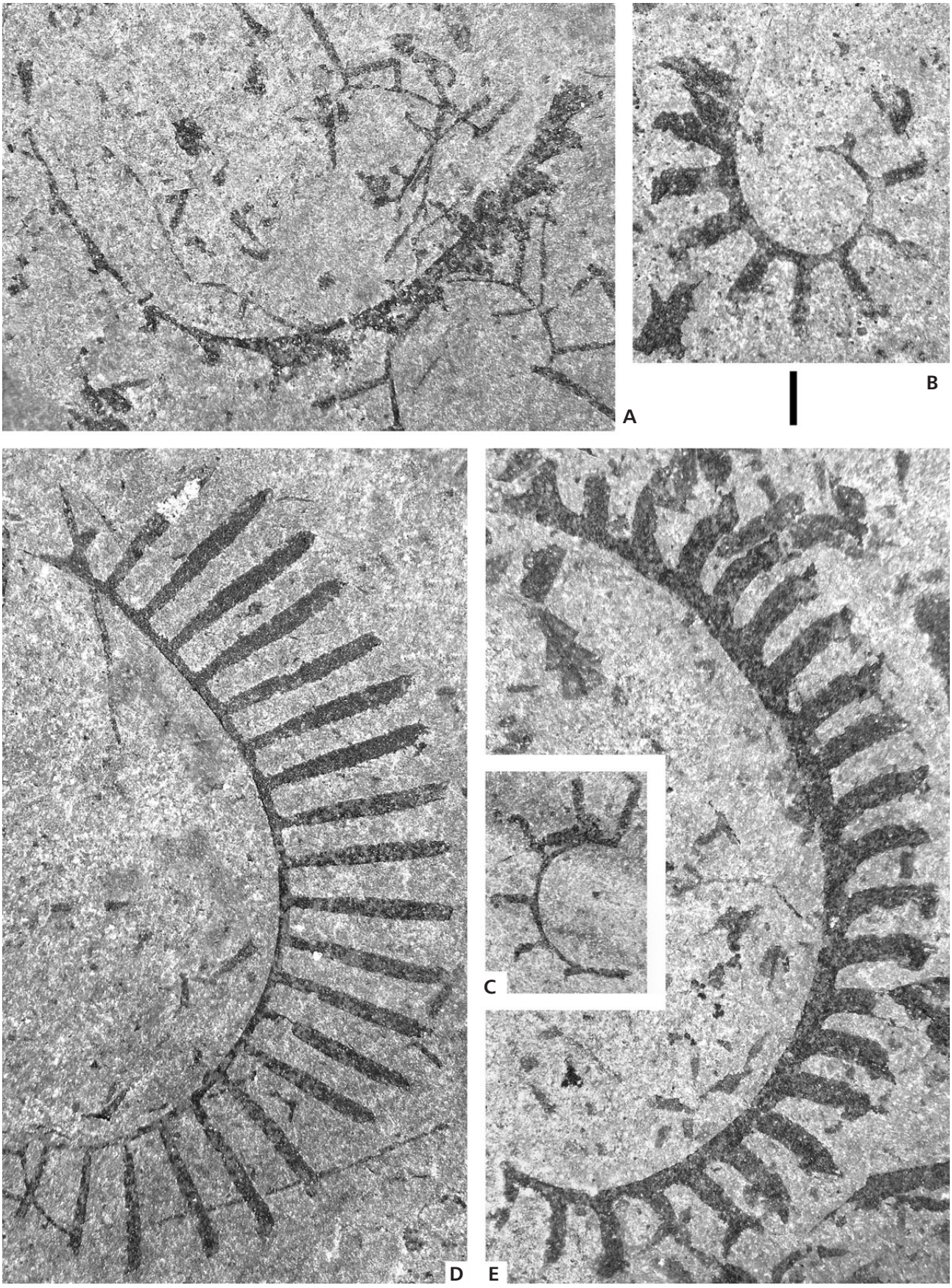
Figures 16D, 18D

1897 *Rastrites peregrinus* var. *longispinus* mihi; Perner, p. 9, pl. 13, figs 32, 35; text-fig. 7.
1914 *Monograptus* (*Rastrites*) *longispinus* (Perner). – Elles & Wood, p. 489, pl. 50, figs 2a–g; text-fig. 344a, b.
1941 *Rastrites longispinus* Perner. – Přibyl, pp. 6–7, pl. 1, figs 1–3; pl. 2, fig. 3; text-fig. 4.
1958 *Rastrites longispinus* (Perner). – Sudbury, p. 525, pl. 21, fig. 71; text-fig. 23.
1970 *Rastrites longispinus* Perner. – Rickards, p. 96, pl. 8, figs 2, ?6; text-fig. 18, fig. 9.
1971 *Rastrites longispinus* Perner. – Schauer, p. 176, pl. 2, figs 1, 2.
1975 *Rastrites longispinus* Perner. – Hutt, pp. 113–114, pl. 25, figs 2, 4, 5; pl. 26, fig. 3 (*non* 6); text-fig. 26, fig. 7.
1975 *Rastrites longispinus* Perner. – Bjerreskov, pp. 82–83, pl. 12, fig. g.

Material. – Twelve more or less complete rhabdosomes.

Description. – Rhabdosome dorsally curved throughout its length with curvature tightened in the proximal part. The sicula has not been found in the limited Všeradice material. The thecae are typical rastritiform, with thread-like prothecae and long isolated tubular metathecae growing approximately perpendicular to the rhabdosome axis. Proximal metathecae are slender, *ca* 1.1 mm high and only 0.1–0.12 mm wide. Proximal prothecae, although flattened, are only 0.08 mm wide. Metathecae of the distal thecae are 0.2 mm wide at their base, widening to 0.32–0.36 mm within the second-third of the length of the metathecal tube. The maximum height of the metatheca, 2.9–3.6 mm, is attained in the distal part of the nearly 20 mm long rhabdosomes at hand. Each metatheca is terminated by a small, proximally facing apertural hook. Distal prothecae are 0.17–0.19 mm wide, slightly broadened before and after the metathecal tube. Considerable variation was recorded in 2TRD which is 1.35–1.9 mm in

Figure 18. A – *Demirastrites*? cf. *toernquisti* (Sudbury, 1958): PŠ 3570. • B, C – *Demirastrites triangulatus* (Harkness, 1851): B – PŠ 3513, immature specimen without sicula and th1; C – PŠ 3643, juvenile rhabdosome showing sicula and th1. • D – *Rastrites longispinus* Perner, 1897: PŠ 3570. • E – *Demirastrites major* (Elles & Wood, 1913): PŠ 3515, specimen with twisted thecae exhibits typical lateral horns on apertural hooks, associated with juvenile *Pseudorthograptus* sp. A–D from the lower *triangulatus* Biozone; E from the lower *pectinatus* Biozone. All figures × 10; scale bar represents 1 mm.


A
B
C
D
E

proximal thecae and 1.55–2.2 mm in distal thecae. The longer the metathecae that are developed in a particular rhabdosome, the shorter are its prothecae and, consequently, lower 2TRD values occur.

Remarks. – The limited number of loose rocks containing *R. longispinus* is consistent with its lowest occurrences recorded well above the base of the *triangulatus* Biozone in bed-by-bed studied sections of the Prague Synform (see Štorch 1994 and Štorch *et al*. 2014) since material from the higher part of the *triangulatus* Biozone is limited in the Všeradice collections. The most proximal part of *R. longispinus* is closely similar to that of *Demirastrites triangulatus* in the form and size of the sicula and in the morphology, inclination and spacing of the isolated metathecae. In *R. longispinus*, however, rastritiform thecae with a narrow base of the metatheca persisted throughout the rhabdosome, becoming also substantially higher than the triangulate metathecae of any *Demirastrites*.

Acknowledgements

The author greatly appreciate the financial support provided by the Institute of Geology of the CAS (RVO 67985831) and the Czech Science Foundation through project 14-16124S. Special thanks are due to David Loydell and Jan Zalasiewicz for their helpful comments on the earlier version of the manuscript and improvement of the English. This paper is a contribution to the IGCP project No. 591 (The Early to Middle Paleozoic Revolution).

References

Barrande, J. 1850. *Graptolites de Bohême*. 74 pp. Published by the author, Prague.

Bates, D.E.B. & Kirk, N.H. 1984. Autecology of Silurian graptolites. *Special Papers in Palaeontology 32*, 121–139.

Bates, D.E.B. & Kirk, N.H. 1987. The role of extrathecal tissue in the construction and functioning of some Ordovician and Silurian retiolitid graptoloids. *Bulletin of the Geological Society of Denmark 35*, 85–102.

Bates, D.E.B. & Kirk, N.H. 1992. The ultrastructure, mode of construction and functioning of a number of Llandovery ancorate diplograptid and retiolitid graptolites. *Modern Geology 17*, 1–270.

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

Bouček, B. 1944. O některých ostnitých diplograptidech českého a saského siluru. *Rozpravy České akademie věd a umění, Třída 2 (1943), 53(25)*, 1–6. [in Czech]

Bouček, B. 1953. Biostratigraphy, development and correlation of the Želkovice and Motol beds of the Silurian of Bohemia. *Sborník Ústředního ústavu geologického, Oddíl paleontologický 20*, 421–484.

Bulman, O.M.B. 1936. *Rhaphidograptus*, a new graptolite genus. *Geological Magazine 73*, 19–26. DOI 10.1017/S001675680008732X

Bulman, O.M.B. 1955. Graptolithina. *In* Moore, R.C. (ed.) *Treatise on invertebrate paleontology. Part V*. 101 pp. Geological Society of America & University of Kansas Press, New York & Lawrence.

Bulman, O.M.B. & Rickards, R.B. 1968. Some new diplograptids from the Llandovery of Britain and Scandinavia. *Palaeontology 11*, 1–15.

Chen Xu & Lin Yao-kun 1978. Lower Silurian graptolites from Tongzi, northern Guizhou. *Memoirs of the Nanjing Institute of Geology and Palaeontology, Academia Sinica 12*, 1–76. [in Chinese]

Churkin, M., Jr. & Carter, C. 1970. Early Silurian graptolites from southeastern Alaska and their correlation with graptolitic sequences in North America and the Arctic. *United States Geological Survey Professional Paper 653*, 1–51.

Desio, A. 1940. Fossili neosilurici del Fezzan occidentale. *Annali del Museo Libico di Storia Naturale 2*, 13–45.

Eisel, R. 1912. Über zonenweise Entwicklung der Rastriten und Demirastriten. *Jahresberichte der Gesellschaft von Freunde der Naturwissenschaften in Gera 53/54*, 27–43.

Elles, G.L. & Wood, E.M.R. 1901–1918. A monograph of British graptolites. *Monograph of the Palaeontographical Society*, *Part 5, 1906, 60(288)*, 181–216; *Part 6, 1907, 61(297)*, 217–272; *Part 7, 1908, 62(305)*, 273–358; *Part 8, 1911, 64(316)*, 359–414; *Part 9, 1913, 66*(323), 415–486; *Part 10, 1914, 67(327)*, 487–526.

Frýda, J. & Štorch, P. 2014. Carbon isotope chemostratigraphy of the Llandovery in northern peri-Gondwana: new data from the Barrandian area, Czech Republic. *Estonian Journal of Earth Sciences 63(4)*, 220–226. DOI 10.3176/earth.2014.22

Harkness, R. 1851. Description of the graptolites found in the black shales of Dumfriesshire. *Quarterly Journal of the Geological Society of London 7*, 58–65. DOI 10.1144/GSL.JGS.1851.007.01-02.16

Hisinger, H. 1837. *Lethaea Suecica seu Petrifacta Suecica, Supplementum 1*. 124 pp. Stockholm.

Hopkinson, J. 1869. On British graptolites. *Journal of Quekett Microscopic Club 1*, 151–166.

Hundt, R. 1942. Beiträge zur Kenntnis des Mitteldeutschen Graptolithenmeeres. *Beiträge zur Geologie von Thüringen 6*, 205–231.

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

Hutt, J.E. 1974b. A new group of Llandovery biform monograptids, 189–203. *In* Rickards, R.B., Jackson, D.E. & Hughes, C.P. (eds) *Graptolite Studies in honour of O.M.B. Bulman. Special Papers in Palaeontology 13*.

Hutt, J.E. 1975. The Llandovery graptolites of the English Lake District. Part 2. *Monograph of the Palaeontographical Society 129(542)*, 57–137.

Hutt, J.E. & Rickards, R.B. 1970. The evolution of the earliest Llandovery monograptids. *Geological Magazine 107*, 67–77. DOI 10.1017/S0016756800054716

Jones, O.T. 1909. The Hartfell-Valentian succession in the district around Plynlimon and Pont Erwyd (North Cardigan-

shire). *Quarterly Journal of the Geological Society of London 65*, 463–537. DOI 10.1144/GSL.JGS.1909.065.01-04.32

Jones, W.D.V. & Rickards, R.B. 1967. *Diplograptus penna* Hopkinson, 1869, and its bearing on vesicular structures. *Paläontologische Zeitschrift 41*, 173–185. DOI 10.1007/BF02988120

Koren', T.N. & Bjerreskov, M. 1997. Early Llandovery monograptids from Bornholm and the southern Urals: taxonomy and evolution. *Bulletin of the Geological Society of Denmark 44*, 1–43.

Koren', T.N. & Melchin, M.J. 2000. Lowermost Silurian graptolites from the Kurama Range, eastern Uzbekistan. *Journal of Paleontology 74*, 1093–1113. DOI 10.1666/0022-3360(2000)074<1093:LSGFTK>2.0.CO;2

Koren', T.N., Mikhaylova, N.F. & Tzai, D.T. 1980. Class Graptolithina. Graptolites, 121–170. *In* Apollonov, M.K., Nikitin, I.F. & Bandaletov, S.M. (eds) *The Ordovician-Silurian boundary in Kazakhstan*. 232 pp. Nauka Kazakh SSR, Alma-Ata. [in Russian]

Koren', T.N. & Rickards, R.B. 1996. Taxonomy and evolution of Llandovery biserial graptoloids from the southern Urals, western Kazakhstan. *Special Papers in Palaeontology 54*, 1–103.

Koren', T.N. & Rickards, R.B. 2004. An unusually diverse Llandovery (Silurian) diplograptid fauna from the southern Urals of Russia and its evolutionary significance. *Palaeontology 47*, 859–918. DOI 10.1111/j.0031-0239.2004.00411.x

Kurck, C. 1882. Några nya graptolitarter från Skåne. *Geologiska Föreningens i Stockholm Förhandlingar 6*, 294–304. DOI 10.1080/11035898209455586

Lapworth, C. 1873. On an improved classification of the Rhabdophora. *Geological Magazine 10(1)*, 500–504, 555–560. DOI 10.1017/S0016756800469256

Lapworth, C. 1876. On Scottish Monograptidae. *Geological Magazine 3(2)*, 308–321, 350–360, 499–507, 544–552. DOI 10.1017/S0016756800154883

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

Legrand, P. 1970. Les couches a Diplograptus du Tassili de Tarit (Ahnet, Sahara algérien). *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 60*, 3–58.

Legrand, P. 1987. Modo de desarrollo del Suborden Diplograptina (Graptolithina) en el Ordovícico Superior y en el Silúrico. Implicaciones taxonómicas. *Revista Española de Paleontología 2*, 59–64.

Legrand, P. 1995. A propos d'un niveau à *Neodiplograptus* dans le Silurien inférieur à l'est de Ouallene, Asejrad (Sahara algérien). Implications stratigraphiques et paléogéographiques. *118e Congres national des Sociétés historiques et scientifique, 4e colloque sur la Géologie africaine, Pau 1993,* 409–424.

Legrand, P. 2002. La formation des argiles de Tedjert (?Ordovicien terminal–Silurien inférieur) au Tassili Oua-n-Ahaggar oriental (Sahara algérien) et sa faune graptolitique. *Annales de la Société géologique du Nord, Série 2 9*, 215–229.

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

Loydell, D.K. 1991. Isolated graptolites from the Llandovery of Kallholen, Sweden. *Palaeontology 34*, 671–693.

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

Loydell, D.K. 2007. Graptolites from the Upper Ordovician and Lower Silurian of Jordan. *Special Papers in Palaeontology 78*, 1–66.

Loydell, D.K. 2012. Graptolite biostratigraphy of the E1-NC174 core, Rhuddanian (lower Llandovery, Silurian), Murzuq Basin, Libya. *Bulletin of Geosciences 87(4)*, 651–660. DOI 10.3140/bull.geosci.1311

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

Loydell, D.K. & Maletz, J. 2009. Isolated graptolites from the *Lituigraptus convolutus* Biozone (Silurian, Llandovery) of Dalarna, Sweden. *Palaeontology 52(2)*, 273–296. DOI 10.1111/j.1475-4983.2008.00843.x

Lukasik, J.J. & Melchin, M.J. 1997. Morphology and classification of some Early Silurian monograptids (Graptoloidea) from the Cape Phillips Formation, Canadian Arctic Islands. *Canadian Journal of Earth Sciences 34*, 1128–1149. DOI 10.1139/e17-091

Melchin, M.J. 1998. Morphology and phylogeny of some early Silurian 'diplograptid' genera from Cornwallis Island, Arctic Canada. *Palaeontology 41*, 263–315.

Melchin, M.J. 1999. Origin of the Retiolitidae from a new graptolite genus from the early Silurian of Arctic Canada. *Lethaia 32*, 261–269. DOI 10.1111/j.1502-3931.1999.tb00544.x

Melchin, M.J. & Koren', T.N. 2001. Morphology and phylogeny of some early Silurian (mid-Rhuddanian) monograptid graptolites from the south Urals of Russia. *Journal of Paleontology 75(1)*, 165–185. DOI 10.1666/0022-3360(2001)075<0165:MAPOSE>2.0.CO;2

Mitchell, C.E. 1987. Evolution and phylogenetic classification of the Diplograptacea. *Palaeontology 30*, 353–405.

Mu En-zhi, Li Ji-jin, Ge Mei-yu, Chen Xu, Ni Yu-nan & Lin Yao-kun 1974. Silurian Graptoloidea, 211–231. *In* Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.) *A handbook of the stratigraphy and palaeontology of south-west China.* 454 pp. Science Press, Beijing. [in Chinese]

Mu En-zhi, Li Ji-jin, Ge Mei-yu, Lin yao-kun & Ni Yu-nan 2002. *Graptolites of China*. 1205 pp. Science Press, Beijing. [in Chinese]

Nicholson, H.A. 1868a. On the nature and zoological position of the Graptolitidae. *Annals and Magazine of Natural History 1(4)*, 55–61. DOI 10.1080/00222936808695638

Nicholson, H.A. 1868b. On the graptolites of the Coniston Flags; with notes on the British species of the genus *Graptolites*. *Quarterly Journal of the Geological Society of London 24*, 521–545. DOI 10.1144/GSL.JGS.1868.024.01-02.67

Nicholson, H.A. 1869. On some new species of graptolites. *Annals and Magazine of Natural History 4(4)*, 231–242. DOI 10.1080/00222936908696041

Ni Yu-nan 1978. Lower Silurian graptolites from Yichang, western Hubei. *Acta Palaeontologica Sinica 17*, 387–416. [in Chinese]

Obut, A.M. 1949. *Polevoi atlas rukovodyashcikh graptolitov verkhnego silura Kirgizkoi SSR*. 56 pp. Izdatelstvo Kirgizskoi Fil. Akademii nauk, SSSR, Frunze. [in Russian]

Obut, A.M. 1965. Graptolity silura Omulevskikh gor (Bassein reky Kolymy), 33–46. *In Stratigrafia i paleontologia asiatskoy chasti USSR*. Nauka, Moskva. [in Russian]

Obut, A.M. & Sobolevskaya, R.F. 1966. *Graptolites of the Lower Silurian in Kazakhstan.* 56 pp. Akademia nauk USSR, Sibirskoe otdelenie, Institut geologii i geofiziki, Moskva. [in Russian]

Obut, A.M., Sobolevskaya, R.F. & Bondarev, V.I. 1965. *Graptolity silura Taimyra*. 120 pp. Akademia nauk USSR, Sibirskoe otdelenie, Institut geologii i geofiziki, Moskva. [in Russian].

Obut, A.M., Sobolevskaya, R.F. & Merkureva, A.P. 1968. *Graptolity Llandoveri v kernach burovych skvazhin Norilskogo rayona*. 162 pp. Akademia nauk USSR, Sibirskoe otdelenie, Institut geologii i geofiziki, Moskva. [in Russian].

Obut, A.M., Sobolevskaya, R.F. & Nikolaev, A.A. 1967. *Graptolites and stratigraphy of the lower Silurian along the margins of the Kolyma massif.* 164 pp. Akademia nauk USSR, Sibirskoe otdelenie, Institut geologii i geofiziki. Ministerstvo geologii SSSR, Nauchno-issledovatel'sky institut geologii Arktiki. [in Russian]

Packham, G.H. 1962. Some diplograptids from the British Lower Silurian. *Palaeontology 5*, 498–526.

Paškevičius, J. 1976. On some new Llandoverian diplograptids of the eastern Baltic, 140–151. *In* Kaljo, D. & Koren', T.N. (eds) *Graptolites and stratigraphy.* 256 pp. Academy of Sciences of Estonian SSR, Tallinn.

Paškevičius, J. 1979. *Biostratigraphy and graptolites of the Lithuanian Silurian*. 266 pp. Mosklas Publishing House, Vilnius. [in Russian]

Pedersen, T.B. 1922. Rastritesskiferen på Bornholm. *Meddelelser fra Dansk Geologisk Forening 6(11)*, 1–29.

Perner, J. 1895. *Études sur les Graptolites de Bohême. IIième Partie. Monographie des Graptolites de l'Étage D.* 31 pp. Raimond Gerhard, Prague.

Perner, J. 1897. *Études sur les graptolites de Bohême. Part 3, section a*. 25 pp. Prag.

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

Přibyl, A. 1942. *Pernerograptus* nov. gen. a jeho zástupci z českého a cizího siluru. *Věstník Královské České společnosti nauk, Třída matematicko-přírodovědecká 1941*, 1–18. [in Czech]

Přibyl, A. 1947. Classification of the Genus Climacograptus Hall, 1865. *Bulletin international de l'Académie tchèque des Sciences 58*, 1–12.

Přibyl, A. 1948. Bibliographic index of Bohemian Silurian graptolites. *Knihovna Státního geologického ústavu České republiky 22*, 1–96.

Přibyl, A. & Münch, A. 1941. Revize středoevropských zástupců rodu *Demirastrites* Eisel. *Rozpravy České akademie věd a umění, Třída 2 51(31)*, 1–29.

Richter, R. 1853. Thüringische Graptolithen. *Zeitschrift der Deutschen geologischen Gesellschaft 5*, 439–464.

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

Rickards, R.B. 1974. A new monograptid genus and the origins of the main monograptid genera, 141–147. *In* Rickards, R.B., Jackson, D.E. & Hughes, C.P. (eds) *Graptolite Studies in honour of O.M.B. Bulman. Special Papers in Palaeontology 13*.

Rickards, R.B. 1976a. Classification of *Monograptus*; a redefinition of some Llandovery graptolite genera, 155–162. *In* Kaljo, D. & Koren', T.N. (eds) *Graptolites and stratigraphy*. Academy of Sciences of Estonian SSR, Institute of Geology, Tallinn.

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

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

Rickards, R.B. & Koren', T.N. 1974. Virgellar meshworks and sicular spinosity in Llandovery graptoloids. *Geological Magazine 111*, 193–204. DOI 10.1017/S0016756800038437

Rickards, R.B., Wright, A.J. & Hamedi, M.A. 2000. Late Ordovician and Early Silurian graptolites from southern Iran. *Records of the Western Australian Museum, Supplement 58*, 103–122.

Russel, J.C., Melchin, M.J. & Koren', T.N. 2000. Development, taxonomy and phylogenetic relationships of species of *Paraclimacograptus* (Graptoloidea) from the Canadian Arctic and the Southern Urals of Russia. *Journal of Paleontology 74*, 84–91. DOI 10.1666/0022-3360(2000)074<0084:DTAPRO>2.0.CO;2

Schauer, M. 1971. Biostratigraphie und Taxionomie der Graptolithen des tieferen Silurs unter besonderer Berucksichtigung der tektonischen Deformation. *Freiberger Forschungshefte, C273 Paläontologie*, 1–185.

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

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

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

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

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

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

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

ŠTORCH, P. 2006. Facies development, depositional settings and sequence stratigraphy across the Ordovician-Silurian boundary: a new perspective from the Barrandian area of the Czech Republic. *Geological Journal 41*, 163–192. DOI 10.1002/gj.1038

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

ŠTORCH, P., MANDA, Š. & TASÁRYOVÁ, Z. 2014. Rhuddanian–Aeronian boundary strata in graptolite-bearing black shale succession of the Barrandian area (Czech Republic), 148–151. *In* ZHAN RENBIN & HUANG BING (eds) *IGCP 591 Field Workshop 2014, Kunming China, 12–21 August 2014, Extended Summary*. Nanjing University Press, Nanjing.

ŠTORCH, P., MITCHELL, C.E., FINNEY, S.C. & MELCHIN, M.J. 2011. Uppermost Ordovician (upper Katian–Hirnantian) graptolites of north-central Nevada, U.S.A. *Bulletin of Geosciences 86(2)*, 301–386. DOI 10.3140/bull.geosci.1264

ŠTORCH, P. & SERPAGLI, E. 1993. Lower Silurian graptolites from southwestern Sardinia. *Bollettino della Società Paleontologica Italiana 32*, 3–57.

STRACHAN, I. 1997. A bibliographic index of British graptolites (Graptoloidea). Part 2. *Monograph of the Palaeontographical Society 151(603)*, 41–155.

SUDBURY, M. 1958. Triangulate monograptids from the *Monograptus gregarius* Zone (Lower Llandovery) of the Rheidol Gorge (northern Cardiganshire). *Philosophical Transactions of the Royal Society of London, Series B 241*, 485–555. DOI 10.1098/rstb.1958.0011

SUESS, F.E. 1851. Über böhmische Graptolithen. *Naturwissenschaftliche Abhandlungen von W. Haidinger 4*, 87–134.

TOGHILL, P. 1968a. A new Lower Llandovery graptolite from Coalpit Bay, County Down. *Geological Magazine 105*, 384–386. DOI 10.1017/S0016756800054443

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

TOGHILL, P. 1968c. The graptolite assemblages and zones of the Birkhill Shales (Lower Silurian) at Dobb's Linn. *Palaeontology 11*, 654–668.

TÖRNQUIST, S.L. 1892. Undersökningar öfver Siljansomradets graptoliter, Part 2. *Lunds Universitets Arsskrifter 28*, 1–47.

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

WILLEFERT, S. 1963. Les Graptolites du Silurien inferieur du jbel Eguer-Iguiguena (SW d'Ito anticlinorium de Kasba-Tadla-Azrou, Maroc central). *Notes et Memoires du Service geologique, Rabat 177*, 1–70.

ZALASIEWICZ, J. 1992. Two new graptolites from the early Silurian (Llandovery: Aeronian) of central Wales: an origin for monoclimacid thecal morphology. *Geological Magazine 129(6)*, 779–785. DOI 10.1017/S0016756800008505

ZALASIEWICZ, J. 1996. Aeronian (Silurian: Llandovery) graptolites from central Wales. *Geologica et Palaeontologica 30*, 1–14.

ZALASIEWICZ, J.A., TAYLOR, L., RUSHTON, W.A., LOYDELL, D.K., RICKARDS, R.B. & WILLIAMS, M. 2009. Graptolites in British stratigraphy. *Geological Magazine 146*, 785–850. DOI 10.1017/S0016756809990434

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

ZALASIEWICZ, J., WILLIAMS, M. & AKHURST, M. 2003. An unlikely evolutionary lineage: the Rhuddanian (Silurian, Llandovery) graptolites *Huttagraptus*? *praematurus* and *Coronograptus cyphus* re-examined. *Scottish Journal of Geology 39(1)*, 89–96. DOI 10.1144/sjg39010089