MIDDLE TO LATE TELYCHIAN (SILURIAN: LLANDOVERY) GRAPTOLOTE ASSEMBLAGES OF CENTRAL WALES

by JAN ZALASIEWICZ

ABSTRACT. Graptolite faunas from the uppermost turriculatus, crispus, griesonii, crenulata and spiralis Biozones of central Wales are described. Detailed collecting integrated with recent BGS mapping has demonstrated a new subzone of Torquigraaptus carnicus in the uppermost turriculatus Biozone, a subdivision of the crispus Biozone into three successive subzones of, in ascending order: Monoclimacis? galaensis, Monograptus crispus, and Streptograptus sartorius; an informal subdivision of the griesonii Biozone into two successive assemblages, and the presence of faunas which can be assigned to the late Telychian crenulata and, probably, the spiralis Biozones. The compositions of these successive assemblages are outlined, and selected graptolites are figured and described. These include two new species: Monograptus pseudocommunis and Streptograptus whitei.

Most early studies of the Llandovery graptolite faunas from central Wales concentrated on assemblages from Rhaudanian and Aeronian strata (e.g. Lapworth 1900; Jones 1909; Davies 1929; Sudbury 1958) and a number of the standard British graptolite biozones stem from those works (see Rickards 1976; Zalasiewicz 1990). Upper Llandovery (Telychian) faunas were, until recently, relatively neglected, because of the great thickness and structural complexity of the Telychian deposits of central Wales. Only one of the early major studies (Wood 1906 on the Tarannon area) focused on this part of the sequence. More recent work has, however, demonstrated the biostratigraphical potential of the well-preserved graptolite faunas preserved within parts of the thick Telychian turbidite sequences of Wales. Loydell (1991, 1992a, 1993b) in particular, has effected a detailed subdivision of the turriculatus Biozone in west-central Wales.

Recent mapping by the British Geological Survey of the Rhayader and Llanilar districts (Text-fig. 1; Davies et al. in press) has enabled many sections yielding faunas referable to the uppermost turriculatus, crispus, griesonii, and crenulata Biozones of the standard British sequence (as outlined in Rickards 1976, 1989; Zalasiewicz 1990) to be examined. This paper summarizes the biostratigraphical results of this BGS work. The sequence of faunas is outlined, and descriptions are made of selected taxa, including two new species. All fossil material referred to is lodged with the British Geological Survey, Keyworth, unless stated otherwise.

GEOLOGICAL SETTING

Details of the stratigraphy, and of the main sections studied, are given in Davies et al. (in press). The succession comprises a number of thick turbidite formations. The hemipelagic intervals between individual turbidites are commonly bioturbated but otherwise unfossiliferous. Some stratigraphical intervals, though, contain hemipelagicites in which a fine primary lamination, the result of deposition in anoxic bottom conditions (Cave 1979) is preserved. Such hemipelagicites contain a well-preserved graptolite fauna as do, locally, some turbidite sandstones. The graptolite-bearing hemipelagicites tend to be most common in strata of late turriculatus and crispus Biozone age; they are rarer in the
**TEXT-FIG. 1.** Location of study area (boxed) in Wales. Outcrop of Llandovery sediments shown by stippled ornament.

*griestoniensis* Biozone and scarce in younger Telychian strata. Continuously anoxic sea floor conditions were re-established close to the Llandovery–Wenlock boundary (Davies *et al.* in press).

**PRESERVATION**

The Llandovery graptolites of the Rhayader and Llanilar district are mainly preserved in partial to full relief. Fragmentary periderm is preserved frequently, and usually surrounds an internal mould of pyrite or limonite. Specimens infilled by sediment or preserved as hollow external moulds are less common. Although often showing well-preserved thecal structures, commonly the graptolites were obtained only as partial rhabdosomes because, during collection, the rock fractured along cleavage and not bedding. This caused particular problems with the recognition of some graptolite taxa, notably the spiraliform monograptids. Graptolites in turbidite sandstones commonly lack a pyrite infill and are mostly diagnostically flattened.

The graptolites are variably deformed, depending on the mode of preservation, degree of tectonism and enclosing lithology. Brittle fracture of pyritized graptolites is typical, the graptolites being broken into segments at their weakest points; the segments tend to be arranged in an imbricate fashion where the long axis of the rhabdosome is perpendicular to the cleavage lineation. Where possible, dimensions of deformed graptolites were taken parallel to this lineation; in this orientation, the pyrite internal moulds tended to resist tectonic compression, while the nature of the brittle fracture indicated that extension parallel to the long axis of the rhabdosome was commonly slight.

**BIOSTRATIGRAPHY**

This paper summarizes the graptolite biostratigraphy from the upper part of the *turriculatus* Biozone to the upper part of the *crenulata* Biozone *sensu* Rickards (1976, 1989), an interval here referred to the *spiralis* Biozone by comparison with sequences in mainland Europe. The
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biostatigraphy outlined here has been applied within the central Welsh Basin; it is not yet known to what extent it is applicable elsewhere. Ranges of taxa reported from other sequences (e.g. Bouček 1953) differ in detail, and it is not yet clear whether this is due largely to faunal diachronity or to problems of identification. The ranges of taxa are given in Text-figure 2.

Spirograptus turriculatus Biozone

Loydell's (1991) subdivision of the turriculatus Biozone was employed during the survey, although often it was not possible to distinguish between the lowest three subzones. One additional subzone, that of Torquigraaptus carnicus, was employed in the survey to characterize strata forming the uppermost part of the turriculatus Biozone. A subsequent zonation by Loydell (1992a) separated a biozone of Spriograpthus guerichi (comprising the runcinatus to lower utilis Subzones) from the lower part of the turriculatus Biozone. The relations of these subzonal schemes is shown in Table 1.

Torquigraaptus carnicus Subzone

This subzone is marked by the incoming of Torquigraaptus carnicus (Gortani, 1923), Streptograpthus whitei sp. nov., S. exigus (Lapworth, 1876) and Monoclimacis? galaensis (Lapworth, 1876). Species ranging up from the proteus and earlier subzones include S. storchi Loydell, 1991, which is common, and the hooked monograptids Monograpthus marri Perner, 1897, and M. rickardsi Hutt, 1975. S. whitei and S. storchi have not yet been found in the overlying crispus Biozone though, in one instance, in the A44 road section near Llangurig (National Grid Reference SN 8580 8198). S. storchi has been found associated with M. aff. crispus, a narrower and more densely thecate form than M. crispus Lapworth, 1876. In the Czech Republic, S. storchi has been noted in the lower part of the crispus Biozone (D. K. Loydell, pers. comm.).

Monograpthus crispus Biozone

This is marked by the incoming of M. crispus Lapworth, 1876, and M. discus Törnquist, 1883 (= M. veles Richter, 1871). Neither is common near the base of the biozone and so recognition of the biozonal boundary locally is difficult. It is not known with certainty which of the two species appears first in central Wales. Bjerrskov (1975) showed the two species as appearing simultaneously on Bornholm, but in a graptolitic level above barren beds. The more continuously fossiliferous sections in Germany (Schauer 1971) and the Czech Republic (Bouček 1953) indicate that M. discus appears before M. crispus. Three successive assemblages can be recognized in the crispus Biozone of central Wales, and these are here formalized as subzones. They are, in ascending order:

1. Monoclimacis? galaensis Subzone

This is a partial-range subzone, its base defined by the overlap of Monoclimacis? galaensis, and T. carnicus with M. crispus, and M. discus. Petalolithus sp. 1 of this paper and Monograpthus aff. crispus are also present. Mcl? galaensis, T. carnicus, Pe. sp. 1, and M. aff. crispus have not been found to range higher in central Wales. M. clintonensis, and S. exigus are common, but M. crispus and M. discus occur only sporadically. The importance of Monoclimacis galaensis as an indicator of high turriculatus to low crispus Biozone strata has been noted by Bjerrskov (1975) and Rickards (1976).

2. Monograpthus crispus Subzone

This is a partial range subzone defined by the overlap of M. crispus and Streptograpthus loydelli Štorch and Serpagli, 1993. Both taxa are abundant.

3. Streptograpthus sartorius Subzone

This is the interval between the disappearance of M. crispus and the first appearance of the monoclimacid monograptids which characterize the griesenonensis Biozone. Torquigraaptus pragensis pragensis (Přibyl, 1943), T. pragensis ruzickai? (Přibyl, 1943), and Streptograpthus sartorius (Törnquist, 1881) appear for the first time.
<table>
<thead>
<tr>
<th>Species</th>
<th>Turriculatus Biozone</th>
<th>Carnicos Subzone</th>
<th>Galenia Subzone</th>
<th>Crispus Biozone</th>
<th>Creationensis Biozone</th>
<th>Lower Part</th>
<th>Upper Part</th>
<th>Spiralis Biozone</th>
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<td>X</td>
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<td>cf.</td>
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<td>cf.</td>
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<td>X</td>
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<tr>
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<td>R</td>
<td>A</td>
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<tr>
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<td>?</td>
<td>X</td>
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<tr>
<td>Monograptus prodon</td>
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<td>X</td>
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<td>?</td>
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<tr>
<td>Torquigrafixus ex. gr. pragensis? (slender form)</td>
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<td>A</td>
<td>A</td>
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<tr>
<td>Monograptidae vormansia vormansia</td>
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<tr>
<td>Monograptidae cf. crenulata sensu Elles and Wood</td>
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<tr>
<td>Monograptidae linnarssonii</td>
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<td>Monograptidae giezeneniensis nicoli</td>
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<td>Monograptus spiralis</td>
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<tr>
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</tbody>
</table>

**TEXT-FIG. 2.** Range-chart of species from the latest *turriculatus* Biozone (*carnicus* Subzone) to the *spiralis* Biozone in the area studied. X, taxon present; A, taxon abundant; R, taxon rare.
<table>
<thead>
<tr>
<th>ZALASIEWICZ: LATE LLANDOVERY GRAPTOLITES</th>
<th>379</th>
</tr>
</thead>
</table>

**Table 1. Subdivisions of the *turriculatus* Biozone used in west and central Wales.**

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td><em>crispus</em> Biozone</td>
<td><em>crispus</em> Biozone</td>
<td><em>carnicus</em> Biozone</td>
</tr>
<tr>
<td>(??) <em>proteus</em> Subzone</td>
<td><em>proteus</em> Subzone</td>
<td><em>proteus</em> Subzone</td>
</tr>
<tr>
<td><em>johnsonae</em> Subzone</td>
<td><em>johnsonae</em> Subzone</td>
<td><em>johnsonae</em> Subzone</td>
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<tr>
<td><em>utilis</em> Subzone</td>
<td><em>utilis</em> Subzone</td>
<td><em>utilis</em> Subzone</td>
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<tr>
<td><em>renaudi</em> Subzone</td>
<td><em>renaudi</em> Subzone</td>
<td><em>renaudi</em> Subzone</td>
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<td><em>gemmatus</em> Subzone</td>
<td><em>gemmatus</em> Subzone</td>
<td><em>gemmatus</em> Subzone</td>
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<tr>
<td><em>runcinatus</em> Subzone</td>
<td><em>runcinatus</em> Subzone</td>
<td>(not recognized)</td>
</tr>
<tr>
<td><em>guerichi</em> Biozone</td>
<td><em>turriculatus</em> Biozone</td>
<td><em>turriculatus</em> Biozone</td>
</tr>
</tbody>
</table>

Many assemblages in this subzone, as in the upper levels of the preceding *turriculatus* Biozone, are dominated by relatively non-diagnostic monograptids resembling *M. marreri* and *M. clintonensis* (sensu Hall, 1852). A comparable interval, lacking both *M. crispus* and monograptacids, was recognized by Wilson (1954) in the Howgill Fells, northern England and by Bjerreroskov (1975) on Bornholm.

**griestoniensis Biozone**

The base of this biozone is recognized by the appearance of two slender monograptids: *Mcl. griestoniensis* (Nicol, 1850), and the distinctive *Mcl. cf. griestoniensis* of Elles and Wood (1911). The latter appears slightly earlier in central Wales (see Zalasiewicz 1990, fig. 2; Davies *et al.* in press) and dominates the lower part of the biozone, along with species extending up from the upper part of the *crispus* Biozone, such as *T. pragensis* *pragensis*, *S. sartorius*, and *T. tullbergi* *spiraloideus* (Pflügl, 1945). *Mcl. griestoniensis*, rare in the lower part of the biozone, becomes common in the upper part.

**crenulata Biozone**

The *crenulata* Biozone, as traditionally recognized in Britain (e.g. Rickards 1976) occurs between the *griestoniensis* Biozone and the *centrifugus* Biozone. In Europe several other biozones have been recognized between a restricted *crenulata* Biozone and the *centrifugus* Biozone (e.g. Bouček 1953; Bjerreroskov 1975). These are difficult to recognize in Britain, partly because of a relative scarcity of anoxic, graptolite-bearing levels, and partly because of a scarcity of diagnostic fossils around the Llandovery–Wenlock boundary. However, elements of this more precise biostratigraphy have been recently identified in the UK (Loydell 1993a; Loydell and Cave 1993), and thus the *crenulata* Biozone has here a correspondingly restricted definition.

The incoming of broad vumeriniids, particularly *Mcl. vomerina vomerina* (Nicholson, 1872) is used to denote the lower boundary of this biozone; the zonal fossil, *Mcl. crenulata* (sensu Elles and Wood 1911) has been recognized at one locality (SO 0817 7417). Accompanying taxa include species continuing from earlier biozones such as *M. discus*, and *Torquigraptus tullbergi tullbergi* (Bouček 1931).

**Monograptus spiralis Biozone**

A single locality (SO 0092 7707) recorded in the highest graptolitic unit in the Dolgau Mudstones (the uppermost Telychian formation of the Rhayader/Llanilar districts; Davies *et al.* in press), yielded newcomer species such as *Monograptus linnarssoni* (Tullberg, 1883), *Monograptus parapriodon* Bouček, 1931, and *M. aff.*
TEXT-FIG. 3. For legend see opposite.
*Petalolithus* sp. 1 of this paper (Text-fig. 3e–g) is a smaller and more densely thecate species than comparable pentalograpidts such as *P. temuis*, and related diplagnostids such as the *Orthograptus* sp. of Hutt et al. (1970). It is more closely resembles *Petalolithus kurcki* (Rickards, 1970; see Text-fig. 3i and redescription in Loydell 1992a) from the *sedgwickii* to lower *turriculatus* Biozones, but differs in having a more convexly curved ventral wall of theca 1.

*Monoclimacus* cf. *griestoniensis* of Elles and Wood (1911) (Text-fig. 6o–r) is narrower than *Monoclimacus crenulata* (sensu Elles and Wood, 1911) (Text-fig. 8h–k; see Loydell et al. 1992 for a discussion of the nomenclature of this species) and more robust than *Monoclimacus griestoniensis* (Text-fig. 6u), with a different proximal and thecal morphology.

The material assigned tentatively to *Monoclimacus griestoniensis* nici R. Rickards, 1965 (Text-fig. 8l–m) resembles the type description. But, except for its narrowness, it also resembles *Mcl. linnarssoni* found at the same horizon; closer study may show that it lies within the latter's range of variability. The material here assigned to *linnarssoni* (Text-fig. 8n–q) agrees well with the detailed description given by Bjerring (1975, p. 55), the only difference being that Bjerring's material has a longer sicula (c. 1.8 mm) and theca 1. Rickards' (1965) material assigned to *Mcl. linnarssoni* from the *centrifugus* Biozone of the Howgill Fells appears not to be conspecific. The rhabosome in that material is more rapidly expanding, reaching 0.7 mm at 10h, has a maximum width of 1.7 mm, and the suprageneric walls appear quite straight rather than possessing a distinct convex curvature.

*Streptograptus storchi* (Text-fig. 3n) is a more robust 'straight streptograptid' than the approximately contemporaneous species *S. pseudobecki* (Bouček and Přibyl, 1942; Text-fig. 3m), which has been redescribed by Loydell (1990a).

*Streptograptus lloydelli* Štorch and Serpagli (Text-fig. 4t–l) can be distinguished from *S. exiguis* (Text-fig. 3b) by its greater width, the more marked distal expansion of the prothecae and by the

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**TEXT-FIG. 3. Graptolites from the *turriculatus* and lower *crispus* Biozones. a–c, *Torquigraptus carnicus* (Gortani, 1923); all on block BGS JZ1034; *turriculatus* Biozone, *carnicus* Subzone; quarry (SN 94457650) E of Cwmgwarwy Farm, 8 km NNW of Rhayader. d, *Streptograptus exiguis* (Nicholson, 1868); BGS JZ2173, *turriculatus* Biozone, *carnicus* Subzone; track section (SN 81876035) Twyi Forest. e–h, *Petalolithus* sp. 1; *crispus* Biozone, probably *galaensis* Subzone; stream section (SN 95875884) SW of Newbridge-on-Wye; e, BGS JZB39; f, BGS JZB40 (counterpart of e); g, BGS JZB35; h, BGS JZB33 (counterpart of g). i, *Petalolithus kurcki* (Rickards, 1970); BGS JZ6160; *turriculatus* Biozone, *tremaudi* Subzone; quarry near Bwch-y-ddual, Dyfed (SN 71096309). j–q, *Monograptus aff. criscus* Lapworth, 1876; BGS DJ3292; probably *turriculatus* Biozone, *carnicus* Subzone; A44 near Llangurig (SN 85808198). k, BGS JZ2984; lower *crispus* Biozone; Cwmgwarwy Farm (SN 94457650). m, *Streptograptus pseudobecki* (Bouček and Přibyl, 1942); BGS JZ6961, *turriculatus* Biozone, *proteus* Subzone; cliff section (SN 55727494) 7 km SSW of Aberystwyth. n, *Streptograptus storchi* Loydell, 1993b; BGS DJ3297; *turriculatus* Biozone, *carnicus* Subzone; road cutting (SN 85809198) near Llangurig. o–q, *Streptograptus whitei* sp. nov.; all *turriculatus* Biozone, *carnicus* Subzone; o, BGS JZ1035; quarry (SN 94457650), 8 km NW of Rhayader; part of near-proximal fragment. p–q, DJ7612 (holotype), section (SN 85086545) by Claerwen Reservoir; mesial and distal parts. All figures ×10 (larger scale bar represents 2 mm) except a, c, ×5 (smaller scale bar represents 2 mm).
TEXT-FIG. 4. For legend see opposite.
higher profile of the metatheca. *S. plumosus* (Baily, 1871), usually attains greater widths (of up to 0·9 mm) and has more robust prothecae (see Loydell 1990b). *Streptograptus aff. lloydelli* (Text-fig. 6i–o) has the same overall dimensions, but differs in being spinoise and in having a narrower thecae 2. It may be related to ‘Monograptus exigus’ C’ of Bjerreskov (1975), which is also spinoise, from the upper *crispus* Biozone of Bornholm. However, the single fragment of that taxon described is slightly narrower (0·5 mm) and has parallel prothecal walls and slightly lower profile metathecae.

The material of *Streptograptus sartorius* (Text-fig. 5a–f) compares well with toptyote material examined (that figured by Törnquist in 1892), with the only observable difference being slightly more widely spaced thecae in that material, with 2TRDs (2TRD = two thecae repeat distance: Howe 1983) of 2·0–2·1 mm. Some other toptyote fragments, however, show widths of up to 0·45 mm in relief, indicating more variation in the Swedish material than has been observed in that from central Wales. The material figured by Bouček and Přibyl (1951) from the *crenulata* Biozone of Bohemia appears different, with possibly hooked metathecae and more distinctively expanding prothecae. Several rhabdosome from one locality are here referred to *S. aff. sartorius* (Text-fig. 5c–k). These differ only in possessing lateral spines, which possibly reflect enhanced preservation of a feature present in all material of *S. sartorius*. *S. sartorius* can be confused with proximal fragments of *Monograptus crispus*; in that species, though, the proximal thecae are considerably more widely spaced (see below).

*Pristiograptus? aff. initialis* (Kirste, 1919) (Text-fig. 8c–d) differs from the typical form (Text-fig. 8c; = *Monoclimacis shottoni* Rickards, 1965) in its greater breadth and increased rate of expansion.

*Torquigraips carnis* (Text-fig. 3a–c) resembles a very slender form of *T. proteus*, with an even more irregular helical spiral than that species possesses. Most fragments are 0·3–0·4 mm wide (max. 0·6 mm) and 2TRDs are c. 3·0 mm. Thecae appear laterally twisted throughout. It may be conspecific with the material described as *Monograptus angustus* Rickards, 1970 by Strachan (1982, p. 163, fig. 2h–i).

The combination of rastriiform thecae proximally and markedly asymmetrical thecae distally renders *Torquigraips pragensis pragensis* (Text-fig. 5l–l) a distinctive species. Previous descriptions of this species (e.g. Storch and Serpagli 1993) have been based on flattened material and so have not shown the lateral twisting of the metatheca. The *pragensis* group does not therefore comprise the latest representatives of the triangulate monograptids (cf. Rickards 1989), but belongs to the *planus–proteus–tullbergi* lineage of monograptids recognized by Bjerreskov (1975), i.e. to *Torquigraips*.

*Torquigraips pragensis ruzickai*? (Text-fig. 5o) differs from *T. pragensis pragensis* in having lower, and fewer, rastriiform thecae proximally, which are inclined at a lower angle to the rhabdosome;

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**TEXT-FIG. 4. Graptolites from the crispus Biozone. A–H, Monograptus crispus Lapworth, 1876. A, BGS DJ7270; b, enlargement of A, to show details of thecal structure. c, BGS SPT1977; sicula and proximal theca. d, BGS DJ7238; mesial theca. e, BGS DJ7268; mesial theca. f, BGS DJ7281; distal theca. g, BGS DJ7281; distal theca. h, BGS DJ7268; distal theca; A–b, B–d, crispus Biozone, crispus Subzone; north bank of Afon Ystwyth (SN 83887547). c, crispus Biozone, crispus Subzone, Afon Claerwen (SN 82176929). i–l, Streptograptus lloydelli Storch and Serpagli, 1993; i–f, l, BGS DJ7223. k, BGS DJ7228; all crispus Biozone, crispus Subzone; Afon Ystwyth (SN 83937548); line denotes cleavage trace. m–o, Torquigraips aff. pergracilis? (Bouček, 1931). m, BGS SPT1916. n–o, BGS SPT1919; crispus Biozone, galaeensis or crispus Subzone; stream section (SN 82016518), 2·15 km S of Claerwen, which is 15 km W of Rhayader, Powys. p–q, Monograptus clintonensis (sensu Hall, 1852); p, BGS DJ8370; crispus Biozone, trackside quarry (SN 89437820) W of Llangurig. q, BGS DJ9343; ?crispus Biozone; stream section (SN 85688020) W of Llangurig.

A, M–N, P–Q, × 10 (smaller scale bar represents 2 mm); B–H, O, × 20 (larger scale bar represents 2 mm).**
TEXT-FIG. 5. For legend see opposite.
it also shows a tendency towards gracilization of the extreme proximal end. In these respects it seems morphologically intermediate between T. pragensis pragensis and torquigriptids possessing a gracile proximal end such as T. proteus and T. tullbergi. The Monograptus pragensis ruzickai described by Hutt (1975), a sedgwickii Biozone taxon, appears to differ in possessing high triangular thecae that are apparently symmetrical throughout the rhabdosome.

Torquigriptus ex. gr. pragensis? (Text-fig. 6r) is tentatively interpreted as a member of the pragensis group, in view of the near-straightness of the fragments and the relative breadth of the common canal. It is narrower distally than T. pragensis pragensis.

Material of Torquigriptus tullbergi tullbergi (Text-fig. 5e-f) differs slightly from the holotype by a more gentle dorsal curve and a slower rate of expansion proximally (width at theca 5 is 0.35 mm and at theca 10 is 0.75 mm; corresponding values for the tullbergi tullbergi holotype are 0.5 mm and 0.8 mm – P. Storch, pers. comm.). This species may be distinguished from other spirally curved torquigriptids by slender, triangular prothecae and a gentle dorsal curvature. T. tullbergi spiralooides (Text-fig. 7f-m) expands more rapidly (width at theca 5 is 0.75-0.9 mm) and has a more coiled rhabdosome; examples of this taxon have been identified as M. spiralis in the past (e.g. Text-fig. 7k-m, from Grieston Quarry, Scotland), but the more slender proximal end of spiralooides serves as a discriminating feature.

Monograptus clintonensis (Text-figs 4p-q, 7n) is a slender, slowly expanding monograptid the hooked thecae of which bear lateral aperture spines which are most noticeable proximally. In the past, it has been confused with Monograptus priodon (Text-fig. 8r; see Loydell 1929b, for full discussion), which expands more rapidly and is more densely thecate proximally. In general dimensions, the species resembles Monograptus marri, which possesses shorter lateral horns, which are not visible in most preservational modes (Hutt et al. 1970; Hutt 1975).

The material placed in affinity with M. falx (Text-fig. 8a-b) resembles M. spiralis in its thecal structure and robust proximal end. However, it appears to be a distinctly shorter form, dorsally curved rather than spirally coiled with a lower rate of expansion, more closely spaced thecae and a maximum observed width (1.0 mm) that is considerably less than the 3.0 mm quoted for M. spiralis s.s. It differs from M. falx in attaining slightly greater lengths than the 12-13 thecae quoted as typical (Pfiiby 1945), and in possessing wider prothecal bases (D. K. Loydell, pers. comm.).

The graptolite here termed Monograptus sp. 1, is spiraloform, the single specimen recovered comprising an incomplete whorl 65 mm in diameter. The thecae (Text-fig. 7o-p) are asymmetrical but not laterally twisted, the right side of the metatheca growing farther than the left, so that the
TEXT-FIG. 6. For legend see opposite.
apertures face diagonally, towards the outside of the spiral. This type of structure is not torquigiraptid (see below); it may be more closely related to that of \textit{Monograptus spiralis} (see Lenz and Melchin 1989) though the apertures are non-spinose.

**SYSTEMATIC PALAEONTOLOGY**

Order \textit{GRAPTOLOIDEA} Lapworth, 1873
Suborder \textit{VIRGELLINA} Fortey and Cooper, 1986
Family \textit{GLYPTOGRAPTIDAE} Fortey and Cooper, 1986
Subfamily \textit{MONOGRAPTINAE} Frech, 1897
Genus \textit{STREPTOGRAPTUS} Yin, 1937 emend. Loydell, 1990

*Type species.* (Designated by Loydell 1990; see Loydell and Chen 1991; \textit{Grapto lithus plumosus} Baily, 1871; from the Llandovery of Tievesvilly, County Down, Northern Ireland.

**\textit{Streptograptus whitei} sp. nov.**

Text-figure 3o-9

*Derivation of name.* After Dr D. E. White, who collected much of the material of this species.

\textit{cf.1931} \textit{Monograptus nodifer}, Haberfelner, p. 136, pl. 11, fig. 7a-c.

\textit{cf.1982} \textit{Monograptus barrandei} group Eilles & Wood, Strachan, p. 163, fig. 2a-d.

*Holotype.* BGS DJ7612, from uppermost \textit{turruculatus} Biozone (\textit{carnicus} Subzone) strata exposed beside Claerwen reservoir (SN 8508 6415) (Text-fig. 3p-q).

*Horizon and localities.* Rare specimens, all from the \textit{carnicus} Subzone of the \textit{turruculatus} Biozone of central Wales.

*Diagnosis.* A long, slowly expanding streptogiraptid with gentle, persistent ventral curvature. Prothecae approximately parallel-sided in the proximal and mesial parts of the rhabdosome, and distally narrowing in the distal part of the rhabdosome.

*Description.* A proximal end with sicaula has not been found. Total rhabdosome length was probably considerably greater than the maximum of 50 mm observed. All fragments show a persistent, gentle ventral curvature. The most proximal fragment is 0.2 mm wide, with a 2TRD of 2.0 mm, and shows no perceptible expansion over 15 mm. The holotype expands from 0.35 mm to 0.7 mm in 35 mm, the 2TRD decreasing from

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\textit{TEXT-FIG. 6.} Graptolites from the \textit{griestoniensis} Biozone. A–I, \textit{Torquigiraptus pergracilis} (Bouček, 1931); all lower \textit{griestoniensis} Biozone; Nant Cerrigyrdagh (SN 85017050), 10 km NW of Rhayader. A, BGS SPT2041; B, detail of A, c, BGS SPT2053; C, detail of C, f, BGS SPT2088; F, BGS SPT2046; G, detail of G, h, BGS SPT2050. I, BGS SPT2056; specimen with sicaula? J–O, \textit{Streptograptus aff. loydelli} Storoch and Serpagli, 1993; lower \textit{griestoniensis} Biozone; landslip section (SN 924749) N of Rhayader. J, BGS JZ942; K, BGS JZ956; F, BGS JZ945; M, BGS JZ964. N, BGS JZ971; O, BGS JZ930; P, \textit{Torquigiraptus ex. gr. pragensis} (Pribil, 1943); BGS JZ3989; upper \textit{griestoniensis} Biozone; track section (SSN 85457831) 6 km WSW of Llangurig, Powys; distal fragment. Q–T, \textit{Monoclimacis} cf. \textit{griestoniensis} of Elles and Wood, 1911; lower \textit{griestoniensis} Biozone; stream section (SO 08436847) E of Abbeycwmhir. Q, BGS JZ2653; distal fragment. R, BGS CAV1853; proximal part. S, BGS JZ2652. T, BGS CAV1853; distal part of T, U, \textit{Monoclimacis griestoniensis griestoniensis} (Nicol, 1850); BGS DJ7517; upper \textit{griestoniensis} Biozone; quarry (SN 92287994), E of Llangurig near-proximal to mesial fragment.

A, C, E–F, H–U, \times 10 (smaller scale bar represents 2 mm); D, G, \times 20 (larger scale bar represents 2 mm).
TEXT-FIG. 7. For legend see opposite.
2:1 mm to 1:6 mm over that distance. Other mesial fragments show slightly more widely spaced thecae, with 2TRDs of up to 2:4 mm. The thecae are of streptograptid type. Proximally and mesially, the protheca are approximately parallel-sided or show slight distal expansion, and comprise approximately half the total rhabdosome width. Distally, protheca show distal contraction, giving this part of the rhabdosome a ‘runcinate’ outline.

Discussion. Monograptus nodifer (sensu Haberfeldner, 1931, also from the upper turriculatus Biozone, of the Carnic Alps) appears similar, differing only in having more closely set thecae, with a 2TRD of c 1:5 mm. M. nodifer s.s., however, is unrelated to the species being described, having radically different thecal morphology (Rickards et al. 1977). Streptograptus? anguinus anguinus (Příbyl, 1941), a spiralis Biozone species, and Streptograptus? anguinus linearis (Chen, 1984) from the turriculatus Biozone of China have a generally similar rhabdosome form; both differ from S. whitei in having parallel-sided protheca throughout and slightly lower profile metathecae which are slightly more widely spaced both proximally and distally.

This rare species is useful stratigraphically in central Wales, having been found only in strata assigned to the uppermost turriculatus Biozone (carnicus Subzone). It may also have been recorded, as ‘M. barrandei group’, from uppermost turriculatus Biozone or lower crispus Biozone strata in south-east Scotland, associated with Monoclimacis? gaulaensis (Strachan 1982).

Genus TORQUIGRAPTUS Loydell, 1993b

Type species. Original designation; Graptolithus Proteus Var. plana Barrande, 1850; from the linnaei Biozone of Zelkovicke, Bohemia.

Discussion. This genus embraces monograptids which possess relatively simple thecal apertures which are laterally twisted towards the reverse (right) side of the rhabdosome. This phenomenon was first noted by Linnarsson (1881) for his species Monograptus dextrorsus from the turriculatus Biozone of Sweden, and then by Törnquist (1899) for his species Monograptus denticulatus from the Aeronian Diplograptus folium Biozone of Scania. The significance of these early findings was not widely appreciated, however, and convincing further evidence of this morphological feature only emerged relatively recently. In particular, Bjerrøs (1975) recognized thecal torsion in a number of Llandovery monograptids from Bornholm: Monograptus planus, M. proteus, M. tullbergi?, and ?Diversograptus sp. and Melchin (1989) showed this feature in M. dextrorsus n. sp. from Cornwallis Island, Canada, while Loydell (1993b) has demonstrated it in the late Aeronian to early Telychian species M. involutus Lapworth, 1876, M. contortus Perner, 1897, and M. cavei Loydell, 1993b from west Wales.

Torquigraptus is restricted to species with fairly simple apertures. Monograptus spiralis (see Lenz and Melchin 1989), M. contortus (see Loydell 1993b) and Spirograptus turriculatus (see Melchin and
TEXT-FIG. 8. For legend see opposite.
Lenz 1986) possess laterally twisted thecae, but also more complex apertures with lateral spines or flanges. Their relationship to Torquigraptus is uncertain. Cyrtograptus species, also possess laterally twisted, and more complex, flange-bearing or spinose apertures (e.g. Lenz and Melchin 1989); this genus, possibly polyphyletic (Lenz and Melchin 1989) may in part have descended from Torquigraptus species. Torquigraptus species have so far been recognized from the Aeronian and Telychian stages (see Loydell for further details). They are mostly, but not exclusively, spirally coiled or dorsally curved.

**Torquigraptus pergracilis?** (Bouček, 1931).

Text-figure 6a–1

| ?1931 | Monograptus pergracilis sp. nov., Bouček, p. 302, text-fig. 10b. |
| ?1933 | Diversograptus? pergracilis (Bouček); Bouček, p. 70, pl. 6, figs 5–6, text-fig. 17b. |
| ?1952 | Diversograptus pergracilis (Bouček); München, p. 132, pl. 44, fig. 2a–c. |
| ?1953 | Diversograptus capitellatus pergracilis (Bouček); Bouček and Přibyl, pp. 500, 561, pl. 1, fig. 4, text-fig. 2, figs 1–6. |

**Material.** Between ten and fifteen fragmentary rhabdosomes from the lower part of the griesstoniensis Biozone, 10 km NW of Rhayader, Wales; SN 8501 7050. One specimen from strata of probable lower griesstoniensis Biozone age collected by R. O. Roberts (1929) from ‘Pentre Brook’ (probably Pandy Brook), near Abycwmhir, Powys, Wales.

**Description.** Fragments at least 16 mm long; all possess a slight dorsal curve. One fragment (Text-fig. 6l) shows a possible proximal end. The apparent sicula is at least 0.8 mm long. Width increases gradually from 0.2 mm proximally to a maximum of 0.3 mm. Thecal shape is consistent throughout. Prothecae are long and nearly parallel-sided; metathecae are small, inconspicuous and appear to be consistently twisted to the right. 2TRDs increase slightly from 2.35 mm proximally to 2.7–3.2 mm distally.

**Remarks.** The almost straight and very slender rhabdosome suggests comparison with pergracilis. P. Storch has kindly re-examined Bouček’s original material and furnished the following description of the poorly preserved type material from Bohemia: ‘Rhabdosome is very slender, either straight or weakly curved (both ventral and dorsal curvature observed). Elongated tube-like thecae overlap for about one-tenth to one-eighth of their length. Metathecae are hooked and, possibly (laterally) twisted. Probably they face proximolaterally. Thecal height is 0.3 mm (0.25–0.35 mm), and 2TRD is 2.4–2.8 mm (mostly 2.6 mm)’. Thus, the Welsh specimens may resemble the type Bohemian material in thecal morphology as well as in overall rhabdosome shape.

Bouček’s species, however, has been recorded from higher horizons (crenulata and spiralis Biozones of Bohemia; Bouček 1953); some of the material showed thecal cladia (Bouček and Přibyl 1953), a feature not seen in the Welsh specimens. If the Welsh material is pergracilis, then the placing

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**TEXT-FIG. 8. Graptolites from the crenulata and spiralis Biozones. a–b, Monograptus aff. falx (Suess, 1851); probably spiralis Biozone; quarry (SO 00927707) NW of Bwch-y-sarnau. a, BGS DJ9943; b, BGS DJ9968. c–d, Pristograptus? aff. initialis (Kirste, 1919); spiralis Biozone; quarry (SO 00927707) NW of Bwch-y-sarnau. c, BGS SPT9. d, BGS DJ9916. e–f, Torquigraptus tullbergi tullbergi (Bouček, 1931); e, BGS JZ4232; probably crenulata Biozone; track section (SO 08177417) E of Bwch-y-sarnau. f, counterpart of e; BGS JZ4233. g, Pristograptus initialis (Kirste, 1919); BGS JZ4256; probably crenulata Biozone; quarry (SO 08177417) E of Bwch-y-sarnau. h–k, Monoclimacis cf. crenulata (sensu Elles and Wood, 1911); probably crenulata Biozone; quarry (SO 08177417) E of Bwch-y-sarnau. l, BGS JZ4218. l, BGS JZ4219. m, BGS JZ4218. k, BGS JZ4217. n, Monoclimacis griesstoniensis nicoil? (Richards, 1965); probably spiralis Biozone; quarry (SO 00927707) NW of Bwch-y-sarnau. l, BGS DJ9970; m, (counterpart of l); BGS DJ9971. n–q, Monoclimacis linnarssonii (Tullberg, 1883); horizon and locality as for l–m. n, BGS SPT20. o, BGS DJ9959. p, BGS DJ9997. q, BGS SPT20. r, Monograptus priedon (Bromn); BGS JZ4218; probably crenulata Biozone; quarry (SO 08177417) E of Bwch-y-sarnau. All ×10 (larger scale bar represents 20 mm), except q, ×5 (smaller scale bar represents 2 mm).
of this taxon by Bouček and Přibyl (1953) as a subspecies of *capillaris* is incorrect, as the latter species has symmetrical thecae (Zalasiewicz, unpublished).

A seemingly allied, but more robust taxon with more widely spaced thecae (2TRD c. 3.8 mm) from *crispus* Biozone strata in central Wales (Text-figs 4m–o) shows lateral twisting of the metathecae. This may be related to German material assigned to *pergracilis* in Bouček's collection, which may be from the *crispus* Biozone (Münch 1952), which has 2TRDs of 3.4–4.2 mm (P. Štorch, pers. comm.).

**Genus** Monograptus Geinitz, 1842

*Type species.* By subsequent designation (Bassler 1915, p. 822) *Lomatoceeras priodon* Bronn, 1835, p. 56, pl. 1, fig. 13; from the Silurian of Germany.

**Monograptus crispus** Lapworth, 1876

Text-figure 4A–H

1876 *Monograptus crispus* sp. nov., Lapworth, p. 503, pl. 120, fig. 7a–c.
1913 *Monograptus crispus* Lapworth; Elles and Wood, p. 456, pl. 45, fig. 6a–f; text-fig. 314a–c.
1951 *Monograptus (Globosograptus) crispus* Lapworth; Bouček and Přibyl, p. 192, pl. 1, fig. 1–7; pl. 2, figs 1–3.
1975 *Monograptus crispus* Lapworth; Hutt, p. 84, pl. 11, figs 8–9, text-fig. 25, fig. 5.
1985 *Prochnyograptus crispus* (Lapworth); Přibyl and Štorch, p. 62, pl. 1, figs 1–2; pl. 2, ?1, ?4.

*Lectotype.* BU 1648, figured Lapworth 1876, pl. 20, fig. 7; from the Gala Beds of Meigle Quarry, Scotland.

*Description.* The material consists of a proximal, dorsally curved portion 0.2–0.25 mm across, with a 2TRD of c. 20 mm; a middle portion which is approximately straight and which varies considerably in length, with a width of 0.25–0.35 mm and 2TRDs of 3.0–4.0 mm; and a ventrally curved distal portion up to 0.9 mm wide, with 2TRDs of 2.0–2.2 mm. The thecae show a progressive distal increase in the amount of coiling. Thecal overlap is negligible throughout and there are no prothecal folds. Proximally, the prothecae are long, and gently distally expanding. The metathecae are coiled through c. 270° (measuring from the local stipe axis). The aperture is gently flared and faces, but is not tightly pressed against, the ventral prothecal wall (Text-fig. 4c). Mesially, the prothecae remain narrow, and become longer. The metathecae are more tightly coiled than in the proximal portion, through c. 360°. The apertures are flared, possessing a distinct lateral flange; they are tightly pressed against the initial part of the metatheca (Text-fig. 4d–f). Distally, the prothecae shorten and become more rapidly distally expanding, the coiled metatheca forming an isolated lobe. The amount of coiling here is c. 450°, the flared apertures facing ventrally and being tightly adpressed against the dorsal-facing wall of the preceding part of the metatheca (Text-fig. 4A–B, G–H).

*Discussion.* The only previous detailed description of the thecal structure of *M. crispus* is in an unpublished Ph.D. thesis (Howe 1982). The main difference of these observations from those of Howe lies in the recognition of the progressive increase in coiling from the mesial to the distal part of the rhabdosome. The affinities of this distinctive thecal type is unknown, though an ancestral relationship to the folded metathecae of *M. knockensis* and *M. singularis*, inferred by Přibyl and Štorch (1985), is possible. The coiled metathecae with their flared apertures suggest an affinity with the streptograptids, but the lack of prothecal folds and the progressive increase in the amount of coiling may indicate otherwise.

**Monograptus aff. crispus**

Text-figure 3r–l

*Material.* Very rare specimens in strata of latest *turriculatus* Biozone (*carnicus* Subzone) to early *crispus* Biozone in age.

*Discussion.* This rare taxon appears to predate slightly *M. crispus* (having been found together with *Streptograptus storchi*, which has not yet been found to co-exist with *M. crispus* s.s. in Wales) and
to overlap with the lower part of its range. It is characterized by more closely-set thecae than is typical of *M. crispus*, with 2TRDs in the range of 1·1–1·5 mm. It is also somewhat less robust, the three distal fragments found not exceeding 0·5 mm in width.

*Mongraptus pseudocommunis* sp. nov.

Text-figure 7A–1

*Derivation of name.* From the superficial resemblance of this taxon to the Aeronian species *Mongraptus communis*.

*Holotype.* SPT 2034 (Text-fig. 7A); from the early *griestoniensis* Biozone in a stream section (SN 8501 7050), 10 km NW of Rhayader, Wales.

*Paratypes.* Five additional specimens from the type locality. In addition, two well-preserved fragments from strata of probable lower *griestoniensis* Biozone age from ‘Pentre Brook’ (probably Pandy Brook), near Abbeycwmhir, Powys were collected by R. O. Roberts (1929).

*Diagnosis.* Rhabdosome strongly dorsally curved, maximum width 1·0 mm; proximal 2–3 thecae slender, elongated; distal thecae triangular, hooked, symmetrical, with slightly laterally expanded, ventrally facing apertures.

*Description.* The short rhabdosome has a dorsal curve, accentuated mesially. The proximal end is gracile, c. 0·15 mm wide with a proximal 2TRD of 2·0 mm. It widens rapidly from theca 2 (0·25 mm) to theca 4 (0·6 mm), and thereafter more gradually to 1·0 mm. Distal 2TRDs are 1·5–1·9 mm. Distal thecae are triangular, hooked, and symmetrical. Two well-preserved thecae (Text-fig. 7H–I) show that the apertural portions of the metathecae are slightly expanded, and that the dorsal apertural wall extends further than the ventral apertural wall, so that the aperture faces ventrally.

*Discussion.* This species closely resembles the Aeronian species *M. communis* in rhabdosomal shape and thecal structure, differing only in being narrower distally (maximum width 1·0 mm as opposed to 1·3–1·4 mm) and having ventrally facing apertures. This may be a true triangulate monograptid; but, as the triangulates, otherwise, appear to have disappeared sometime around the beginning of the Telychian, it is possible that derivation was from *Torquigraptus*. If so, it would constitute an example of iterative evolution – independently re-creating the *communis* morphology – and also reverse evolution, 'straightening out' the laterally twisted thecae.

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