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

by JAN ZALASIEWICZ

ABSTRACT. Graptolite faunas from the uppermost *turriculatus*, *crispus*, *griestoniensis*, *crenulata* and *spiralis* Biozones of central Wales are described. Detailed collecting integrated with recent BGS mapping has demonstrated a new subzone of *Torquigraptus 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 *griestoniensis* 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 Rhuddanian 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, 1992*a*, 1993*b*) 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*, *griestoniensis*, 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 hemipelagites in which a fine primary lamination, the result of deposition in anoxic bottom conditions (Cave 1979) is preserved. Such hemipelagites contain a well-preserved graptolite fauna as do, locally, some turbidite sandstones. The graptolite-bearing hemipelagites tend to be most common in strata of late *turriculatus* and *crispus* Biozone age; they are rarer in the

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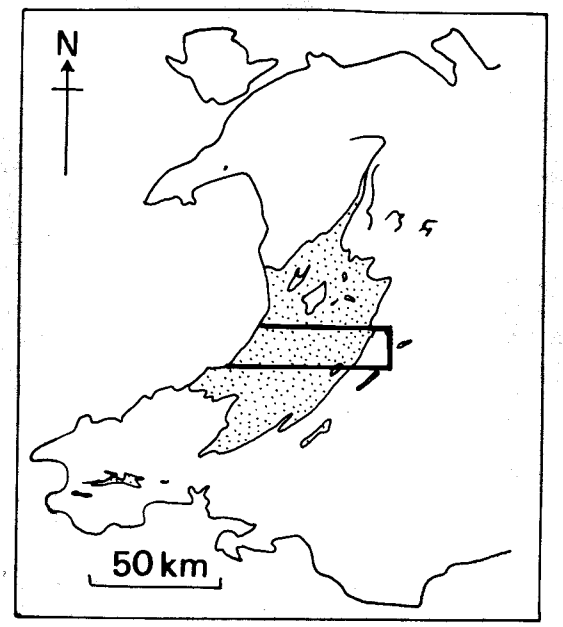


TEXT-FIG. 1. Location of study area (boxed) in Wales. Outcrop of Llandovery sediments shown by stippled ornament.

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 diagenetically 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

biostratigraphy 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 diachroneity 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 *Torquigraptus carnicus*, was employed in the survey to characterize strata forming the uppermost part of the *turriculatus* Biozone. A subsequent zonation by Loydell (1992*a*) separated a biozone of *Spirograptus 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.

Torquigraptus carnicus *Subzone*

This subzone is marked by the incoming of *Torquigraptus carnicus* (Gortani, 1923), *Streptograptus whitei* sp. nov., *S. exiguus* (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 *Monograptus 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.).

Monograptus 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. Bjerreskov (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 *Monograptus* 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. exiguus* 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 Bjerreskov (1975) and Rickards (1976).

2. *Monograptus crispus* Subzone

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

3. *Streptograptus sartorius* Subzone

This is the interval between the disappearance of *M. crispus* and the first appearance of the monoclimacid monograptids which characterize the *griestoniensis* Biozone. *Torquigraptus pragensis pragensis* (Přibyl, 1943), *T. pragensis ruzickai*? (Přibyl, 1943), and *Streptograptus sartorius* (Törnquist, 1881) appear for the first time.

	turriculatus Biozone		*crispus* Biozone			*griestoniensis* Biozone		*crenulata* Biozone	*spiralis* Biozone
	(earlier subzones) ← *proteus* Subzone	*carnicus* Subzone	*galaensis* Subzone	*crispus* Subzone	*sartorius* Subzone	(lower part)	(upper part)		
Pristiograptus nudus s.l.	X	X	X	X	X	X	X	X	X
Spirograptus turriculatus	X	X	X	?					
Monograptus bjerreskovae	X	?							
Normalograptus? nebula	X	X	?	?	?	X	X		
Monograptus marri	X	cf.	cf.	cf.	cf.	cf.	cf.		
Streptograptus storchi	X	A							
Monograptus rickardsi	X	X	X	X	X				
Petalolithus tenuis s.l.	X	X	X	X					
Streptograptus pseudobecki	X								
Torquigraptus proteus	X	X							
Monoclimacis? galaensis	?	X	X						
Monograptus aff. *rickardsi* (slender form)		X							
Torquigraptus carnicus		X	X						
Streptograptus whitei		X							
Monograptus aff. *crispus*		R	X						
Streptograptus exiguus		X	A	X	X	X			
Monograptus clintonensis		?	X	X	X	X			
Streptograptus mustadi Howe 1982 ms			R						
Monograptus crispus			X	A					
Monograptus discus			X	X	X	X	X	L	
Petalolithus sp. 1			X						
Streptograptus loydelli				A	?				
Retiolites geinitzianus subspp.				X	X	X	X	X	X
Torquigraptus pragensis ruzickai?					R				
Torquigraptus pragensis pragensis					X	X			
Streptograptus aff. *sartorius*					X				
Streptograptus sartorius					X	X			
Torquigraptus tullbergi spiraloides					?	X	X		
Monoclimacis cf. *griestoniensis* of Elles and Wood						A	R		
Monoclimacis griestoniensis s.s.						R	A		
Torquigraptus tullbergi tullbergi						X	?	X	
Streptograptus aff. *loydelli*						X			
Monograptus priodon						X	X	X	X
Monograptus pseudocommunis						X			
Torquigraptus pergracilis?						X			
Monograptus sp. 1						X			
Pristiograptus initialis						?	?	X	
Torquigraptus ex. gr. *pragensis?* (slender form)							X		
Monoclimacis vomerina vomerina								A	A
Monoclimacis cf. *crenulata sensu* Elles and Wood								L	
Monoclimacis linnarssoni									X
Monoclimacis griestoniensis nicoli									?
Monograptus spiralis									X
Monograptus aff. *falx*									X
Monograptus parapriodon									X
Pristiograptus? aff. *initialis* (broad form)									X

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

	Loydell (1991)	Loydell (1992*a*)	Davies *et al.* (1994)	
	crispus Biozone		*crispus* Biozone	
turriculatus Biozone	(?) *proteus* Subzone *johnsonae* Subzone *utilis* Subzone	*turriculatus* Biozone	*carnicus* Subzone *proteus* Subzone *johnsonae* Subzone *utilis* Subzone	*turriculatus* Biozone
	renaudi Subzone *gemmatus* Subzone *runcinatus* Subzone	*guerichi* Biozone	*renaudi* Subzone *gemmatus* Subzone *runcinatus* Subzone (not recognized)	

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

griestoniensis *Biozone*

The base of this biozone is recognized by the appearance of two slender monoclimacids: *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 spiraloides* (Přibyl, 1945). *Mcl. griestoniensis*, rare in the lower part of the biozone, becomes common in the upper part.

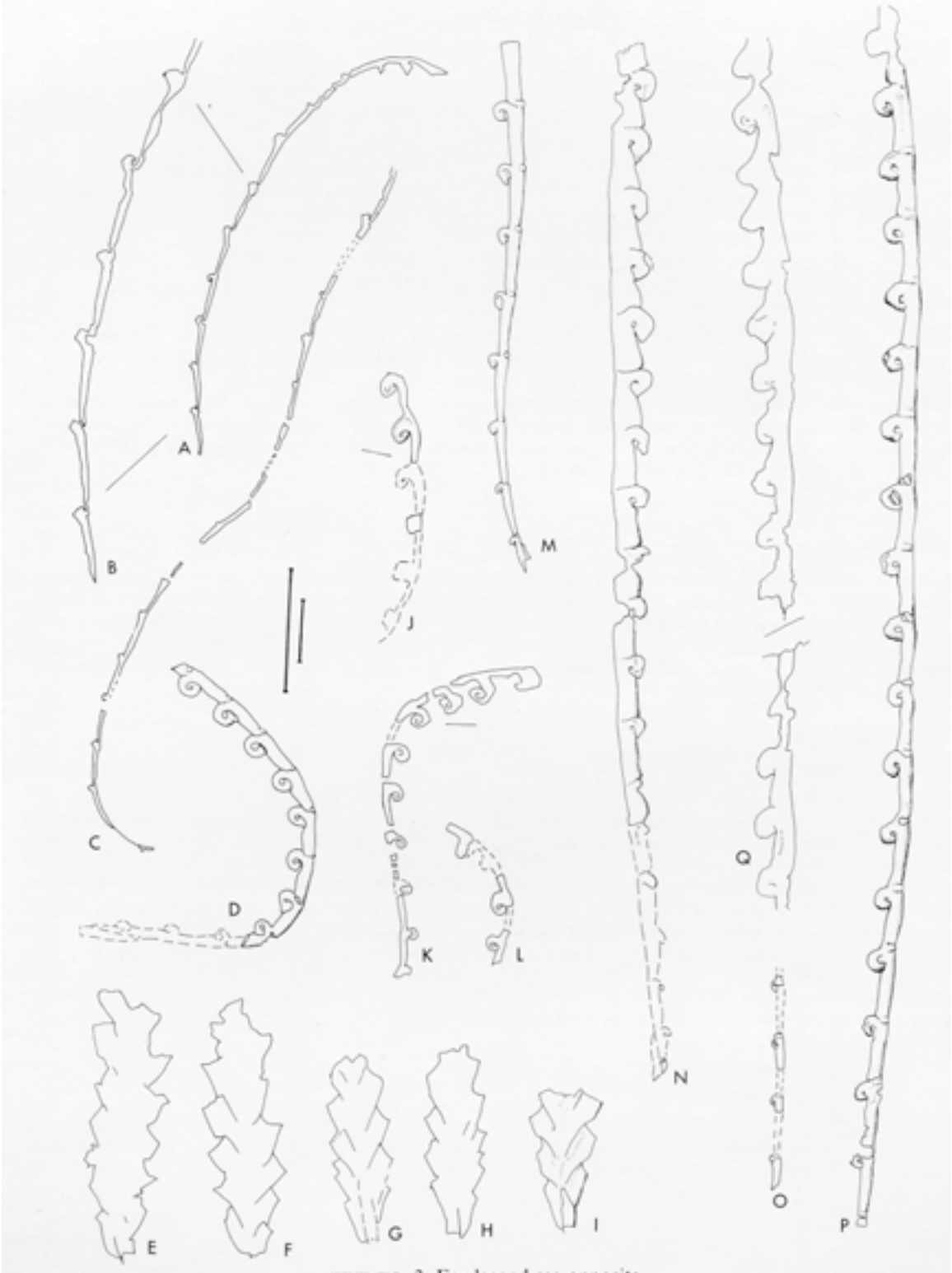
crenulata *Biozone*

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; Bjerreskov 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 1993*a*; Loydell and Cave 1993), and thus the *crenulata* Biozone has here a correspondingly restricted definition.

The incoming of broad vomerinids, 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 *Monoclimacis linnarssoni* (Tullberg, 1883), *Monograptus parapriodon* Bouček, 1931, and *M.* aff.



TEXT-FIG. 3. For legend see opposite.

falx (Suess, 1851), while *M. discus* and *T. tullbergi* subspecies are absent. This assemblage seems to correlate with the upper part of the *spiralis* Biozone of Bjerreskov (1975), and with the *spiralis* Biozone of Bouček (1953). *Monograptus spiralis* (Geinitz, 1842) has been found only rarely elsewhere, occurring in isolated localities without any diagnostic accompanying fauna.

PALAEONTOLOGICAL NOTES

Petalolithus sp. 1 of this paper (Text-fig. 3E–H) is a smaller and more densely thecate species than comparable petalograptids such as *P. tenuis*, and related diplograptids such as the *Orthograptus* sp. of Hutt *et al.* (1970). It most closely resembles *Petalolithus kurcki* (Rickards, 1970; see Text-fig. 3I and redescription in Loydell 1992*a*) from the *sedgwickii* to lower *turriculatus* Biozones, but differs in having a more convexly curved ventral wall of theca 1[1].

Monoclimacis cf. *griestoniensis* of Elles and Wood (1911) (Text-fig. 6Q–T) is narrower than *Monoclimacis 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 *Monoclimacis griestoniensis* (Text-fig. 6U), with a different proximal and thecal morphology.

The material assigned tentatively to *Monoclimacis griestoniensis nicoli* 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 Bjerreskov (1975, p. 55), the only difference being that Bjerreskov'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 rhabdosome in that material is more rapidly expanding, reaching 0·7 mm at th10, has a maximum width of 1·7 mm, and the supragenicular 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 (1990*a*).

Streptograptus loydelli Štorch and Serpagli (Text-fig. 4I–L) can be distinguished from *S. exiguus* (Text-fig. 3D) by its greater width, the more marked distal expansion of the prothecae and by the

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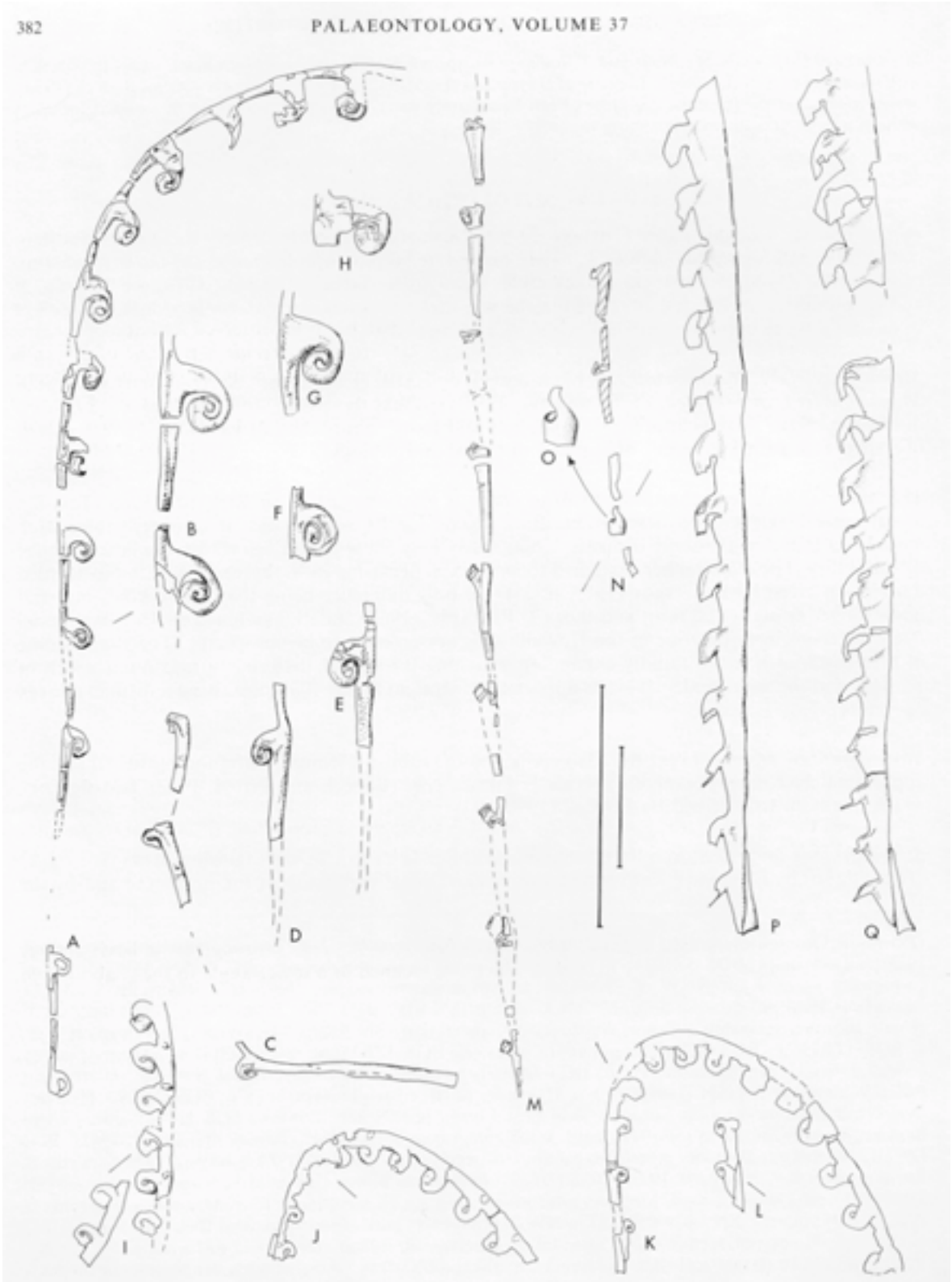
TEXT-FIG. 3. Graptolites from the *turriculatus* and lower *crispus* Biozones. A–C, *Torquigraptus carnicus* (Gortani, 1923); all on block BGS JZ1034; *turriculatus* Biozone, *carnicus* Subzone; quarry (SN 94457650) E of Cwmgwary Farm, 8 km NNW of Rhayader. D, *Streptograptus exiguus* (Nicholson, 1868); 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, ?*renaudi* Subzone; quarry near Bwlch-y-ddault, Dyfed (SN 71096309). J–L, *Monograptus* aff. *crispus* Lapworth, 1876; BGS DJ8292; probably *turriculatus* Biozone, *carnicus* Subzone; A44 near Llangurig (SN 85808198). K, BGS JZ984; lower *crispus* Biozone; Cwmgwary 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, 1993*b*; BGS DJ8297; *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 metathecae. *S. plumosus* (Baily, 1871), usually attains greater widths (of up to 0·9 mm) and has more robust prothecae (see Loydell 1990*b*). *Streptograptus* aff. *loydelli* (Text-fig. 6J–O) has the same overall dimensions, but differs in being spinose and in having a narrower theca 2. It may be related to '*Monograptus exiguus* C' of Bjerreskov (1975), which is also spinose, 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 topotype 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 theca repeat distance: Howe 1983) of 2·0–2·1 mm. Some other topotype 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 distinctly expanding prothecae. Several rhabdosomes from one locality are here referred to *S.* aff. *sartorius* (Text-fig. 5G–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).

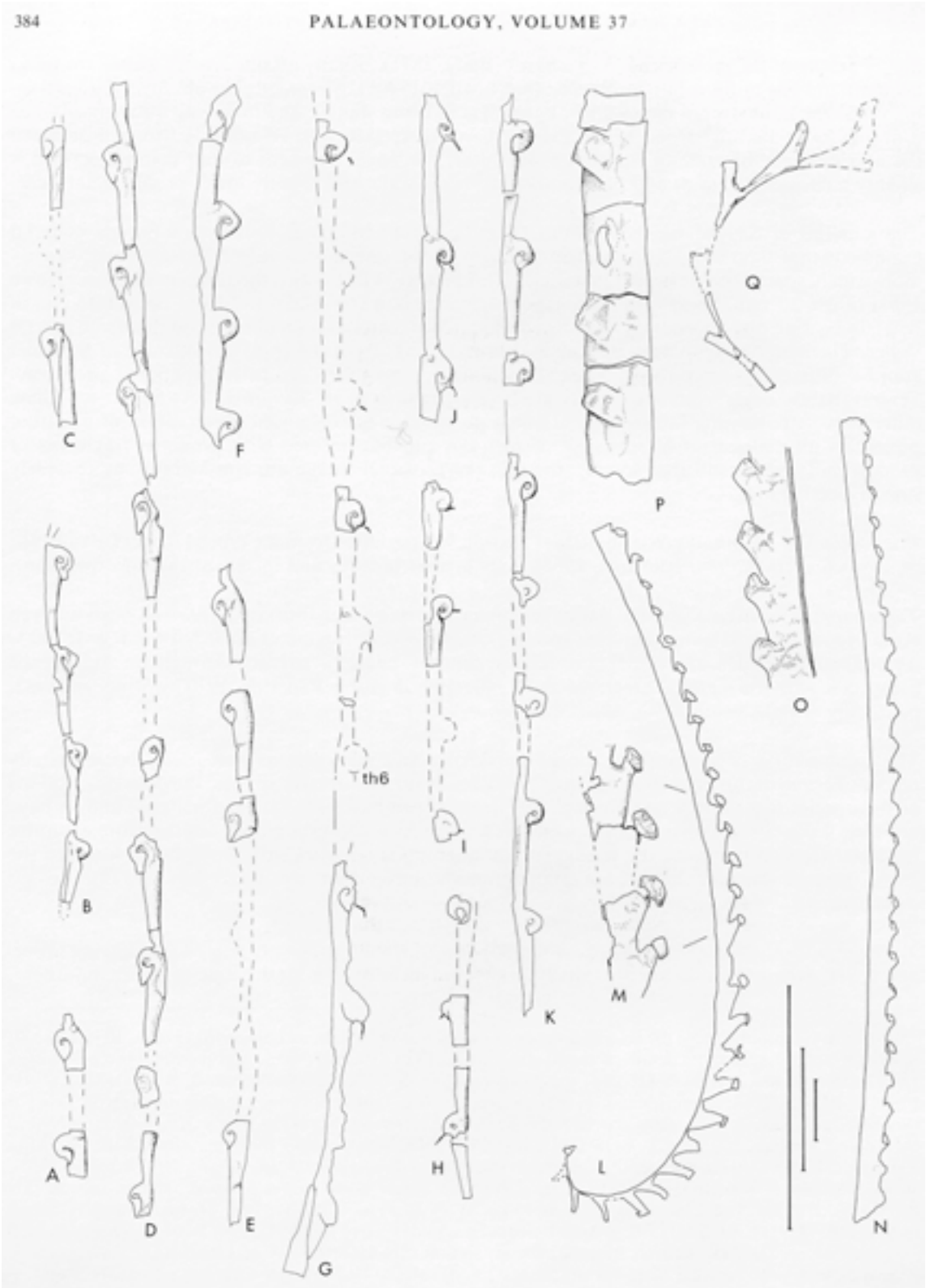
Pristiograptus? aff. *initialis* (Kirste, 1919) (Text-fig. 8C–D) differs from the typical form (Text-fig. 8G; = *Monoclimacis shottoni* Rickards, 1965) in its greater breadth and increased rate of expansion.

Torquigraptus carnicus (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 rastritiform thecae proximally and markedly asymmetrical thecae distally renders *Torquigraptus pragensis pragensis* (Text-fig. 5L–P) a distinctive species. Previous descriptions of this species (e.g. Štorch and Serpagli 1993) have been based on flattened material and so have not shown the lateral twisting of the metathecae. 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 *Torquigraptus*.

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

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 thecae. 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, D–H, *crispus* Biozone, *crispus* Subzone; north bank of Afon Ystwyth (SN 83887547). C, *crispus* Biozone, *crispus* Subzone, Afon Claerwen (SN 82176929). I–L, *Streptograptus loydelli* Štorch and Serpagli, 1993; I–J, L, BGS DJ7223. K, BGS DJ7228; all *crispus* Biozone, *crispus* Subzone; Afon Ystwyth (SN 83937548); line denotes cleavage trace. M–O, *Torquigraptus* aff. *pergracilis*? (Bouček, 1931). M, BGS SPT1916. N–O, BGS SPT1919; *crispus* Biozone, *galaensis* 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 torquigraptids 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 triangulate thecae that are apparently symmetrical throughout the rhabdosome.

Torquigraptus ex. gr. *pragensis*? (Text-fig. 6P) 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 *Torquigraptus tullbergi tullbergi* (Text-fig. 8E–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. Štorch, pers. comm.). This species may be distinguished from other spirally curved torquigraptids by slender, triangular prothecae and a gentle dorsal curvature. *T. tullbergi spiraloides* (Text-fig. 7J–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 *spiraloides* 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 apertural spines which are most noticeable proximally. In the past, it has been confused with *Monograptus priodon* (Text-fig. 8R; see Loydell 1992*b*, 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 (Přibyl 1945), and in possessing wider prothecal bases (D. K. Loydell, pers. comm.).

The graptolite here termed *Monograptus* sp. 1, is spiraliform, 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

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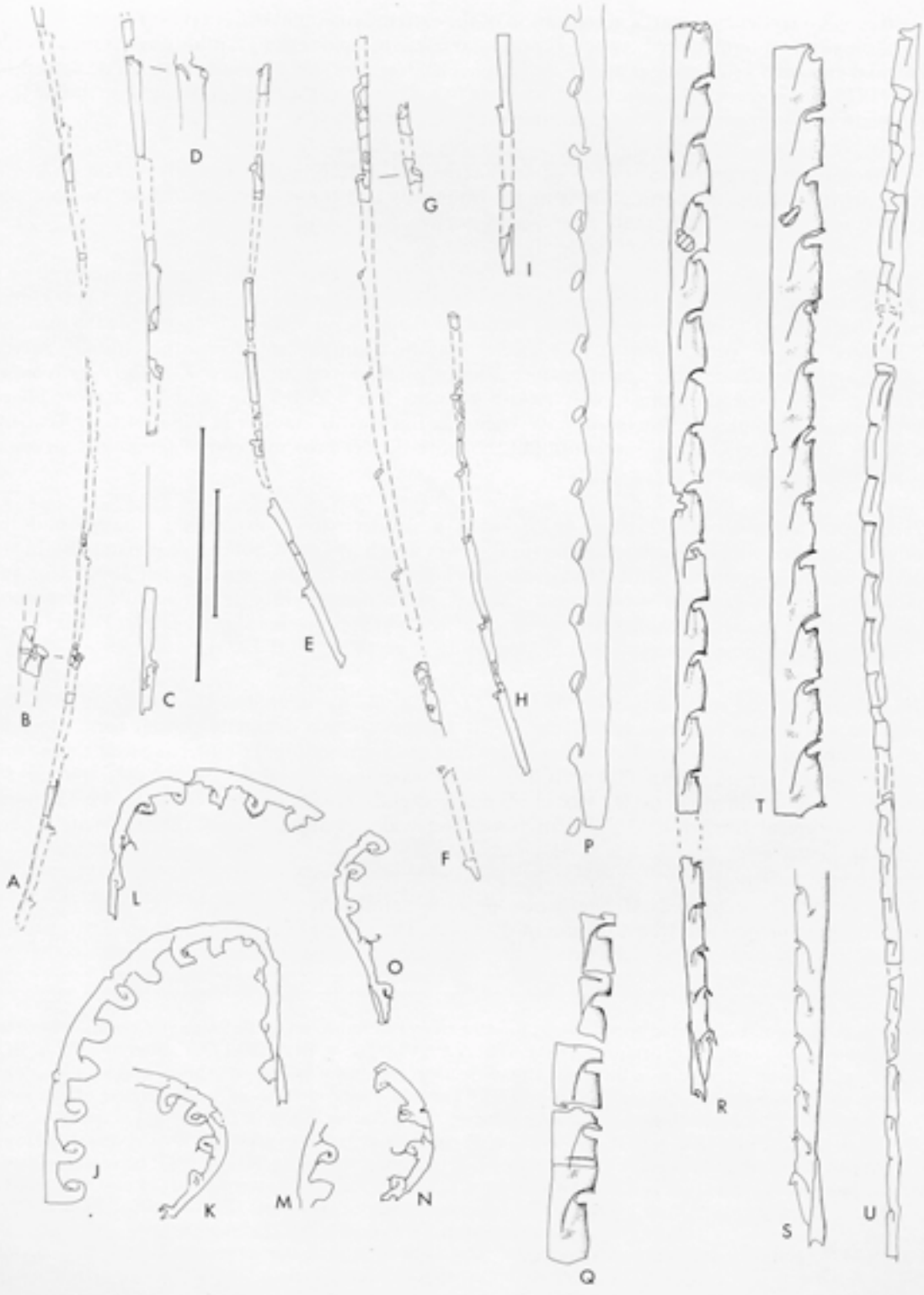
TEXT-FIG. 5. Graptolites from the upper *crispus* Biozone (*sartorius* Subzone) to the lower *griestoniensis* Biozone. A–F, *Streptograptus sartorius* (Törnquist, 1881). A, BGS CAV1851. B–E, BGS SPT173. C, BGS SPT177. F, BGS JZ2692. A, F, lower *griestoniensis* Biozone; stream section (SO 08436847) E of Abbeycwmhir. B–E, *crispus* Biozone, *sartorius* Subzone; quarry (SN 99757477) 2 km S of Pant-y-dwr. G–K, *Streptograptus* aff. *sartorius* (Törnquist, 1881); all *crispus* Biozone, *sartorius* Subzone; track cutting (SN 89007777) W of Llangurig. G, BGS DJ8476. H, I, K, BGS DJ8502. J, BGS DJ8488. L–P, *Torquigraptus pragensis pragensis* (Přibyl, 1943); all lower *griestoniensis* Biozone; stream section (SO 08436847) E of Abbeycwmhir. L, BGS JZ2683; proximal to mesial part of rhabdosome. M, part of L. N, same specimen as L; more distal part. O, counterpart of part of N. P, BGS JZ2682; distal fragment, ventral aspect. Q, *Torquigraptus pragensis ruzickai*? (Přibyl, 1943); BGS DJ7179, upper *crispus* Biozone; Afon Ystwyth (SN 84227559).

A–K, ×20 (largest scale bar represents 2 mm); L, N, ×5 (smallest scale bar represents 2 mm); M, O–Q, ×10 (intermediate scale bar represents 2 mm).



TEXT-FIG. 6. For legend see opposite.

apertures face diagonally, towards the outside of the spiral. This type of structure is not torquigraptid (see below); it may be more closely related to that of *Monograptus spiralis* (see Lenz and Melchin 1989) though the apertures are non-spinose.

SYSTEMATIC PALAEONTOLOGY

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

Type species. (Designated by Loydell 1990; see Loydell and Chen 1991); *Graptolithus plumosus* Baily, 1871; from the Llandovery of Tievesvilly, County Down, Northern Ireland.

Streptograptus whitei sp. nov.

Text-figure 3O–Q

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

cf.1931 *Monograptus nodifer*, Haberfelner, p. 136, pl. 11, fig. 7*a–c*.
cf.1982 *Monograptus barrandei* group Elles & Wood, Strachan, p. 163, fig. 2A–D.

Holotype. BGS DJ7612, from uppermost *turriculatus* Biozone (*carnicus* Subzone) strata exposed beside Claerwen reservoir (SN 8508 6415) (Text-fig. 3P–Q).

Horizon and localities. Rare specimens, all from the *carnicus* Subzone of the *turriculatus* Biozone of central Wales.

Diagnosis. A long, slowly expanding streptograptid 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 sicula 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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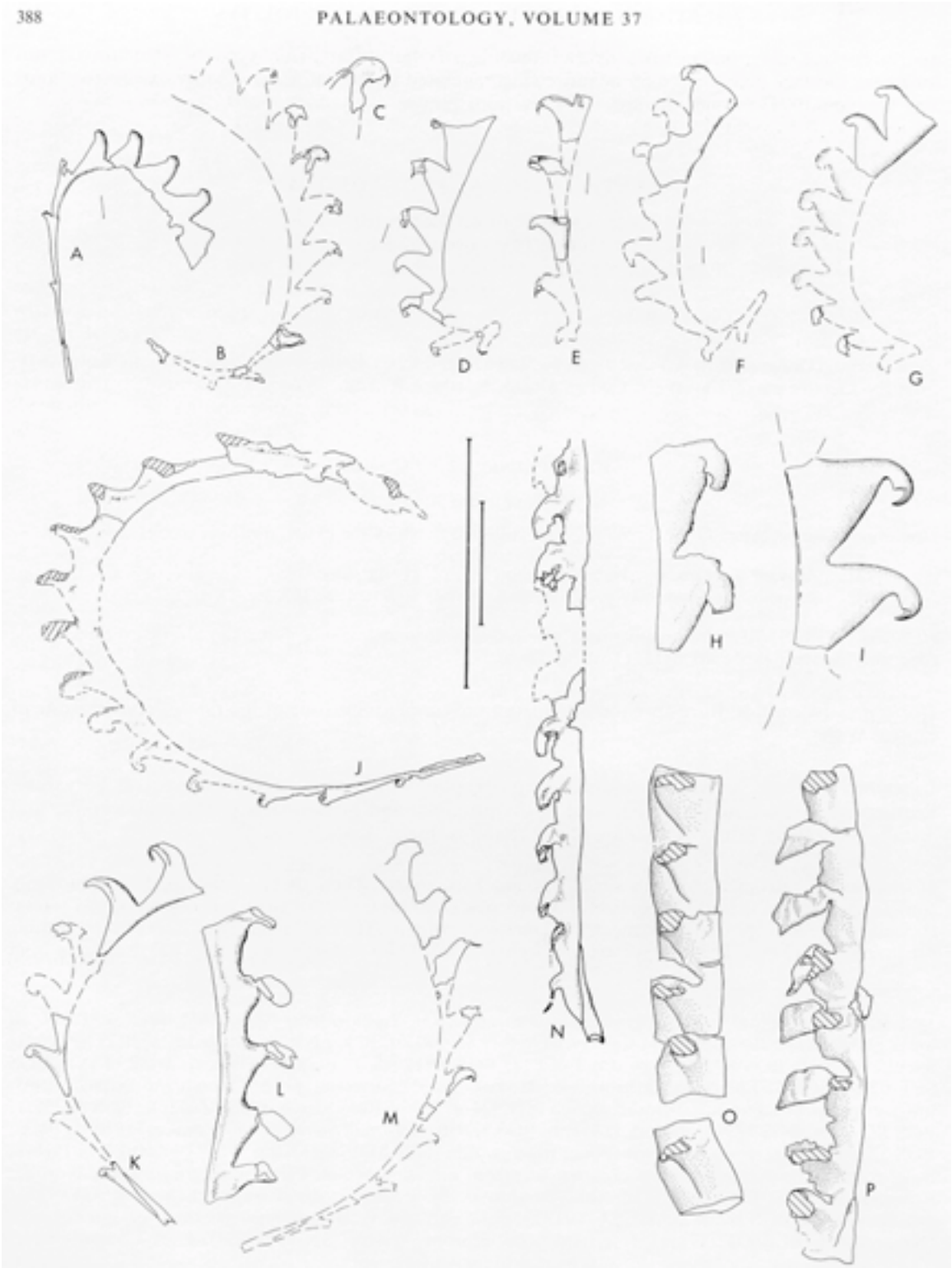
TEXT-FIG. 6. Graptolites from the *griestoniensis* Biozone. A–I, *Torquigraptus pergracilis*? (Bouček, 1931); all lower *griestoniensis* Biozone; Nant Cerrigyrhdyg (SN 85017050), 10 km NW of Rhayader. A, BGS SPT2041; B, detail of A. C, BGS SPT2053. D, detail of C. E, BGS SPT2088. F, BGS SPT2046. G, detail of F. H, BGS SPT2050. I, BGS SPT2056; specimen with sicula? J–O, *Streptograptus* aff. *loydelli* Štorch and Serpagli, 1993; lower *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, *Torquigraptus* ex. gr. *pragensis*? (Přibyl, 1943); BGS JZ3989; upper *griestoniensis* Biozone; track section (SSN 85457831) 6 km WSW of Llangurig, Powys; distal fragment. Q–T, *Monoclimacis* cf. *griestoniensis* of Elles and Wood, 1911; lower *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 R. U, *Monoclimacis griestoniensis griestoniensis* (Nicol, 1850); BGS DJ7517; upper *griestoniensis* Biozone; quarry (SN 92587994), E of Llangurig near-proximal to mesial fragment.

A, C, E–F, H–U, ×10 (smaller scale bar represents 2 mm); D, G, ×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 prothecae are approximately parallel-sided or show slight distal expansion, and comprise approximately half the total rhabdosome width. Distally, prothecae show distal contraction, giving this part of the rhabdosome a 'runcinate' outline.

Discussion. Monograptus nodifer (*sensu* Haberfelner, 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* (Přibyl, 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 prothecae 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? galaensis* (Strachan 1982).

Genus TORQUIGRAPTUS Loydell, 1993*b*

Type species. Original designation; *Graptolithus Proteus* Var. *plana* Barrande, 1850; from the *linnaei* Biozone of Zelkovice, 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, Bjerreskov (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. ssp. from Cornwallis Island, Canada, while Loydell (1993*b*) has demonstrated it in the late Aeronian to early Telychian species *M. involutus* Lapworth, 1876, *M. contortus* Perner, 1897, and *M. cavei* Loydell, 1993*b* from west Wales.

Torquigraptus is restricted to species with fairly simple apertures. *Monograptus spiralis* (see Lenz and Melchin 1989), *M. contortus* (see Loydell 1993*b*) and *Spirograptus turriculatus* (see Melchin and

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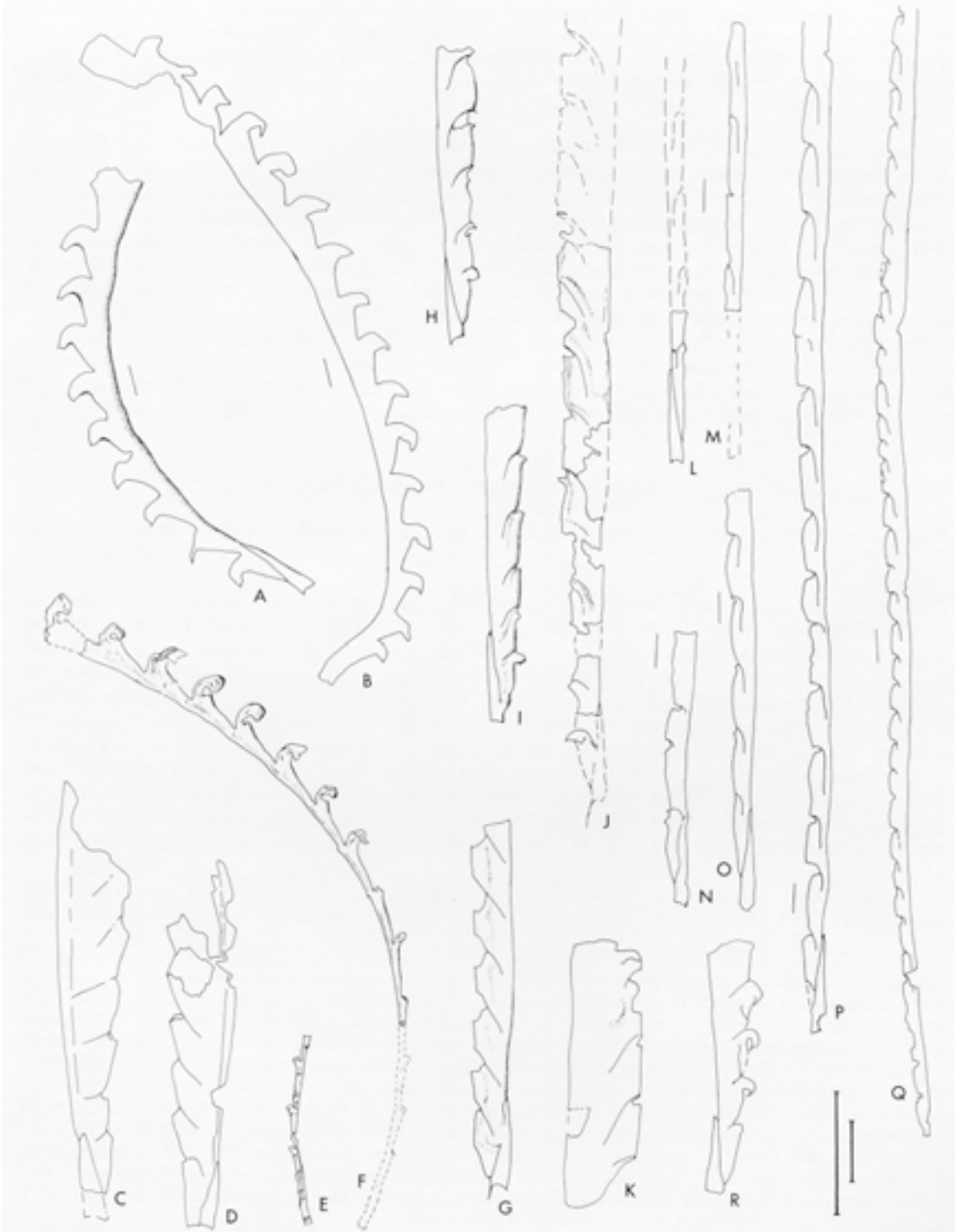
TEXT-FIG. 7. Graptolites from the *griestoniensis* Biozone. A–I, *Monograptus pseudocommunis* sp. nov.; A–F, all lower *griestoniensis* Biozone; from Nant Cerrigyrhydyg (SN 85017050), 10 km NW of Rhayader. A, BGS SPT2034; latex cast of holotype. B, BGS SPT2088. C, detail of B. D, BGS SPT2050. E, BGS SPT2079. F, BGS SPT2067. G–I, probably lower *griestoniensis* Biozone; specimens collected by R. O. Roberts (1929) from 'Pentre Brook' (= Pandy Brook). G, ROR63 (R. O. Roberts collection, Cambridge Univ.). H–I, ROR570 (R. O. Roberts collection); ventrolateral and lateral aspects respectively. J, *Torquigraptus tullbergi* cf. *spiraloides* (Přibyl, 1943); BGS JZ4496*a*; lower *griestoniensis* Biozone, section (SO 05877280); N of Abbeycwmhir. K–M, *Torquigraptus tullbergi spiraloides* (Přibyl, 1945); respectively K–L, BGS GSM11801 and M, BGS Geol. Soc. Coll. 6951; *griestoniensis* Zone; Grieston Quarry, Innerleithen, Scotland. N, *Monograptus clintonensis* (*sensu* Hall, 1852); BGS JZ2710; lower *griestoniensis* Biozone; stream section (SO 08436847) E of Abbeycwmhir. O, *Monograptus* sp. 1, BGS JZ2707; lower *griestoniensis* Biozone; stream section (SO 08436847), E of Abbeycwmhir.

A–B, D–G, J–N, × 10 (smaller scale bar represents 2 mm); C, H–I, O, × 20 (larger scale bar represents 2 mm).



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–I

?1931 *Monograptus pergracilis* sp. nov., Bouček, p. 302, text-fig. 10*b*.
?1933 *Diversograptus*? *pergracilis* (Bouček); Bouček, p. 70, pl. 6, figs 5–6, text-fig. 17*b*.
?1952 *Diversograptus pergracilis* (Bouček); Münch, p. 132, pl. 44, fig. 2*a–c*.
?1953 *Diversograptus capillaris 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 *griestoniensis* Biozone, 10 km NW of Rhayader, Wales; SN 8501 7050. One specimen from strata of probable lower *griestoniensis* Biozone age collected by R. O. Roberts (1929) from 'Pentre Brook' (probably Pandy Brook), near Abbeycwmhir, 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. Štorch 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 Bwich-y-sarnau. A, BGS DJ9943; B, BGS DJ9968. C–D, *Pristiograptus*? aff. *initialis* (Kirste, 1919); *spiralis* Biozone; quarry (SO 00927707) NW of Bwlch-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 Bwlch-y-Sarnau. F, counterpart of E; BGS JZ4233. G, *Pristiograptus initialis* (Kirste, 1919); BGS JZ4256; probably *crenulata* Biozone; quarry (SO 08177417) E of Bwlch-y-Sarnau. H–K, *Monoclimacis* cf. *crenulata* (*sensu* Elles and Wood, 1911); probably *crenulata* Biozone; quarry (SO 08177417) E of Bwlch-y-Sarnau. H, BGS JZ4218. I, BGS JZ4191. J, BGS JZ4178. K, BGS JZ4178. L–M, *Monoclimacis griestoniensis nicoli*? Rickards, 1965; probably *spiralis* Biozone; quarry (SO 00927707) NW of Bwlch-y-Sarnau. L, BGS DJ9970; M, (counterpart of L) BGS DJ9971). N–Q, *Monoclimacis linnarssoni* (Tullberg, 1883); horizon and locality as for L–M. N, BGS SPT20. O, BGS DJ9959. P, BGS DJ9997. Q, BGS SPT20. R, *Monograptus priodon* (Bronn); BGS JZ4218; probably *crenulata* Biozone; quarry (SO 08177417) E of Bwlch-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) *Lomatoceras 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. 7*a–c*.
1913 *Monograptus crispus* Lapworth; Elles and Wood, p. 456, pl. 45, fig. 6*a–f*; text-fig. 314*a–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 *Prochnygraptus 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.* 2·0 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 3J–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.

Monograptus pseudocommunis sp. nov.

Text-figure 7A–I

Derivation of name. From the superficial resemblance of this taxon to the Aeronian species *Monograptus 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 triangulate, 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 triangulate, 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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