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Graptolites in British stratigraphy

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Abstract – 697 taxa of planktonic graptolites are recorded, and their stratigraphical ranges are given, through 60 biozones and subzones in the Ordovician and Silurian strata of England, Wales and Scotland, in the first such stratigraphical compilation for Great Britain since the synthesis of Elles & Wood (1901–1918).

Keywords: graptolites, graptolite zones, biozones, biostratigraphy, Britain.

1. Introduction

Graptolites are extinct colonial hemichordates, generally considered to be closely related to the present-day pterobranchs. They range in age from the middle of the Cambrian to the Carboniferous. The graptolites include the exclusively planktonic graptoloids, the largely benthic dendroids and also the benthic crustoids, tuboids, cameroids and dithecoids (Rickards & Durman, 2006). The graptoloids are the focus of this account. They provide the primary means of correlation of Ordovician and Silurian strata in the UK, and are fundamental to resolving the stratigraphical and structural architecture of these rocks (e.g. Zalasiewicz, 2001), which were laid down in sedimentary basins on the margins of the Palaeozoic Iapetus Ocean. Major outcrops are in the Southern Uplands of Scotland, the Lake District and the Howgill Fells of northern England, and Wales and the Welsh Borderland. Outside Great Britain, graptolites are important also in early Devonian successions.

The British graptolite biozonal and subzonal schemes are shown in Figures 1 and 2. In the early Ordovician, planktonic dendroids, and then the dichograptid graptoloids, were the most important groups. These were succeeded by the diplograptids, which were dominant throughout the rest of the Ordovician. Dicranograptids and nemagraptids were also important elements at various times in the mid- to late Ordovician. (Such terms are used here in a general sense; higher-level graptolite taxonomy is discussed in more detail in Mitchell, 1987 and Mitchell *et al.* 2007).

Following near-extinction during the latest Ordovician glaciation, a few species of diplograptids survived into the earliest Silurian. These gave rise to the monograptids, which diversified to dominate the Silurian and Devonian seas worldwide (although in Great Britain, graptolites disappeared from the shallowing marine basins late in the Ludlow). Normal diplograptids persisted for a short while into the Silurian, while retiolitid ('meshwork') graptolites were locally common and survived into the Ludlow. The morphologically diverse and rapidly evolving monograptids provide a fine resolution for the Silurian, with graptolite zones lasting, on average, well under a million years (Rickards, 1976, 1989; Zalasiewicz, 1990; Hughes, 1995; Melchin, Cooper & Sadler, 2004); by contrast, the duration of graptolite zones in the British Ordovician averages *c.* 2 Ma (Rushton, 1990, cf. Cooper & Sadler, 2004).

2. Palaeoecology, provincialism and distribution

Graptolites are commonly held to be 'ideal' zone fossils, because they were widely distributed in marine waters and so not bound by facies. The situation, though, is not as simple as this. The graptoloids were probably holoplanktonic, although there is still much debate about whether they floated more or less passively (e.g. Bulman, 1964; see also discussion in Rigby & Rickards, 1990 and Palmer & Rickards, 1991) or actively propelled themselves through the water (e.g. Kirk, 1978; Bates & Kirk, 1984, 1985; Rickards *et al.* 1998; Melchin & DeMont, 1995).

Planktonic graptolites have long been interpreted as largely 'open ocean' dwellers, common in offshore pelagic and hemipelagic sequences ('graptolite facies'), and rare or absent in shallow water deposits ('shelly facies'). Subsequent elaborations of this general observation included suggestions that graptolites were subject to depth control, with near-surface and deep-living taxa (e.g. Berry & Boucot, 1972; Bates &

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Time: Period	Time: Epoch	Chronostratigraphy: International standard stages	Chronostratigraphy: British regional series	Chronostratigraphy: British regional stages	Age (Ma)	British Ordovician graptolite biostratigraphy: England and Wales graptolite zones and subzones	British Ordovician graptolite biostratigraphy: Scotland graptolite zones and subzones
Ordovician	Late	Hirnantian	Ashgill	Hirnantian	443.7	*Normalograptus persculptus*	*Normalograptus persculptus*
					445.6	? ? *Dicellograptus anceps* ? ?	*Normalograptus extraordinarius*
		Katian		Rawtheyan			*D. anceps - pacificus* Subz
							D. anceps - complexus Subz
						Pleurograptus linearis	? ? *Dicellograptus complanatus* ? ?
				Cautleyan			*Pleurograptus linearis*
				Pusgillian			
			Caradoc	Streffordian		*Dicranograptus clingani* Zone - *D. morrisi* Subz	*Dicranograptus clingani* Zone - *D. morrisi* Subz
				Cheneyan		*Dicranograptus clingani* Zone - *E. caudatus* Subz	*Dicranograptus clingani* Zone - *E. caudatus* Subz
		Sandbian		Burrellian	455.8	*Diplograptus foliaceus*	*Climacograptus bicornis* Zone *wilsoni* Subz
				Aurelucian			*Climacograptus bicornis* Zone *apiculatus-ziczac* Subz
						Nemagraptus gracilis	*Nemagraptus gracilis*
	Mid	Darriwilian	Llanvirn	Llandeilian	460.9	*Hustedograptus teretiusculus*	Darriwilian Da4
				Abereiddian		*Didymograptus murchisoni*	
						Didymograptus artus	Darriwilian Da3
							Darriwilian Da2
			Arenig	Fennian		*Aulograptus cucullus*	Darriwilian Da1
		Dapingian			468.1	*Isograptus gibberulus*	Yapeenian Ya1-2
							Castlemanian Ca3-4
				Whitlandian		*Isograptus victoriae victoriae*	Castlemanian Ca1-2
	Early	Floian			471.8	*Expansograptus simulans*	Chewtonian Ch1-2
				Moridunian		*Corymb. varicosus*	Bendigonian Be3-4
						Tetragraptus phyllograptoides	Bendigonian Be1-2
							Lancefieldian La3
		Tremadocian	Tremadoc	Migneintian	478.6	*Araneograptus murrayi*	Lancefieldian La2
						[no graptolites]	
				Cressagian		*Adelograptus tenellus*	
					488.3	*Rh. flabelliformis*	

Figure 1. British Ordovician graptolite biozones and subzones. Zonal scheme based on that proposed by Fortey *et al*. (1995), and adopted in the Ordovician Correlation Report of Fortey *et al*. (2000), with subsequent modification to the Arenig to early Llanvirn by Cooper *et al.* (2004), refinement of the Caradoc by Bettley, Fortey & Siveter (2001), while the Caradoc/Ashgill section of England and Wales shows the modified correlations suggested by Rickards (2002). Chronostratigraphy and radiometric dates after Ogg, Ogg & Gradstein (2008).

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Chronostratigraphy Epoch	Stage	Age (Ma)	Rickards (1976)	Zalasiewicz *et al.*, this study: Zones	Subzones
Ludlow	Ludfordian		No later zones recorded in Britain	No later zones recorded in Britain	
			Bohemograptus	*Bohemograptus*	
		421.3	*Saetograptus leintwardinensis*	*Saetograptus leintwardinensis*	
	Gorstian		*Saetograptus incipiens*	*Saetograptus incipiens*	
			Lobograptus scanicus	*Lobograptus scanicus*	
		422.9	*Neodiversograptus nilssoni*	*Neodiversograptus nilssoni*	
Wenlock	Homerian		*Monograptus ludensis*	*Monograptus ludensis*	
			Gothograptus nassa	*Gothograptus nassa*	
			Cyrtograptus lundgreni	*Cyrtograptus lundgreni*	
		426.2	*Cyrtograptus ellesae*		
	Sheinwoodian		*Cyrtograptus linnarssoni*	*Cyrtograptus rigidus*	
			Cyrtograptus rigidus	*Pristiograptus dubius*	
			Monograptus riccartonensis	*Monograptus riccartonensis*	
				Monograptus firmus	
		428.2	*Cyrtograptus murchisoni*	*Cyrtograptus murchisoni*	
	?				
Llandovery	Telychian		*Cyrtograptus centrifugus*	*Cyrtograptus centrifugus*	
			Monoclimacis crenulata	*Cyrtograptus insectus*	
				Cyrtograptus lapworthi	
				Oktavites spiralis	
				Monoclimacis crenulata	*Streptograptus loydelli* *Monoclimacis? galaensis*
			Monoclimacis griestoniensis	*Monoclimacis griestoniensis*	
			Monograptus crispus	*Streptograptus sartorius*	*Torquigraptus carnicus* *Torquigraptus proteus* *Streptograptus johnsonae* *Stimulograptus utilis* *Pristiograptus renaudi* *Monograptus gemmatus* *Paradiv. runcinatus*
				'Monograptus' crispus	
			Monograptus turriculatus (*Ra. maximus* Subz)	*Spirograptus turriculatus*	
		436		*Spirograptus guerichi*	
	Aeronian		*Monograptus sedgwickii*	*Stimulograptus halli*	
				Stimulograptus sedgwickii	
			Monograptus convolutus	*Lituigraptus convolutus*	
			Pribylograptus leptotheca	*Pribylograptus leptotheca*	
			Diplograptus magnus	*Neodiplograptus magnus*	
		439	*Monograptus triangulatus*	*Monograptus triangulatus*	
	Rhuddanian		*Coronograptus cyphus*	*Monograptus revolutus*	
			Lagarograptus acinaces	*Huttagraptus acinaces*	
			Atavograptus atavus	*Atavograptus atavus*	
		443.7	*Orthograptus acuminatus*	*A. ascenus-P. acuminatus*	

Figure 2. British Silurian graptolite biozones and subzones. Zonal scheme follows Rickards (1976, depicted) with modifications from Loydell (1992–1993*a*), Zalasiewicz (1994), Loydell & Cave (1993, 1996), Zalasiewicz & Williams (1999) and those proposed herein. Chronostratigraphy and radiometric dates after Ogg, Ogg & Gradstein (2008).

Kirk, 1984; Erdtmann, 1976) or that they were controlled by 'water mass specificity' with particular assemblages of taxa adapted to particular conditions of temperature and chemistry (Finney, 1986), while competition from other (soft-bodied) macrozooplankton may also have restricted their occurrence (Zalasiewicz, 2001). Finney & Berry (1997) disputed the notion of graptolites as truly ocean-going, noting

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their absence from many deep-water, anoxic deposits, and suggested that they were largely confined to the region of the outer shelf and continental slope.

Provincialism in the graptolites was particularly marked in the Ordovician, with well-defined 'Atlantic' and 'Pacific' provinces between which it is often difficult to correlate. This may have been due in part to pronounced climatic gradients (Skevington, 1974), the Atlantic province representing temperate, and the Pacific representing equatorial, waters. More local provincialism is also common, however, with apparently coeval faunas of markedly different composition being reported from different regions of the USA interior (Finney, 1986), and from the western and eastern parts of the Welsh Basin (e.g. compare the faunal successions in Hughes, 1989 and Zalasiewicz, 1992*a*). Provincialism is less pronounced in the Silurian (Melchin, 1989), and the British biozonal system can be applied for much of the Silurian throughout much of the world, with relatively minor modifications (see Koren' *et al.* 1996 and Melchin, Cooper & Sadler, 2004).

3. Taxonomy

One of the fundamental constraints on graptolite biostratigraphy is the ability to discriminate consistently between taxa. Many graptolites have a complex morphology, with many identifiable features that can be measured and tabulated. Nevertheless, the identification of graptolites is not by any means universally straightforward, partly because of the difficulty of assessing levels of intraspecific variation and partly because of preservational factors (see below).

Furthermore, in some early Ordovician dichograptids, while new thecae were being added to the growing tips of the colony, the early-formed thecae continued to grow; this gave rise to mature rhabdosomes that have a markedly different appearance from juvenile ones (Williams & Stevens, 1988, p. 49). Later Ordovician diplograptid taxa are often difficult to classify because the phylogenetically significant patterns of the very earliest growth stages (e.g. Mitchell, 1987) can be recognized only in very well-preserved material.

The Silurian monograptids are arguably more tractable. The development of a single stipe led to a great diversity in rhabdosome shape, with different types of straight, curved or plane- to helically spiralled forms (Figs 11–19). This was accompanied by the evolution of a wide range of thecal types, many of which can be recognized even in indifferently preserved material. The Silurian monograptids were thus very 'expressive' morphologically. Evolution is easy to see in them, although it is uncertain whether it was actually more rapid than in the less easily interpreted Ordovician taxa.

Taxonomic uncertainties continue to be the most severe constraint upon the use of graptolites in biostratigraphy. Many species are poorly understood or inadequately described, and those, particularly in the older literature, can 'mutate' in subsequent descriptions to become, in the words of N. F. Hughes, imprecise 'balloon' taxa. There are many instances of the type material of a 'classical' species being too poorly preserved, or inadequately described, to serve as a reference specimen by modern standards. It has been common, also, for several distinct taxa to be described, at various times, as the same species. Conversely, Loydell (1993*b*, pp. 330–1) has shown how *Stomatograptus longus* Obut, 1949 has, over time, acquired five additional species names (junior synonyms). There remains much taxonomic 'housekeeping' to do, much of it straightforward but time-consuming. Better definition of taxa, for instance by the wholesale refiguring of type material (Zalasiewicz *et al.* 2000; Zalasiewicz & Rushton, 2008) should lead to greater refinement in graptolite biostratigraphy.

4. Preservation

The widespread occurrence of graptolites in British early Palaeozoic successions is due to a phenomenon which is absent from recent oceans: that of prolonged, widespread periods of sea-floor anoxia (Page *et al.* 2007 and references therein). Thus, graptolites are typically found in finely laminated hemipelagic deposits ('graptolite shales') laid down in anoxic conditions that excluded benthos. In Britain, graptolites are generally rare or absent in rocks that were laid down under oxygenated sea-floor conditions and that were colonized, and bioturbated, by a benthic fauna (e.g. Davies *et al.* 1997).

British Ordovician and Silurian deep-water sequences characteristically show an alternation of oxic facies ('barren beds') and anoxic facies ('graptolite shales') (Rickards, 1964; Cave, 1979; Davies *et al.* 1997). These are most clearly seen in condensed, pelagic deposits such as the Moffat Shale Group of Scotland and the Skelgill Beds of the Lake District, where individual graptolite biozones tend to be only a few metres thick. In coarser clastic successions, such as the kilometres-thick Silurian turbidite deposits of the Welsh Basin, the 'graptolite shales' take the form of millimetre- to centimetre-thick units between individual turbidites.

The relative proportion of 'graptolite shales' and 'barren beds' exerts a strong control on the preservation of graptolites, and hence on the resolution of graptolite biostratigraphy. In the Caradoc of Scotland and Wales, for instance, the *clingani* Biozone is locally preserved within continuously anoxic facies, and this has enabled detailed range charts (e.g. Williams, 1982*a*; Zalasiewicz, Rushton & Owen, 1995) to be constructed, allowing the incomings and extinctions of species to be established, thus offering the prospect of very detailed correlation. The *complanatus* Biozone of the lower Ashgill, by contrast, is preserved in the Southern Uplands of Scotland only as two 5 cm thick beds within a sequence of 'barren beds' several metres thick. In Wales, the *complanatus* Biozone has not been recognized, probably due to an absence of anoxic facies of that age.

In highly expanded successions, such as the Skiddaw Group of the Lake District, graptolites can be rare simply through dilution by clastic sediment. Most of the Skiddaw graptolites have been found not at exposure, but by searching through extensive screes (Cooper *et al*. 1995, 2004). The Manx Slates of the Isle of Man are the equivalents of the Skiddaw Group but, as there are few screes on the Isle of Man, graptolites have only ever been found on two occasions, a century apart (Bolton, 1899; Rushton, 1993). Further, one 'Manx Slate' lithofacies was recently shown to contain late Wenlock graptolites (Howe, 1999), necessitating a radical revision of geological interpretations of that island.

Graptolites are preserved either diagenetically flattened or in partial to full relief. Flattened specimens, common in condensed black shale successions, may originally have been encased in gelatinous 'marine snow' or microbial mats on the sea floor (Jones, Zalasiewicz & Rickards, 2002). The pyritized relief material which is common, for instance, in the Llandovery turbiditic sequences of Wales, generally shows more morphological information than can be gleaned from flattened material. However, relief material may occasionally be more difficult to identify than the 'simple' flattened silhouettes on which many specific descriptions were originally based; for example, the characteristic apertural spines of the zone fossil *Stimulograptus sedgwickii* are normally not visible on relief specimens, being either broken off or embedded in the rock matrix. Graptolites that can be dissolved from limestones or cherts to provide exquisitely preserved isolated specimens are rare in British sequences (a notable exception is the Balclatchie fauna from Scotland: Bulman, 1944–1947); however, little use has been made of the graptolite fragments that are encountered while preparing samples for conodonts or chitinozoans.

5. Graptolite biozones

The distinctiveness and usefulness of graptolite assemblages were recognized midway through the nineteenth century, notably by Joachim Barrande (1850) in Bohemia, James Hall (1865) in Canada, Gustav Linnarsson (1871) in Sweden, and Charles Lapworth (1878) in the Southern Uplands of Scotland. Barrande and Lapworth both worked in areas that are now realized to be characterized by many structural dislocations and repetitions. Barrande believed that in any area, these repeated assemblages were environmentally controlled, successively 'colonizing' it whenever conditions were right. Lapworth interpreted his assemblages to be temporally restricted and used them to demonstrate the multiple structural repetitions of the Southern Uplands, thus simultaneously solving a major controversy of British regional geology and providing one of the most precise correlative tools in geology.

Lapworth's graptolite biozones, as modified by Elles & Wood (1901–1918) are essentially those in use today, though further refined and subdivided (e.g. Rickards, 1976; Loydell, 1992–1993*a*; Loydell & Cave, 1996). They are broadly assemblage biozones, named after a species, ideally with a restricted vertical range and a wide horizontal distribution (see Rickards, 1995). A name-giving species may be restricted to its biozone, with its incoming being used to define the zonal base (e.g. *Monograptus riccartonensis*, *'Monograptus' crispus*). It may, equally, range outside 'its' biozone, either above its upper boundary (e.g. *Spirograptus turriculatus, Monograptus firmus*) or exceptionally below it (e.g. *Bohemograptus*). What are important in the recognition of a biozone are the total assemblage and the incoming species. Strictly speaking, they are thus the Oppel biozones of the North American Stratigraphic Code, but in practice, assemblage biozones are essentially the same. Where the base of a biozone is defined by the incoming of more than one species, it is realized that these species may not appear exactly synchronously, but in practical biostratigraphical collecting they commonly seem to do so, particularly in condensed sequences.

Graptolite biozones, like biozones generally and unlike chronostratigraphical units, are not fixed within sections by 'golden spikes'. They may, though, have type sections, where they were originally described, enabling clear, original definitions and forming the starting point for subsequent redefinition either there or elsewhere in the world.

An alternative to the use of assemblage biozones is the use of evolutionary lineages. These are not so widely applied in the case of graptolites, largely because the use of assemblage biozones is so successful. Their use is also constrained by the relatively small amount of detailed work that has been done on graptolite evolutionary lineages, particularly with regard to determining whether these lineages show gradualistic or punctuational change. In gradualistic lineages, arbitrary 'snips' of a continuum must be selected, while punctuational lineages are 'naturally' broken up into discrete taxon ranges. It might be said that the latter show evolution to be working in a 'digital' fashion compared to the 'analogue' mechanism of the former. Both punctuational and gradualistic modes of evolution may be inferred in the graptolite record. Punctuation may be invoked where distinctive species, such as *Aulograptus cucullus*, seem to 'appear' globally without any trace of a direct ancestor, though this observation must be viewed in the knowledge that the evolution of such species may have taken place 'elsewhere' (and perhaps slowly), that is, in some marine basin that has not yet been located. Gradualistic modes of evolution have also been recorded (e.g. Urbanek, 1966; Sudbury, 1958); it should be remembered, however, that even 'established' lineages are only hypotheses.

There have been several modifications of graptolite biozones. Numerical notation, giving biozones numbers rather than names, has been used by some authors. This practice is a corruption of Elles & Wood (1901–1918), who numbered their biozones as well as naming them. Elles and Wood, though, were simply providing a count. The numbering of biozones is not as well standardized as are names, and the use of different numerical schemes for different regions is a recipe for chaos. Numerical notation is best avoided.

Interregna are low-diversity levels that may have value in practical correlation, even defined on the occurrence of long-ranging species (and thus on the absence of other species). A familiar example is the Wenlock *Gothograptus nassa/Pristiograptus dubius* Interregnum established by Jaeger (1959). *P. dubius* is one of the longest-ranging graptolite species known (early Wenlock to late Ludlow), while *G. nassa* has been recorded from significantly below the interregnum up to the basal Ludlow (though outside Britain this species seems to be almost confined to its biozone: Porębska, Kozłowska-Dawidziuk & Masiak, 2004). Thus, certain identification of this interregnum hinges on the recognition of the underlying or overlying biozone. The *nassa/dubius* level has been subsequently treated and referred to as a biozone by most workers. Other 'interregna' have been recognized (e.g. a low diversity interval dominated by monograptids with hooked thecae in the upper *turriculatus* Biozone of central Wales: Davies *et al.* 1997) and used informally. Some well-established biozones, also, effectively comprise low-diversity intervals separating more diverse and distinctive biozonal assemblages. For example, the use of the *peltifer* Biozone in Scotland was defined on the basis of few incoming taxa, but many species of the underlying *gracilis* Biozone are absent, while those defining the overlying *wilsoni* Biozone have not yet appeared. The difficulty of recognizing the *peltifer* Biozone led Williams *et al.* (2004) to propose an alternative biozonal arrangement for the lower Caradoc interval, as discussed below.

The duration of graptolite biozones has been assessed in a number of ways. Average duration is estimated by dividing radiometric estimates for the duration of periods or epochs by the number of biozones (e.g. Hughes, 1995). Ordovician biozones are significantly longer, averaging some 2 Ma (Rushton, 1990), than Silurian biozones, which average < 1 Ma, and < 0.5 Ma if subzones and informal subdivisions are taken into account (Zalasiewicz, 1990). Within-period inequalities in length have been assessed by using radiometric dates that constrain epoch rather than period boundaries; in this way, Hughes (1995) estimated average biozone durations, respectively, of 1.0, 0.44, 1.0 and 1.43 Ma for the Llandovery, Wenlock, Ludlow and Přídolí epochs. Finer-scale estimates have been made by using thicknesses of distal, deep-sea graptolitic mudrocks, assuming sedimentation rates to be roughly constant, and cross-checking by comparing sections in different parts of the world, and then applying radiometric age constraints. In this way, Churkin, Carter & Johnson (1977) estimated the *persculptus* Biozone as < 1 Ma in duration, while the *gracilis* Biozone apparently represents some 8 Ma.

Some of the most precise correlation achieved has been effected by bypassing the zonal concept altogether, and cross-correlating the first and last appearances of individual species in selected well-studied sections. Cooper & Lindholm (1990) used such data to effect graphical correlation of early to mid-Ordovician sections; they showed that, globally, the appearances and disappearances of graptolites form a coherent pattern in time, enabling subdivision into about 50 time-slices within a 20 Ma interval. Further refinement of this approach has involved, for example, the 'constrained optimization' (CONOP) method described by Cooper & Sadler (2004) that aimed at extracting the maximum information from individual species ranges, and that further refined estimates of the durations of individual biozones. Within depositional basins or graptolite provinces, such methodologies should see progessive advances in precision; between provinces, endemism and diachronous species ranges will limit progress.

6. British graptoloid biostratigraphy: a summary of previous work

Charles Lapworth (1878) first applied the concept of graptolite zones in Britain while working in the Southern Uplands of Scotland. Having examined a large number of sections, and following the Swedish work of Linnarsson (Hamilton, 2001), he was able to subdivide the Hartfell and Birkhill Shale formations into eleven units based on distinct lithological differences, and found that these corresponded with differences in their accompanying graptolite assemblages which he called 'zones'. He provided detailed lithological logs of the best sections, as well as a chart outlining the vertical ranges of all observed taxa from the sections studied. This was to be the model of procedure for all future biostratigraphical work involving graptolites. In the following year, Lapworth (1879–1880*a*) extended his study of graptolite zones to include all British and international material, identifying twenty zones for the Late Cambrian to Silurian interval. He provided range charts for the graptolite genera and species then known, and suggested that these could form a basis for detailed temporal subdivision of early Palaeozoic strata. His work was immediately put to the test by the Geological Survey of Scotland and was found to be of the greatest value (Rushton, 2001*a*).

These zones were recognizable in other parts of Britain, as later papers indicated, notably in the Stockdale Shales (Marr & Nicholson, 1888) and the Skiddaw Slates (Marr, 1894) of the Lake District. Key biostratigraphical work in Wales and the Welsh Borderland increased the number of known British graptolite species and biozones. Elles's (1900) study of the Wenlock Shales of the Welsh Borderland, Wood's (1900) on the Lower Ludlow Formation of the Welsh Borderland, and Herbert Lapworth's (1900) work

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on the Silurian sequence at Rhayader in mid-Wales, all provide detailed lithostratigraphies combined with species range charts; new biozones were introduced and existing ones altered, reflecting distinct local variations in the composition of the graptolite assemblages. Wood (1900) subdivided part of the Ludlow succession at Long Mountain into subzones. These workers also compared their range charts and faunal lists with information available from the rest of Britain and abroad, particularly Sweden.

'A monograph of British graptolites' (Elles & Wood, 1901–1918) is a complete account of all the British planktonic graptolite species and subspecies known at that time (apart from *Rhabdinopora* and *Corynoides*), providing descriptions and figures of each taxon. The stratigraphical ranges of all the taxa were collated into a biostratigraphy comprising 36 graptolite biozones and subzones. This was the first time that one study on British graptolites had unified the taxonomy, biostratigraphy and chronostratigraphical importance of the group to such an extent. The monograph continues to provide the basis for British graptolite biostratigraphy, and its influence on global correlation remains profound, although many of the individual taxon descriptions and ranges have been revised in subsequent studies.

Graptolites were now established as a fundamental part of British Early Palaeozoic stratigraphical studies (e.g. Jones, 1909, 1947; Davies, 1929; Jones & Pugh, 1935). Later, Sudbury (1958) beautifully demonstrated patterns of fine-scale evolution in the Llandovery triangulate monograptids of the Rheidol Gorge, Wales. Toghill (1968*a*) updated the graptolite assemblages and biozones of the early Silurian Birkhill Shale Formation of Scotland. Studies on the Silurian strata of Northern England included accounts of the Wenlock and Ludlow (Rickards, 1967) and Llandovery (Rickards, 1970) graptolites of the Howgill Fells and of the Lake District (Hutt, 1974–1975). The results of these studies were collated into a major revision of British Silurian graptolite ranges and zonal descriptions (Rickards, 1976). No corresponding update of Elles & Wood's Ordovician range charts was produced prior to the one we provide in this report, although Jackson (1962) provided a synthesis of the Arenig biostratigraphy of the Skiddaw Group of the Lake District.

Subsequent work includes Williams's descriptions of the classic Dob's Linn section (1982*b*, 1988), which became the Ordovician–Silurian boundary stratotype (Bassett, 1985), and in the Moffat and Girvan districts (Williams, 1982*a*, 1987, 1994). Zalasiewicz (1984, 1986) described early Ordovician graptolite material from North Wales, and Fortey & Owens (1978, 1987) from South Wales.

Major British Geological Survey (BGS) mapping programmes in Wales, the Lake District and southern Scotland were all underpinned by graptolite biostratigraphy; large collections were made and described, and the biozonation itself was considerably refined. Rushton's (*in* Cooper *et al.* 2004) reorganization of Arenig graptolite biostratigraphy in the Skiddaw Group formed part of this work, as did the report of graptolites of Arenig age in the Ballantrae ophiolite complex in SW Scotland (Stone & Rushton, 1983). Studies of younger Ordovician strata included those of Zalasiewicz (1992*a*), Zalasiewicz, Rushton & Owen (1995), Cave & Rushton (1996) and Williams *et al.* (2003*a*, 2004), while the compilation of Scottish records by Rushton *et al.* (1996) demonstrated the continued importance of graptolite work in the stratigraphy and structure of the Southern Uplands of Scotland.

Remapping of central Wales by BGS prompted refinement of Llandovery and Wenlock graptolite biostratigraphy. There were studies of early to mid-Llandovery (Rhuddanian–Aeronian) sections and graptolite assemblages (Zalasiewicz, 1992*b*, 1996; Zalasiewicz & Tunnicliff, 1994). Spectacular progress was made in late Llandovery (Telychian) successions (Loydell, 1991*a*, 1992–1993*a*, 1993*b*; Loydell & Cave, 1993, 1996; Zalasiewicz, 1994; Zalasiewicz, Loydell & Štorch, 1995; Davies *et al.* 1997). For example, the former *Monograptus turriculatus* Biozone was split into two separate biozones, each with several component subzones, and the former *Monoclimacis crenulata* Biozone into four separate biozones. Work on Elles's (1900) original Wenlock biozonal localities near Builth Wells (Zalasiewicz & Williams, 1999; Williams & Zalasiewicz, 2004) resulted in a reorganization of graptolite biozones for that part of the stratigraphical column. Nevertheless, substantial sections of British early Palaeozoic biostratigraphy remain relatively neglected, for example, the Ludlow successions, and further refinement may be expected. The current biozonal schemes for the British Ordovician and Silurian are given in Figures 1 and 2.

7. Notes on the range charts

Two separate graptoloid range charts are given for the British Ordovician, one representing England and Wales (Figs 3–7) and the other Scotland (Figs 8–10), because significant regional differences in graptolite faunas exist. The separation of Scotland from England and Wales by the Iapetus Ocean resulted in faunal provincialism during the Ordovician, and for graptolites, this remained the case even upon the closure of Iapetus at the end of the period, probably as a result of environmental factors (Zalasiewicz, Rushton & Owen, 1995). Fewer such problems exist in the Silurian, and a single sequence of graptolite biozones has been recognized throughout the UK (Figs 11–19). Sources for the ranges are provided (Tables 1–3) and, for ease of use, an index to taxa (Table 4).

Elles & Wood (1901–1918) assigned their species to relatively few genera. There has since been an expansion of generic concepts; those used here mostly follow Strachan's (1996–1997) review of British graptolites. Strachan gave full bibliographic references to the species known to him, and those references are

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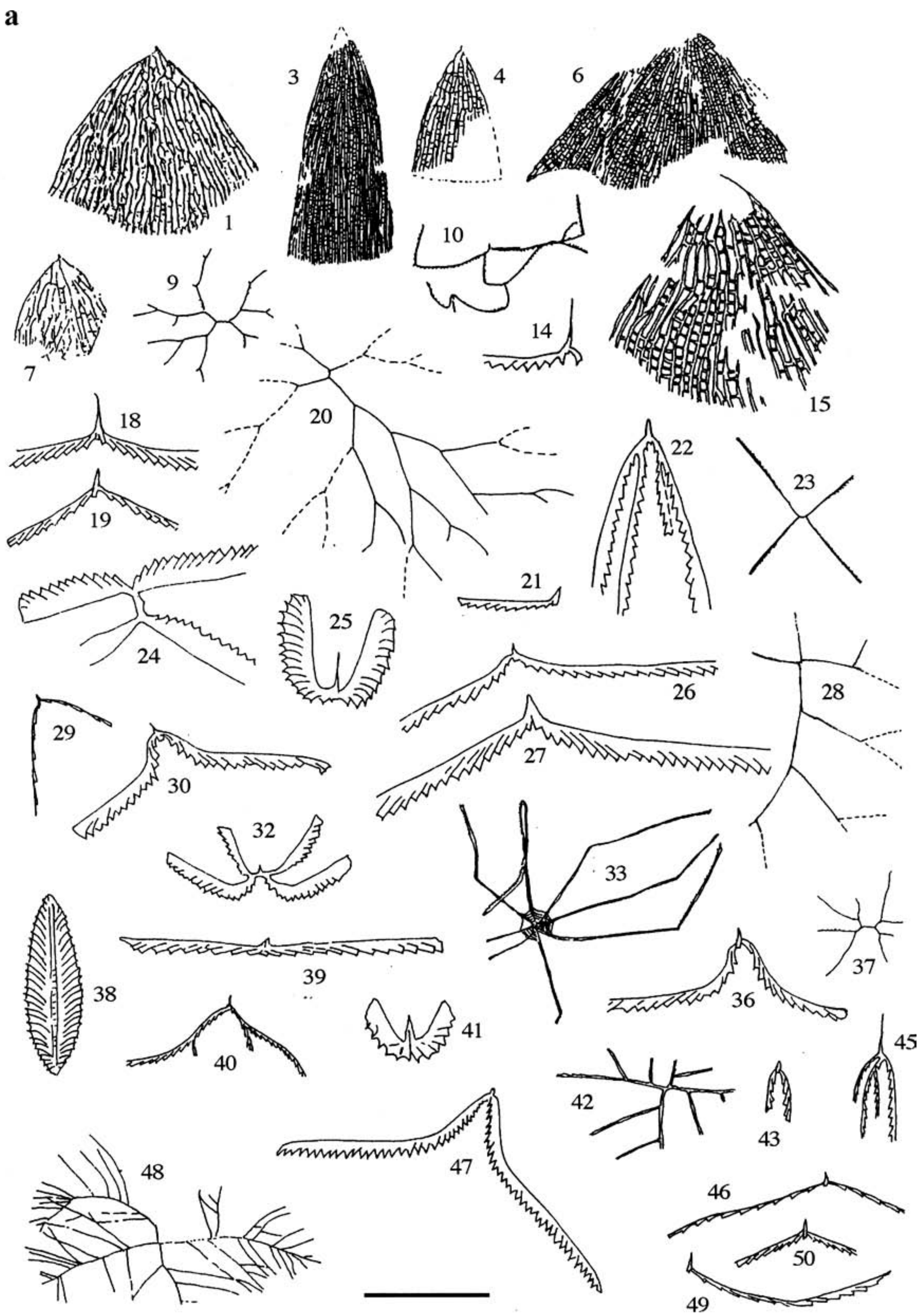

Figure 3. For legend see facing page.

not repeated here, though references are given here for species recognized in Britain subsequent to Strachan's compilation.

These range charts were commenced by JAZ and AWAR in work for the British Geological Survey, substantially developed by LT during Ph.D. studies, and subsequently added to by the other authors. Species recorded in the range charts have been fully documented in papers, monographs or memoirs. Records in conference abstracts are not included.

In the range charts: X – present; A – abundant; L – present in lower part; M – present in middle part;

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b

No.	Taxa	flabell.	tenellus	(salop.)	(sedg.)	murrayi	Phyllog.	varic.	simulans	victoriae	gibberul.	cuccul.	artus	Sources
1	*Rhabdinopora flabelliformis* cf. *parabola* (Bulman, 1954)	L												41
2	*Rhabdinopora flabelliformis* cf. *desmograptoides* (Hahn, 1912)	L												41
3	*Rhabdinopora flabelliformis socialis* (Salter, 1857)	X		?										42, 43, 44
4	*Rhabdinopora flabelliformis flabelliformis* (Eichwald, 1840)	X	X	aff. (L)										42, 45
5	*Rhabdinopora flabelliformis belgica* (Bulman, 1971)	X		aff. (L)										45
6	*Rhabdinopora flabelliformis patula* (Bulman, 1973)	X		X (L)										45
7	*Rhabdinopora flabelliformis anglica* (Bulman, 1927)		L	cf. (L)										44, 45
8	*Rhabdinopora flabelliformis bryograptoides* (Bulman, 1954)			cf. (L)										45
9	*Adelograptus tenellus* (Linnarsson, 1871)		X											42,45, 47
10	*Adelograptus hunnebergensis* (Moberg, 1892)		X											42, 45, 47
11	*Adelograptus hians* (Moberg, 1892)		X											47
12	*Adelograptus sarmentosus* (Moberg, 1892)		X											42, 43
13	*Anisograptus* cf. *norvegicus* Bulman, 1954		X											45
14	*Kiaerograptus quasimodo* Rushton, 1981		?											46
15	*Araneograptus murrayi* (Hall, 1865)					X								7, 10, 22
16	*Acrograptus*? cf. *sinensis* (Lee & Chen, 1962)					X								7, 10, 22
17	*'Didymograptus'* sp. (declined) of Molyneux & Rushton, 1988					X								7, 22
18	*Didymograptus (s.l.) protobalticus* Monsen, 1937						X							7
19	*Acrograptus*? *rigoletto* (Maletz, Rushton & Lindholm, 1991)						X							7, 21
20	*Temnograptus multiplex* (Nicholson, 1868)						X	?						7
21	*Azygograptus validus*? Törnquist, 1904						?	?						7
22	*Tetragraptus* (*Pendeograptus*) *fruticosus* (Hall, 1858)						cf. X	X						7
23	*Tetragraptus quadribrachiatus* (Hall, 1858)						X	X	X	X	X	X		7
24	*Tetragraptus amii* Elles & Wood, 1902						X?	?	X	?	X	X		7
25	*Tetragraptus pseudobigsbyi* Skevington, 1965						?	?	X	X	X	X		7
26	*Baltograptus vacillans attenuatus* (Monsen, 1937)							X						7
27	*Didymograptus s.l. balticus* Tullberg, 1881							X						7
28	*Trochograptus diffusus* Holm, 1881							X	?	?				7, 14
29	*Acrograptus filiformis* Tullberg, 1880							X	X					7
30	*Corymbograptus varicosus* (Wang, 1974)							X	X					7
31	*'Didymograptus'* cf. *decens* Törnquist, 1889							L	L					7
32	*Tetragraptus reclinatus* Elles & Wood, 1902							X	X	X	X	?		7, 33
33	*Dichograptus octobrachiatus* (Hall, 1858)							X	X	?	X	X		7
34	*Corymbograptus* cf. *kunmingensis* Ni, 1979							U						7
35	*Dichograptus octobrachiatus sedgwickii* Salter, 1863							U	X	?	X	?		7
36	*Corymbograptus deflexus* (Elles & Wood, 1901)							U	X	L		cf.		7, 28, 33
37	*Dichograptus separatus* Elles, 1898							U?				X		7
38	*Pseudophyllograptus angustifolius* (Hall, 1858)							U	X	X	X	X	X	7, 28
39	*Expansograptus similis* (Hall, 1865)							cf.	?					7
40	*Adelograptus*? *divergens* (Elles & Wood, 1902)								X					7
41	*Isograptus* cf. *primulus* Harris, 1933								X					7
42	*Schizograptus reticulatus* (Nicholson, 1868)								X					7
43	*Didymograptus* (*Didymograptellus*) *minutus* Törnquist, 1879								X					7
44	*Tetragraptus postlethwaitei* Elles, 1898								X					7, 14
45	*Tetragraptus pendens* Elles, 1898								X					7
46	*Acrograptus gracilis* (Törnquist, 1891)								X					7, 28
47	*Corymbograptus v-fractus v-fractus* (Salter, 1863)								?					14
48	*Holograptus deani* Elles & Wood, 1902								?	?				14
49	*Azygograptus eivionicus* Elles, 1922								X	L				2, 7, 33
50	*Acrograptus infrequens* Kraft, 1973								X	L				7

Figure 3. Ordovician graptolites (a) and their stratigraphical ranges (b) in England and Wales, *flabelliformis* to *artus* biozones. Scale bar represents 10 mm except for: 1, 23, 32, 40, 45, 47 (20 mm); 3, 4, 6, 7, 9, 10, 15, 23, 37, 42 (40 mm); 20, 28 (57 mm); 33 (80 mm); and 48 (320 mm). Key to symbols used in range charts: X – present; A – abundant; L – present in lower part; M – present in middle part; U – present in upper part; cf. – similar to but not certainly identified; aff. – related to but not identical; ? – doubtful; ?? – very doubtful; < – range extends lower; > – range extends higher.

U – present in upper part; cf. – similar to but not certainly identified; aff. – related to but not identical to named species; ? – doubtful record; ?? – very doubtful; < – range extends lower; > – range extends higher.

The thumbnail sketches of the graptolite taxa on the pages facing the charts are intended to remind the general reader of the overall character of the various species. They are not adequate for identification.

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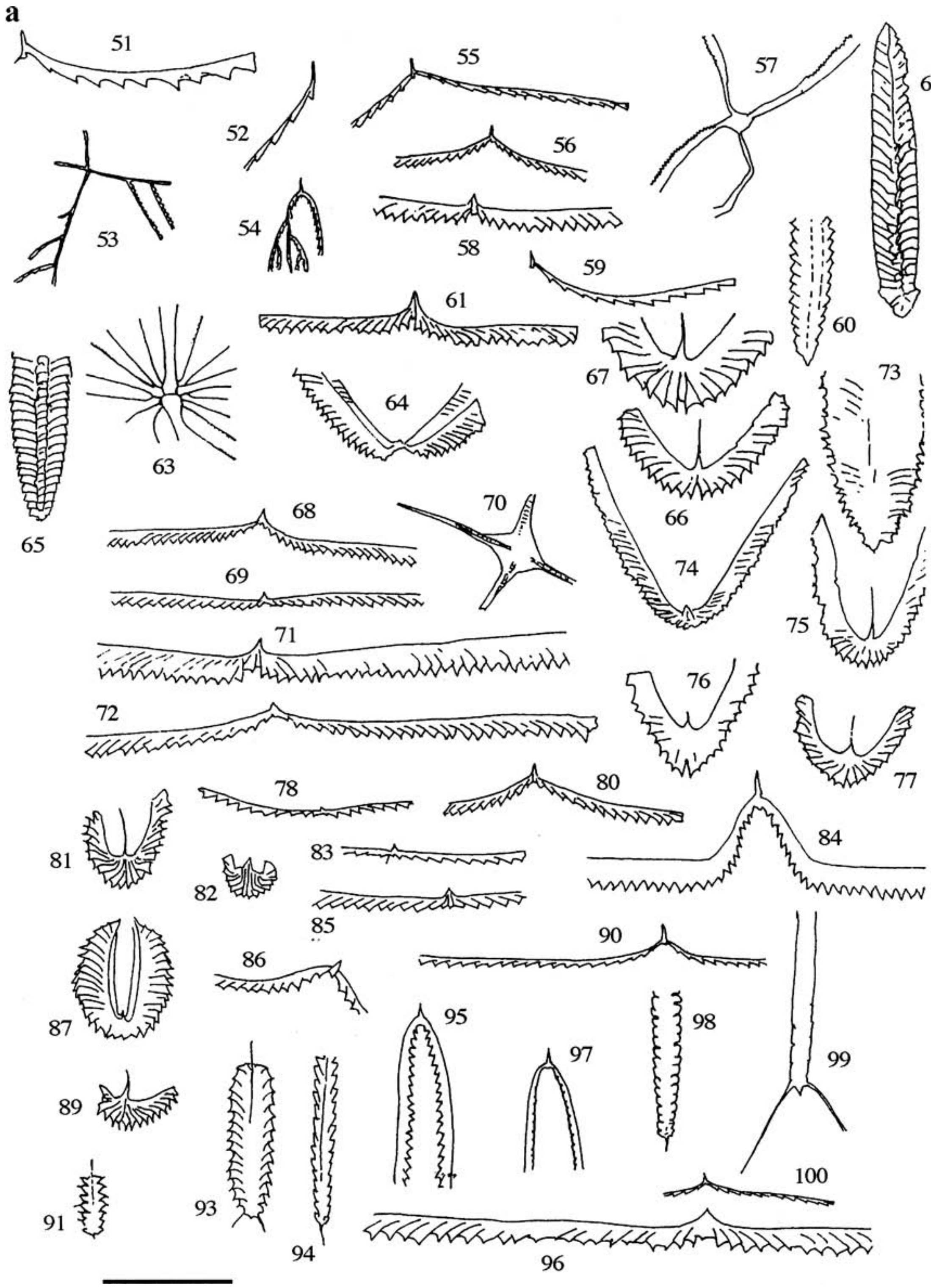

Figure 4. For legend see facing page.

8. Ordovician

R. A. Cooper (1999) discussed the global correlation of Tremadocian graptolites, recognized nine graptolite chronozones, and in his figure 1 showed the ranges of the main types of graptolites in the Tremadocian. In Britain, only a few of those chronozones are recognized. They are distributed between two locally defined stages proposed by Fortey *et al*. (1995), the Cressagian below and the Migneintian. In Britain, the upper Tremadocian is almost devoid of graptolites, with two widely recognized trilobite biozones, the *Conophrys salopiensis* and *Angelina sedgwickii* zones, occupying most of the Migneintian (Fig. 1, 3*b*).

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b

No.	Taxa	simul.	victor.	gibber.	cucull.	artus	murch.	teretius.	gracilis	Sources
51	*Azygograptus hicksii* (Hopkinson, 1875)	X								2, 15
52	*Azygograptus ellesi* Monsen, 1937	X	aff.							2, 7
53	*Schizograptus tardifurcatus* Elles, 1898	X	?							7
54	*Pseudobryograptus cumbrensis* (Elles, 1898)	X	L							8, 26
55	*Acrograptus kurcki* (Törnquist, 1901)	X	L							7
56	*Expansograptus simulans* (Elles & Wood, 1901)	X	L	cf.						7, 10, 28, 33
57	*Tetragraptus crucifer* (Hall, 1858)	X		X						7
58	*Expansograptus* cf. *praenuntius* (Törnquist, 1901)	X	X	?						3, 7, 28, 33
59	*Azygograptus lapworthi* Nicholson, 1875	?	?	?						2, 7
60	*Pseudotrigonograptus minor* (Mu & Lee, 1958)	X	X	X	?					3, 7
61	*Expansograptus goldschmidti* (Monsen *sensu* Kraft, 1977)	?	X	X	?					7, 15, 16
62	*Pseudotrigonograptus ensiformis* (Hall, 1858)	?	X	X	?	?				7
63	*Loganograptus logani* (Hall, 1858)	X		X	X					7
64	*Tetragraptus serra* (Brongniart, 1828)	X	X	X	X	?				7, 24
65	*Phyllograptus densus* Törnquist, 1879		X							7
66	*Isograptus victoriae victoriae* Harris, 1933		X							7, 10
67	*Isograptus victoriae* cf. *maximus* Harris, 1933		X							7, 19
68	*Corymbograptus*? *uniformis lepidus* (Ni, 1979)		X	X						3, 7, 15, 16
69	*Expansograptus extensus linearis* (Monsen, 1937)		X	X						3, 7, 10
70	*Tetragraptus headi* (Hall, 1858)		X	X						7
71	*Expansograptus hirundo* (Salter, 1863)		X	X	X					3, 7, 8, 28, 37
72	*Expansograptus nitidus* (Hall, 1858)		?	X	X					7, 28
73	*Phyllograptus* cf. *typus* Hall, 1858				?	MU	L?			7, 28, 31, 32, 36
74	*Isograptus victoriae divergens* Harris, 1933 (of Jenkins)			X						19
75	*Isograptus gibberulus* (Nicholson, 1875)			X						3, 7, 8, 10, 19
76	*Isograptus caduceus* ssp. (large)			X						7
77	*Isograptus caduceus* cf. *imitatus* Harris, 1933			X						7, 19
78	*Expansograptus distinctus* (Harris & Thomas, 1935)			X						3, 7, 16
79	*Pseudisograptus* n. sp. A of Jenkins, 1982			X						7
80	*Corymbograptus*? *uniformis* (Elles & Wood, 1901)			X						7, 16
81	*Pseudisograptus angel* Jenkins, 1982			X						3, 7, 19
82	*Pseudisograptus dumosus* (Harris, 1933)			?						3
83	*Xiphograptus svalbardensis* (Fortey & Archer, 1974)			X	?					7
84	*Corymbograptus v-fractus volucer* (Nicholson, 1890)			X	?					7, 16
85	*Expansograptus suecicus* (Tullberg, 1880)			cf.	cf.					28
86	*Corymbograptus* cf. *inflexus* (Chen & Xia, 1979)			cf.	cf.					28
87	*Tetragraptus bigsbyi bigsbyi* (Hall, 1865)			X	X	?	?			7, 28, 32
88	*'Thamnograptus' doveri* Nicholson, 1875			U						7
89	*Pseudisograptus* cf. *geniculatus* (Skevington, 1965)				?					28
90	*Acrograptus nicholsoni planus* (Elles & Wood, 1901)				X					7, 16
91	*Undulograptus sinicus* (Mu & Lee, 1958)				X					7
92	*Cardiograptus* sp.				X					7
93	*Cryptograptus hopkinsoni* (Nicholson, 1869)				X					7, 16
94	*Eoglyptograptus shelvensis* (Bulman, 1963)				X	cf.				7, 16, 28
95	*Didymograptus protobifidus* Elles, 1933				X	L				7, 12
96	*Expansograptus sparsus* (Hopkinson, 1875)				X	?				7, 16, 28
97	*Aulograptus cucullus* (Bulman, 1932)				X	X				7, 16, 24, 26
98	*Undulograptus cumbrensis* (Bulman, 1963)				X	X				7, 16, 26
99	*Cryptograptus antennarius* (Hall, 1865)				X	X				7, 16, 24
100	*Didymograptus* sp. A of Skevington				X	X				7, 15, 16

Figure 4. Ordovician graptolites (a) and their stratigraphical ranges (b) in England and Wales, *simulans* to *gracilis* biozones. Scale bar represents 10 mm except for: 54, 64 (20 mm); 53, 57, 63, 70 (40 mm). For key to symbols in range charts, see Figure 3.

8.a. *Rhabdinopora flabelliformis* Biozone

The appearance of *Rhabdinopora flabelliformis* (formerly *Dictyonema flabelliforme*) has for a long time been taken as a marker for the beginning of the Tremadocian. Although the base of the Ordovician, as currently defined, is now taken at the appearance of the conodont *Iapetognathus fluctivagus* (Cooper, Nowlan & Williams, 2001), the appearance of the earliest subspecies of *Rhabdinopora*

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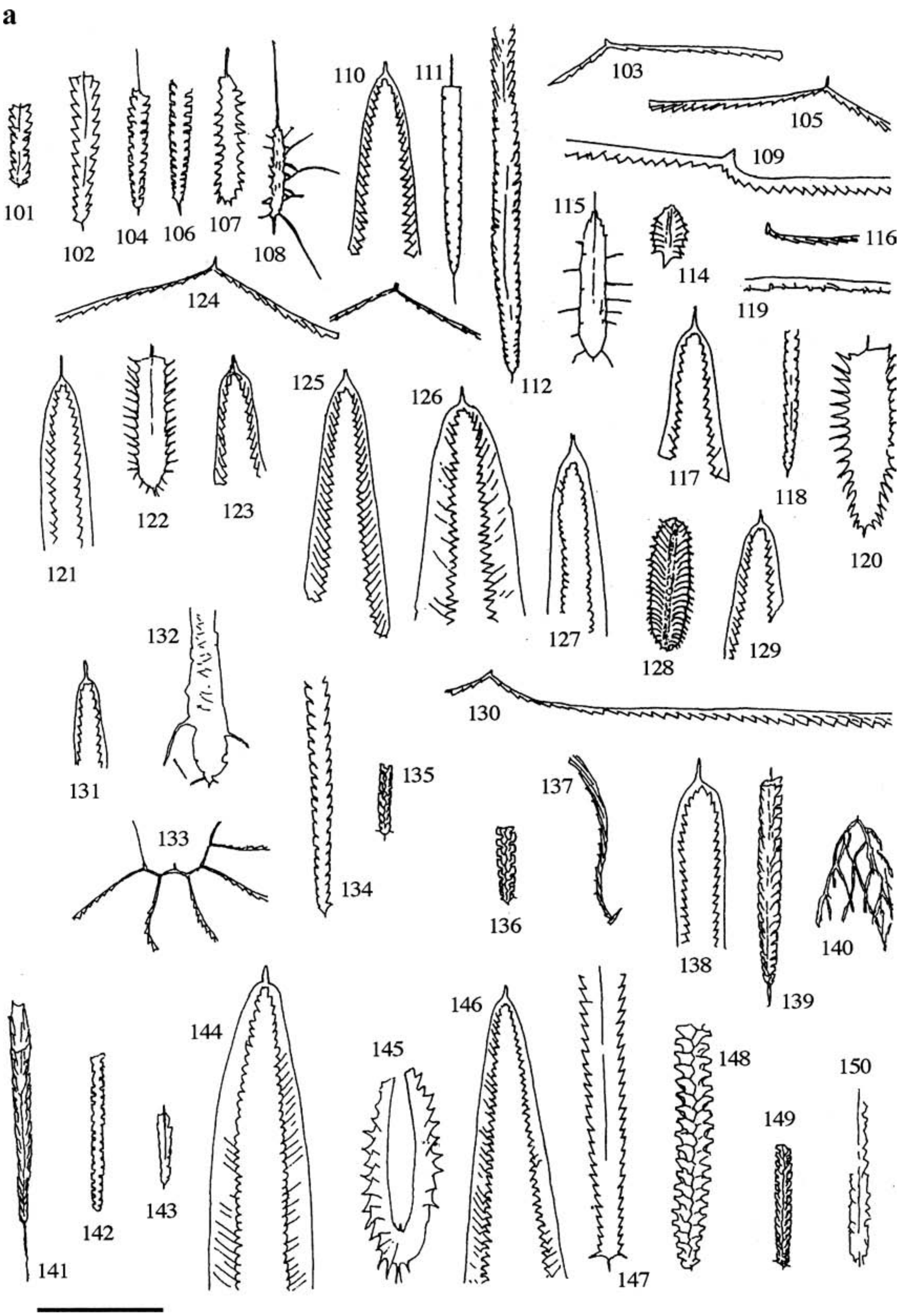

Figure 5. For legend see facing page.

flabelliformis remains a good approximation to the base of the Ordovician and is applicable in clastic sequences where conodonts are rare (Landing *et al.* 2000).

The lowest of Cooper's biozones, that of *Rhabdinopora praeparabola*, is not yet known in Britain. The *flabelliformis* Biozone in Britain appears to include the equivalents of Cooper's *parabola* and *matanensis* biozones, and possibly part of the overlying *anglica* Biozone. At Brin-llin-fawr, North Wales, the occurrence of taxa closely comparable to the early subspecies *Rhabdinopora flabelliformis parabola* and *R. f.*

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b

No.	Taxa	cucull.	artus	murch.	teret.	gracilis	foliac.	caudat.	Sources
101	*Oelandograptus austrodentatus anglicus* (Bulman, 1963)	X	X						7, 26
102	*Eoglyptograptus dentatus* (Brongniart, 1828)	X	X	L?					7, 16, 26, 28
103	*Acrograptus affinis* (Nicholson, 1869)	X	X	X					7, 16, 26
104	*Climacograptus biformis* Mu & Lee, 1958	cf.		?					7
105	*Acrograptus acutidens* (Elles & Wood, 1901)	U	X	X					7, 16, 24, 26, 28
106	*Amplexograptus confertus* (Lapworth, 1875)	U?	LM	L					3, 8, 28, 32
107	*Cryptograptus tricornis schaeferi* Lapworth, 1880b	U?	X	L	X	?			3, 17, 26, 28, 32
107A	*Isograptus*? *caduceus* cf. *nanus* (Ruedemann, 1904)		?						48
108	*Paraglossograptus* sp.		L						7
109	*Expansograptus robustus* (Ekström, 1937)		X	cf.					7, 26
110	*Didymograptus acutus* Ekström, 1937		X						7, 26
111	*Climacograptus angustatus* Ekström, 1937		X?						7, 25
112	*Diplograptus ellesi* Bulman, 1963		X						3, 26
113	*Didymograptus* cf. *dubitatus* Harris, 1935		X						7
114	*Pseudophyllograptus glossograptoides* (Ekström, 1937)		X						26, 28
115	*Glossograptus armatus* (Nicholson, 1869)		X						7, 28
116	*Azygograptus coelebs* Lapworth, 1880b		X						2
117	*Didymograptus spinulosus* Perner, 1895		X	?					3, 7, 8, 43, 44
118	*Climacograptus tailbertensis* Skevington, 1970		X						7, 16, 26
119	*Holmograptus lentus* (Törnquist, 1911)		X						7, 26
120	*Glossograptus acanthus* Elles & Wood, 1908		X						7, 28
121	*Didymograptus stabilis* Elles & Wood, 1901		X						7, 26, 28
122	*Glossograptus fimbriatus* (Hopkinson, 1872)		X	X	X	X			17, 28
123	*Didymograptus pluto* Jenkins, 1963		X						20, 28
124	*Acrograptus nicholsoni nicholsoni* (Lapworth, 1875)		X	cf.					7, 14
125	*'Didymograptus bifidus'* auctt.		X	?					26, 32
126	*Didymograptus geminus* (Hisinger, 1840)		X	X					5, 7
127	*Didymograptus pakrianus* Jaanusson, 1960		X	?					7, 26, 32
128	*Pseudophyllograptus*? *nobilis* (Harris & Keble, 1932)		?	?					7
129	*Didymograptus artus* Elles & Wood, 1901		X	L?					7, 15, 26, 43
130	*Didymograptus euodus* Lapworth, 1875		X	L		X?			15, 26, 32
131	*Didymograptus miserabilis* Bulman, 1931		X	cf.					7, 28
132	*Lonchograptus* sp. of Rushton *in* Gibbons & McCarroll, 1993		M						8
133	*Trichograptus fragilis* (Nicholson, 1869)		M						26
134	*Diplograptus hollingworthi* Skevington, 1970		M						7, 26
135	*Pseudoclimacograptus angulatus* (Bulman, 1953)		M						7, 26
136	*Pseudoclimacograptus scharenbergi* (Lapworth, 1876)		MU	X	X	X	X		7, 14, 17, 28
137	*Nicholsonograptus fasciculatus* (Nicholson, 1869)		X						25
138	*Didymograptus nanus* Lapworth, 1875		U	L					7, 26, 27
139	*Amplexograptus caelatus* (Lapworth, 1875)		Ucf.	M		X			17
140	*Pterograptus elegans*? Holm, 1881			L					32
141	*Pseudoclimacograptus angulatus magnus* (Berry, 1964)			X					32
142	*Pseudoclimacograptus angulatus micidus*? (Berry, 1964)			X					32
143	*'Climacograptus' pauperatus* Bulman, 1953			X					27
144	*Didymograptus murchisoni* (Beck, 1839)			X					13, 28, 32
145	*Isograptus ovatus davidensis* Skevington & Jackson, 1976			X					39
146	*Didymograptus speciosus* Ekström, 1937			X?					5, 6, 20, 28, 32
147	*Orthograptus calcaratus priscus* Elles & Wood, 1907			X	L?				13, 32
148	*Lasiograptus retusus* Lapworth, 1880b			LM	L				5, 17
149	*Pseudoclimacograptus angulatus sebyensis* Jaanusson, 1960			X	L				5, 17
150	*Cryptograptus tricornis* (Carruthers, 1859)			X	X	X	L		14, 17

Figure 5. Ordovician graptolites (a) and their stratigraphical ranges (b) in England and Wales, *cucullus* Biozone to *caudatus* Subzone. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

desmograptoides at the base of the *flabelliformis* Biozone (Legrand *in* Rushton *et al.* 1999, fig. 7.4) suggests that the *parabola* Biozone may prove recognizable. Higher in the *flabelliformis* Biozone, *R. flabelliformis flabelliformis* and *R. f. socialis* are the most widely recognized forms, and are known from north Wales, Shropshire and numerous boreholes in Warwickshire and Buckinghamshire (Bulman & Rushton, 1973; Old, Sumbler & Ambrose, 1987; Bridge *et al.* 1998). Although *Rhabdinopora f. anglica* appears

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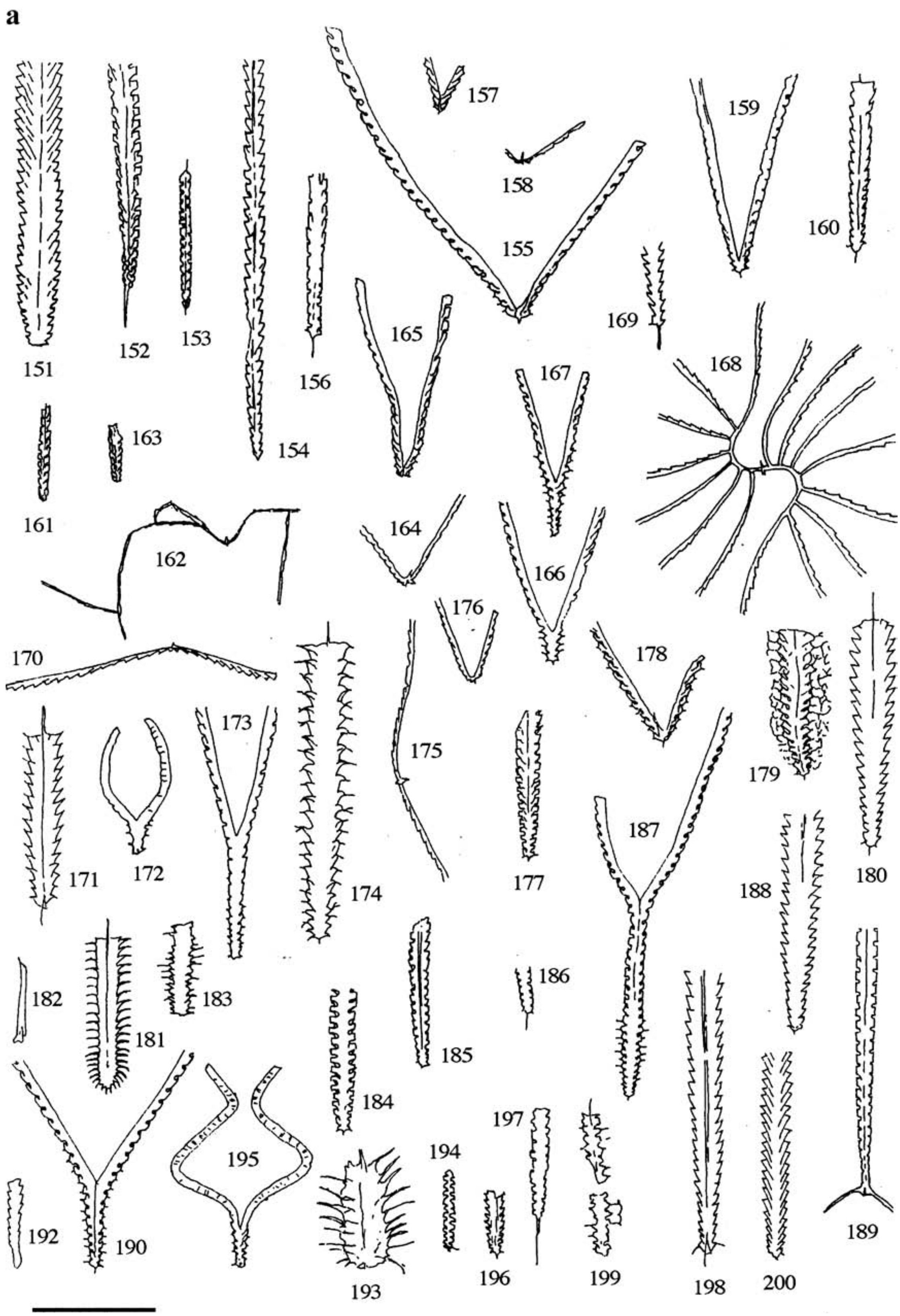

Figure 6. For legend see facing page.

to occur high in the *flabelliformis* Biozone, it is not yet clear whether a separate *anglica* Biozone can be recognized. The borehole record of *Kiaerograptus quasimodo* Rushton, 1981 is anomalous because it lies in the midst of borehole records proving the *flabelliformis* Biozone (Old, Sumbler & Ambrose, 1987), whereas *Kiaerograptus* occurs typically in the equivalents of the Migneintian Stage.

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b

No.	Taxa	murch.	teret.	gracilis	foliaceus	caudatus	morrisi	linearis	complan.	anceps	persculp.	Sources
151	*Diplograptus foliaceus* (Murchison, 1839)	X	X	X	X							17, 28, 31, 44
152	*Diplograptus*? *decoratus* (Harris & Thomas, 1935)	MU	LM									5, 17, 28, 31, 34
153	*Normalograptus brevis* (Elles & Wood, 1906)	U	X	X	X	cf.						5, 29
154	*Normalograptus euglyphus* (Lapworth, 1880b)		X?	X								5, 17, 28, 29, 34, 43
155	*Dicellograptus divaricatus divaricatus* (Hall, 1859)		X	M								17, 31
156	*Climacograptus antiquus* Lapworth, 1873		X	X	X	X						17, 28, 29
157	*Dicranograptus irregularis* Hadding, 1913		MU	L								17
158	*Dicellograptus geniculatus* Bulman, 1932		MU	X								5, 17, 28, 29, 31
159	*Dicellograptus intortus* Lapworth, 1880b		MU	X	L							5, 17, 28
160	*Hustedograptus teretiusculus* (Hisinger, 1840)		MU	L	LM							5, 17, 28, 29
161	*Climacograptus sheldoni* Hughes, 1989		U	L								17, 28, 29, 31
162	*Nemagraptus* cf. *subtilis* Hadding, 1913		U	X								5, 17
163	*Pseudoclimacograptus modestus* (Ruedemann, 1908)		U	X	L							5, 17
164	*Dicellograptus salopiensis* Elles & Wood, 1904		U	X	LM							5, 7, 17, 28, 34
165	*Dicellograptus cambriensis* Hughes, 1989		U	LM	LM							17, 28, 29, 34
166	*Dicranograptus brevicaulis* Elles & Wood, 1904		U	LU	X							17, 28
167	*Dicranograptus rectus* Hopkinson, 1872 *sensu* Elles & Wood		U	X	X							17, 28, 29
168	*Nemagraptus gracilis* (Hall, 1847)			X								17, 28, 29
169	*Orthograptus uplandicus* (Wiman, 1895)			X								17, 28, 29
170	*Expansograptus*? *superstes* (Lapworth, 1876)			X								28, 43
171	*Orthograptus whitfieldi* (Hall, 1859)			X								29
172	*Dicranograptus furcatus minimus* Lapworth, 1876			X								14
173	*Dicranograptus ramosus* (Hall, 1847)			X								14
174	*Hallograptus mucronatus* (Hall, 1847)			X	?							43
175	*Leptograptus validus validus* Elles & Wood, 1903			X	L							17, 28, 29
176	*Dicellograptus sextans exilis* Elles & Wood, 1904			X	L							43
177	*Diplograptus leptotheca* Bulman, 1946			X	LM							29
178	*Dicellograptus sextans sextans* (Hall, 1843)			X	X							5, 28
179	*Lasiograptus costatus* (Lapworth, 1873)			X	X	X						44, 29
180	*Orthograptus apiculatus* Elles & Wood, 1907			LU?	X	Laff.						5, 17, 28, 29, 38
181	*Glossograptus hincksii hincksii* (Hopkinson, 1872)			MU	LM							29
182	*Corynoides curtus* Lapworth, 1876			MU	X	X						5, 17, 28, 34, 36
183	*Lasiograptus pusillus* Ruedemann, 1947			U								34
184	*Amplexograptus perexcavatus* (Lapworth, 1876)			U	X							5, 29
185	*Amplexograptus arctus* Elles & Wood, 1907			U	X							5, 29, 44
186	*Diplograptus molestus* Thorslund, 1948			U	X							5, 34, 44
187	*Dicranograptus ramosus spinifer* Elles & Wood, 1904			U	X							5, 17, 29, 34
188	*Orthograptus calcaratus acutus* Elles & Wood, 1907			U	X							29, 43
189	*Climacograptus bicornis* (Hall, 1847)			U	X							17, 28, 29
190	*Dicranograptus nicholsoni nicholsoni* Hopkinson, 1870			U	X	X						29, 36
191	*Climacograptus* cf. *bekkeri* (Öpik, 1927)			?	?							43
192	*Climacograptus* cf. *putillus* (Hall, 1865)			?	?							43
193	*Glossograptus* cf. *ciliatus* Emmons, 1855			?	?							43
194	*Pseudoclimacograptus isknos* Zalasiewicz, 1992				X							34, 44
195	*Dicranograptus ziczac* Lapworth, 1876				X							29
196	*'Glyptograptus' plurithecatus* Obut & Sobolevskaya, 1964				X							34
197	*Climacograptus meridionalis* (Ruedemann, 1947)				?							34
198	*Orthograptus calcaratus* group				X	X	X	LM				5, 29, 36
199	*Lasiograptus harknessi* (Nicholson, 1867)				X	X	X	?				5, 29, 34, 36, 44
200	*Orthograptus amplexicaulis* (Hall, 1847)				X	X	X	X	X			17, 36, 37

Figure 6. Ordovician graptolites (a) and their stratigraphical ranges (b) in England and Wales, *murchisoni* to *persculptus* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

8.b. *Adelograptus tenellus* Biozone

This biozone is recognized by the appearance of *Adelograptus* (formerly *Clonograptus*) *tenellus* and *A. hunnebergensis*. Cooper (1999) recognized an *Adelograptus* Biozone above the *Rhabdinopora flabelliformis anglica* Biozone, but these are not readily separated in Britain. In the 'Transition Beds' of the Shineton Shales of Shropshire, *Rhabdinopora flabelliformis* subspp., including *R. f. anglica*, alternate with *Adelograptus* spp. through a relatively small thickness of strata, above which *Rhabdinopora* disappears. It appears that an equivalent situation pertains to the English subcrop.

8.c. Higher Tremadocian zones

Above the *tenellus* Biozone, graptolites are practically absent from strata in Britain until the top of the

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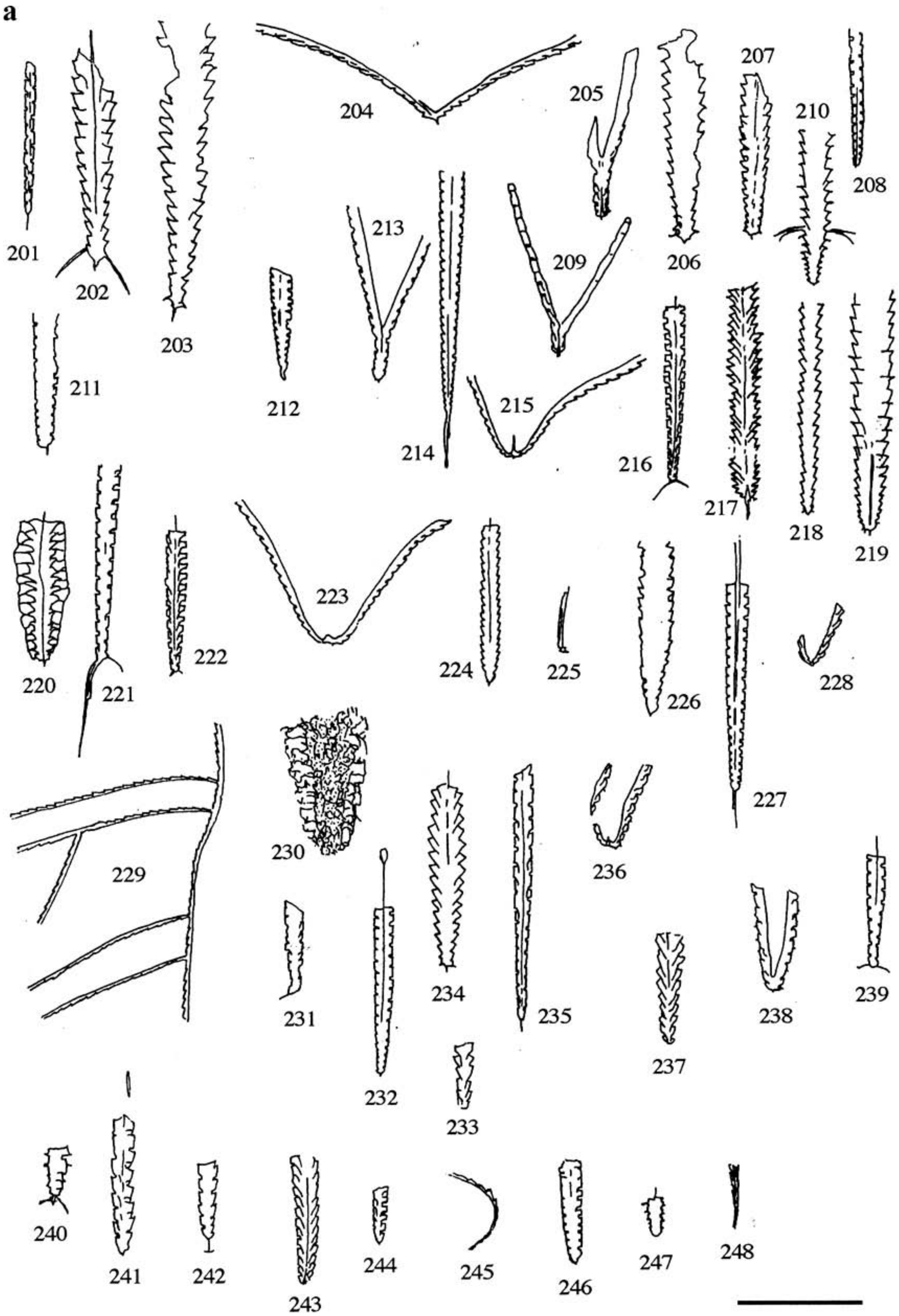

Figure 7. For legend see facing page.

Tremadocian, and Migneintian biostratigraphy has depended on evidence from trilobites and acritarchs. There are, however, two records of *Rhabdinopora flabelliformis* subspp. from strata referred to the *Conophrys salopiensis* trilobite Biozone as recognized on the basis of trilobites and acritarchs: one from the Deanshanger Borehole in Buckinghamshire (Bulman & Rushton, 1973), the other from the 'Upper *Dictyonema* Band' in the Gwynant Valley, north of Cadair Idris (Pratt, Woodhall & Howells, 1995, p. 16). Both

b

No.	Taxa	foliaceus	caudatus	morrisi	linearis	complan.	anceps	persculp.	Sources
201	*Norm. angustus* (Perner, 1895) (= *C. miserabilis* Elles & Wood, 1906)	X	Xcf.	Xcf.	X	X	?	?>	36, 38
202	*Orthograptus calcaratus tenuicornis* Elles & Wood, 1907	M	U						29
203	*Orthograptus calcaratus vulgatus* Elles & Wood, 1907	M	U						29
204	*Dicellograptus patulosus* Lapworth, 1880	U							29
205	*Dicranograptus nicholsoni minor* Bulman, 1945	U							6, 34
206	*Orthograptus calcaratus basilicus* Elles & Wood, 1907	U	MU	X	Lcf.				29, 43
207	*Amplexograptus compactus* (Elles & Wood, 1907)	U	X	X					29, 36, 37, 43
208	*Normalograptus mohawkensis* Ruedemann, 1912 (=*minimus* E&W)	?	cf.	X	X	X			4, 5, 38, 44
209	*Dicranograptus clingani resicis* Williams & Bruton, 1983	?	?	?					37
210	*Orthograptus* cf. *mucronatus spinigerus* (Lapworth, 1976)		L						5
211	*Climacograptus* aff. *antiquus* (broad) Lapworth, 1873?		L						5
212	*Normalograptus pollex* Rushton & Zalasiewicz, 1999		X						5, 37, 9
213	*Dicranograptus clingani clingani* Carruthers, 1868		X						5, 29, 36, 43, 44
214	*Ensigraptus* cf. *caudatus* (Lapworth, 1876)		X						5, 38
215	*Dicellograptus flexuosus* Lapworth, 1876		L?	X	X?				7, 29, 36, 38, 44
216	*Climacograptus spiniferus* Ruedemann, 1912		X	L					5, 36, 38
217	*Orthograptus pageanus micracanthus* Elles & Wood, 1907		X	X					38
218	*Orthograptus truncatus pauperatus* Elles & Wood, 1907		X	X	cf.				4, 38, 43
219	*Orthograptus quadrimucronatus quadrimucronatus* (Hall, 1865)		X	X	cf.				4, 5, 29, 36, 44
220	*Neurograptus margaritatus* (Lapworth, 1876)		U	L?					36, 38
221	*Appendispinograptus lanceolatus* (Vandenberg 1990)		?U	?L					38
222	*Climacograptus dorotheus* Riva, 1976		U	X					36, 38, 44
223	*Dicellograptus morrisi* Hopkinson, 1871			X	X	?			4, 29, 36, 38, 44
224	*'Glyptograptus' daviesi* Williams, 1982			X	X				4, 36, 38
225	*Corynoides ultimus* Ruedemann, 1925			U	L				36, 38
226	*Normalograptus* (broad form) of Zalasiewicz, Rushton & Owen, 1995				LM				7, 36
227	*Climacograptus tubuliferus* Lapworth, 1876				X				38
228	*Dicellograptus johnstrupi* Hadding, 1915				X				4
229	*Pleurograptus linearis* (Carruthers, 1858)				cf.				4
230	*Plegmatograptus nebula* Elles & Wood, 1908			X	cf.				4, 44
231	*Pseudoclimacograptus clevensis* Skoglund, 1963				X				4
232	*Climacograptus styloideus* Elles & Wood, 1906				X				4
233	*Glyptograptus occidentalis* (Ruedemann, 1947)				X				4
234	*Orthograptus abbreviatus* Elles & Wood, 1907				X	?	A		4
235	*Normalograptus normalis* (Lapworth, 1877)				X	X	X	?>	1, 4, 18, 23, 25, 30, 35
236	*Dicellograptus praeanceps* Rickards, 2002				U				4
237	*Orthograptus amplexicaulis ashgillensis* (Davies, 1929)				U	?	?		11, 4
238	*Dicellograptus anceps* (Nicholson, 1867)					?	X		44
239	*Appendispinograptus supernus* (Elles & Wood, 1906)					?	X		40
240	*Climacograptus tuberculatus* Nicholson, 1869							L	14
241	*'Climacograptus?' indivisus* Davies, 1929					?	?		11
242	*Glyptograptus avitus* Davies, 1929							X>	11, 25, 35
243	*Normalograptus persculptus* (Elles & Wood, 1907)							X>	35
244	*Normalograptus parvulus* (H. Lapworth, 1900)							X>	35
245	*Atavograptus ceryx* (Rickards & Hutt, 1970)							X>	18
246	*Normalograptus medius* (Törnquist, 1897)							X>	1, 18, 25, 35
247	*Paraclimacograptus innotatus* (Nicholson, 1869)							?>	30
248	*Akidograptus ascensus* Davies, 1929							?U>	18, 30, 35

Figure 7. Ordovician graptolites (a) and their stratigraphical ranges (b) in England and Wales, *foliaceus* to *persculptus* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

records presumably represent a late development of Cooper's 'Assemblage 3' (Cooper, 1979) and pre-date his *P. antiquus* and *Kiaerograptus* biozones.

8.d. *Araneograptus murrayi* Biozone

This biozone was first used in Britain by Cooper *et al.* (1995), in reference to the Skiddaw Group from the English Lake District. The *A. murrayi* Biozone is currently the only recognizable upper Tremadocian graptoloid biozone in the British sequence. The base is taken on the appearance of the biozone fossil accompanied by *Acrograptus*? cf. *sinensis* and a declined *Didymograptus* (*s.l.*) sp. (Molyneux & Rushton, 1988).

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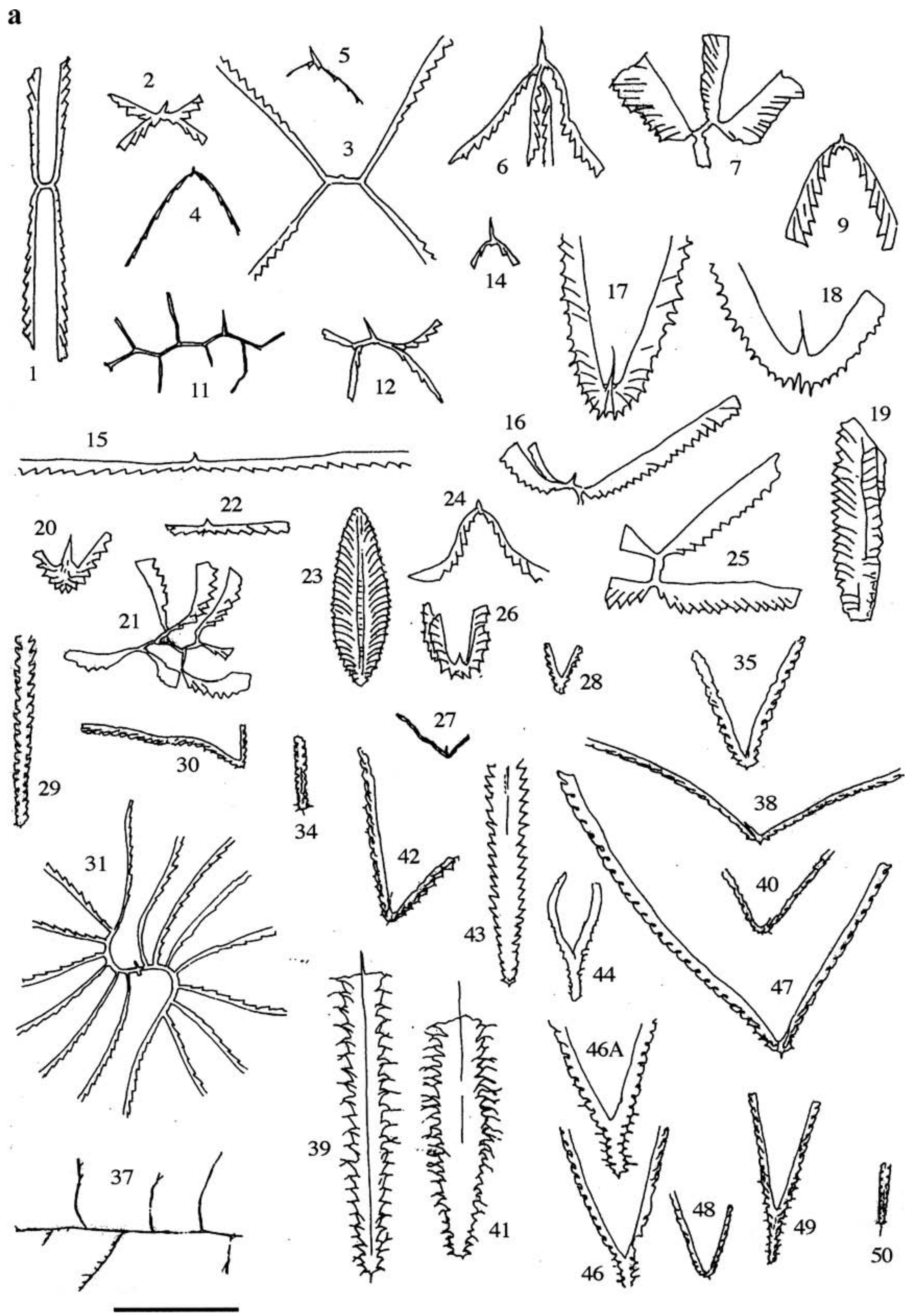

Figure 8. For legend see facing page.

8.e. *Tetragraptus phyllograptoides* Biozone

The base of this biozone equates to that of the Floian Stage of the Ordovician (Bergström, Löfgren & Maletz, 2004). Cooper *et al.* (1995) adopted the *T. phyllograptoides* Biozone, an established Scandinavian interval (Lindholm, 1991), based on the similarity between the Skiddaw Group assemblages and those characteristic of the upper part of this biozone in Scandinavia (Maletz, Rushton & Lindholm, 1991). The biozone fossil is not known from the Lake District, but this biozone may be recognized by the

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No.	Taxa	Lanc2	Lanc3	Be1-2	Be3-4	Ch1-2	Ch3-4	Ca1-2	Ca3	Ca4-Ya	Da1-2	Da3	gracilis	ap.-zic.	wilsoni	Sources
1	*Tetragraptus approximatus* Nicholson, 1873		?	X												4
2	*Tetragraptus* cf. *decipiens* T.S. Hall, 1899			X												2
3	*Tetragraptus quadribrachiatus* (Hall, 1858)			X												2, 4
4	*Acrograptus* cf. *filiformis* (Tullberg, 1880)			X												2
5	*Paradelograptus* sp. A of Rushton et al. 1986			X												2
6	*Tetragraptus (Pendeograptus) fruticosus* (Hall, 1858)			X		?										4
7	*Tetragraptus serra* (Brongniart, 1828)			cf.		X				aff.						2, 4, 5, 17
8	*Expansograptus*? aff. *geometricus* (Törnquist, 1901)					X										4
9	*Didymograptus* cf. *protomurchisoni* Decker, 1944					X										4
10	*Tetragraptus bigsbyi* cf. *askerensis* Monsen, 1937					X										4
11	*Sigmagraptus praecursor* Ruedemann, 1904					X										4
12	*Tetragraptus* cf. *kindlei* Ruedemann, 1947					X										4
13	*Paradelograptus* sp. B of Rushton *et al.*, 1986					X										2, 4
14	*Didymograptus* cf. *protoindentus* Monsen, 1937					X										4
15	*Expansograptus extensus* (Hall, 1858)					X				aff.						4, 5, 17
16	*Tetragraptus reclinatus* Elles & Wood, 1902					X				cf.						4, 5, 17
17	*Isograptus caduceus* cf. *australis* Cooper, 1973									X						5, 17
18	*Isograptus victoriae victoriae* Harris, 1933									X						5, 17
19	*Pseudotrigonograptus ensiformis* (Hall, 1858)									X						17
20	*Pseudisograptus initialis* Maletz, 2001									X						17
21	*Dichograptus* aff. *maccoyi densus* Cooper & Fortey, 1982									X						17
22	*Xiphograptus lofuensis* (Lee, 1961)									X						17
23	*Pseudophyllograptus angustifolius* (Hall, 1858)									X						5, 17
24	*Yutagraptus*? *v-deflexus* (Harris, 1924)									X						5, 17
25	*Tetragraptus amii* Elles & Wood, 1902									X						5, 17
26	*Tetragraptus pseudobigsbyi* Skevington, 1965									X						5, 17
27	*Dicellograptus geniculatus* Bulman, 1932												X			24
28	*Dicranograptus irregularis* Hadding, 1913												X			19, 24
29	*Diplograptus notabilis* Hadding, 1913												X			18, 24
30	*Dicellograptus alabamensis* Ruedemann, 1908												X			1, 18, 24
31	*Nemagraptus gracilis* (Hall, 1847)												X			3, 6, 13,16, 24
31A	*Nemagraptus subtilis* Hadding, 1913												X	L		24
32	*Nemagraptus explanatus pertenuis* (Lapworth, 1876)												X	L		6, 16, 24
33	*Acrograptus*? *serratulus* (Hall, 1847)												X	L		6, 13, 24
34	*Pseudoclimacograptus setosus* Rushton, 2003												X			20
35	*Dicellograptus formosus* Hopkinson												?			21
36	*Corynoides*? *pristinus* Ruedemann												cf.	?		10, 13
36A	*Leptograptus validus s.l.*												X	X		24
37	*Thamnogr. scoticus* Lapworth, 1876 (?=*capillaris* Hall, 1859)												?	X		3, 6, 13, 24
38	*Dicellograptus patulosus* Lapworth, 1880												X	L		3, 6, 10, 24
39	*Hallograptus mucronatus* (Hall, 1847)												?	L		6, 13, 16, 24
40	*Dicellograptus salopiensis* Elles & Wood, 1904												X	X		1, 3, 6, 18, 24
41	*Hallograptus bimucronatus* (Nicholson, 1869)												X	?		6, 13
42	*Dicellograptus sextans sextans* (Hall, 1843)												?	X		6, 13, 16, 24
43	*Orthograptus calcaratus acutus* Elles & Wood, 1907												X	?		6, 13
44	*Dicranograptus furcatus furcatus* (Hall, 1847)												X	X		6, 13, 24
45	*Dicellograptus divaricatus rigidus* Lapworth, 1880												?	X		6, 13, 24
46	*Dicranograptus brevicaulis* Elles & Wood, 1904												X	X		3, 6, 13, 24
46A	*Dicranograptus celticus* Elles & Wood, 1904												?	X		13, 24
47	*Dicellograptus divaricatus s.l.* (Hall, 1859)												X	X		6, 13, 24
48	*Dicellograptus sextans exilis* Elles & Wood, 1904												?	X		6, 13, 14, 16, 24
49	*Dicranograptus rectus* Hopkinson, 1872												X	X		6, 13, 24
50	*Pseudoclimacograptus modestus* (Ruedemann, 1908)												X	X	L	1, 3, 6, 18, 24

Figure 8. Ordovician graptolites (a) and their stratigraphical ranges (b) in Scotland, Lancefieldian 2 to *wilsoni* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

appearance of *Acrograptus*? *protobalticus*, *A.*? *rigoletto* and *Temnograptus multiplex*. Other taxa appearing are *Tetragraptus quadribrachiatus* and *Tetragraptus* (*Pendeograptus*) cf. *fruticosus*. Species diversity is still relatively low in the *phyllograptoides* Biozone, although greater than that of the previous biozone, and includes the first tetragraptids and a temnograptid (Fig. 3). This interval has not been recorded elsewhere in Britain (Cooper *et al.* 1995, 2004).

In Scotland, graptoloid assemblages from the lower to middle part of the Ordovician sequence resemble those in Australasia more closely than the English and

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a

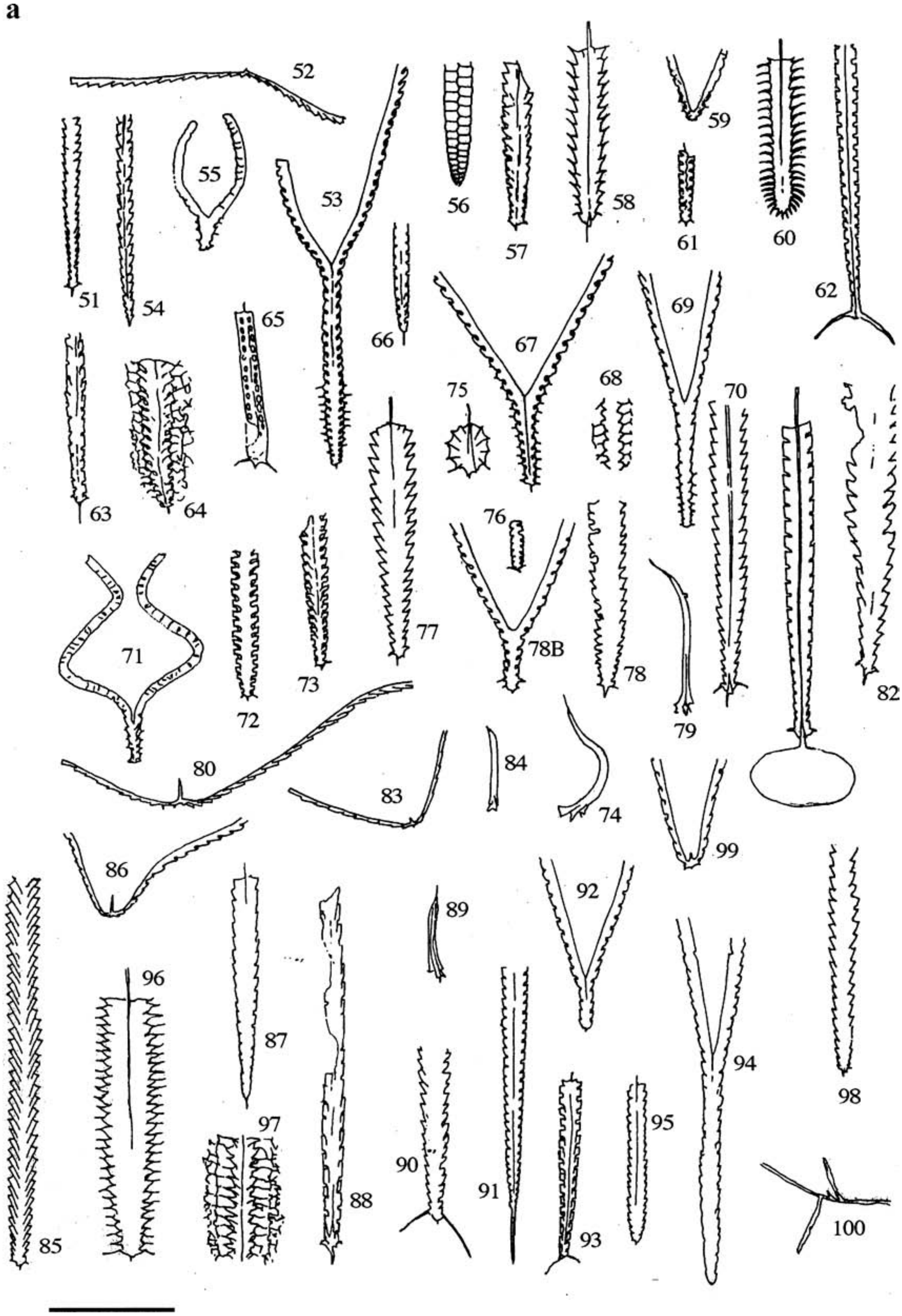

Figure 9. For legend see facing page.

Welsh assemblages. This prompted Stone & Rushton (1983) to use the Australasian graptolite biostratigraphical scheme (VandenBerg & Cooper, 1992) during their work on the faunas of the Ballantrae ophiolite complex. The earliest assemblages from Ballantrae contain *Tetragraptus approximatus*, either by itself or associated with *T.* (*Pendeograptus*) *fruticosus*. The latter association is characteristic of the lowermost Bendigonian (Be1), but the former could originate from the Lancefieldian (La3). Assemblages from Pinbain that contain *T.* cf. *decipiens*, *Acrograptus* cf. *filiformis* and *Paradelograptus* sp. are less definite, but suggest an early Bendigonian (Be1–2) age (Rushton *et al.* 1986).

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b

No.	Taxa	gracilis	ap.-zic.	wilsoni	caudat.	morrisi	linearis	Sources
51	*Hustedograptus teretiusculus* (Hisinger, 1840)	X	X					1, 3, 13, 24
52	*Expansograptus*? *superstes* (Lapworth, 1876)	x	L					3, 6, 13, 24
53	*Dicranograptus ramosus spinifer* Elles & Wood, 1904	?	X					6, 13, 24
54	*Normalograptus euglyphus* (Lapworth, 1880b)	X	X					1, 3, 6, 13, 14, 24
55	*Dicranograptus furcatus minimus* Lapworth, 1876	?	L					6, 13
56	*Reteograptus geinitzianus* Hall, 1859	X	X					1, 3, 6
57	*Amplexograptus compactus* (Elles & Wood, 1907)	?	X	?	cf.			6, 11, 24
58	*Orthograptus whitfieldi* (Hall, 1859)	?	X	L	cf?			6, 24
59	*Dicellograptus intortus* Lapworth, 1880	X	X	Lcf.				3, 6, 10, 13, 24
60	*Glossograptus hincksii hincksii* (Hopkinson, 1872)	?	X	L				6, 10, 13, 24
61	*Pseudoclimacograptus scharenbergi* (Lapworth, 1876)	X	X	X				3, 6, 10, 13, 24
62	*Climacograptus bicornis* (Hall, 1847)	?	X	X				6, 10,11, 13, 14, 24
63	*Climacograptus antiquus* Lapworth, 1873	X	X	X	X			6, 10, 11, 13, 14, 24
64	*Lasiograptus costatus* Lapworth, 1873	?	X	X	X			6, 10, 13, 24
65	*Cryptograptus tricornis* (Carruthers, 1858)	X	X	X	X	L		1, 3, 6, 10, 11, 16, 24
66	*Normalograptus brevis* (Elles & Wood, 1906)	X	X	X	X	X	L	6, 10, 11, 24
67	*Dicranograptus nicholsoni nicholsoni* Hopkinson, 1870	?	X	X	X	?		6, 10, 11, 13, 14, 24
68	*Lasiograptus harknessi* (Nicholson, 1867)	?	X	X	X	?		6, 11, 13, 24
69	*Dicranograptus ramosus ramosus* (Hall, 1847)	X	X	X	X	X		6, 7, 13, 24
70	*Orthograptus calcaratus* (group)	X	X	X	X	X	X	6, 13, 24
71	*Dicranograptus ziczac* Lapworth, 1876	?	X					6, 10, 13, 24
72	*Amplexograptus perexcavatus* (Lapworth, 1876)	?	X	?				6, 13, 24
73	*Diplograptus leptotheca* Bulman, 1946	?	X	L				6, 10, 13, 24
74	*Corynoides serpens* Strachan,1949		X					14, 24
75	*Rogercooperia phylloides* (Elles & Wood, 1908)	?						22
75A	*Dicranograptus tardiusculus* Elles & Wood, 1904		L					24
75B	*Leptograptus ascendens* Elles & Wood, 1903		L					24
75C	*Leptograptus validus incisus* Elles & Wood, 1903		L					24
75D	*Amplexograptus arctus* Elles & Wood, 1907		L					24
75E	*Hallograptus bimucronatus nobilis* Elles & Wood, 1908		L					24
75F	*Dicranograptus cyathiformis* Elles & Wood, 1904		X					24
75G	*Glossograptus armatus* (Nicholson, 1867)		X					24
76	*Pseudoclimacograptus isknos* Zalasiewicz, 1992		cf.					13
77	*Orthograptus apiculatus* Elles & Wood, 1907		X					6, 13, 24
78	*Diplograptus foliaceus* (Murchison, 1839)		X	?				6, 11, 24
78A	*Dicranograptus nicholsoni minor* Bulman, 1945		X	?				13
78B	*Dicranograptus pringlei* Bulman, 1945		X	?				13
78C	*Pseudoclimacograptus stenostoma* (Bulman, 1947)		X	?				13, 24
79	*Corynoides calicularis* Nicholson, 1867		X	X	X	?		6, 10, 11, 14, 24
80	*Leptograptus flaccidus* (Hall, 1865)		?	?	?	?	X	6, 14, 16, 24
81	*Climacograptus wilsoni* Lapworth, 1876			X				6, 10, 11, 24
82	*Orthograptus calcaratus vulgatus* Elles & Wood, 1907			X	X	LM		6, 11, 14
83	*Dicellograptus angulatus* Elles & Wood, 1904			X	X	X		6
84	*Corynoides curtus* Lapworth, 1876			X	X	X	?	6, 11, 14
85	*Orthograptus amplexicaulis* (Hall, 1847)			X	X	X	X	6, 7, 10, 11
86	*Dicellograptus flexuosus* Lapworth, 1876			?	X	X	?	6, 7, 10, 11, 13
87	*Diplograptus pilatus* Williams, 1982				L			7
88	*Climacograptus antiquus lineatus* Elles & Wood, 1907				X			10
89	*Corynoides incurvus* Hadding, 1915				X			11
90	*Orthograptus calcaratus tenuicornis* Elles & Wood, 1907				X			11,13
91	*Ensigraptus caudatus* (Lapworth, 1876)				X			6, 10, 11, 13
92	*Dicranograptus clingani* Carruthers, 1868				X			7, 11, 14
93	*Climacograptus spiniferus* Ruedemann, 1912				X	L		6, 10, 11, 14
94	*Dicranograptus ramosus longicaulis* Elles & Wood, 1904				X	X	X	6, 13, 14, 16
95	*Glyptograptus daviesi* Williams, 1982				X	X		7, 11
96	*Orthograptus pageanus* Elles & Wood, 1973				X	X	?	6, 16
97	*Neurograptus fibratus* (Lapworth, 1876)				X	X	?	6
98	*Orthograptus truncatus intermedius* Elles & Wood, 1907				X	X	?	6, 11, 14
100	*Amphigraptus divergens radiatus* Lapworth, 1876				X	X	X	6

Figure 9. Ordovician graptolites (a) and their stratigraphical ranges (b) in Scotland, *gracilis* to *linearis* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

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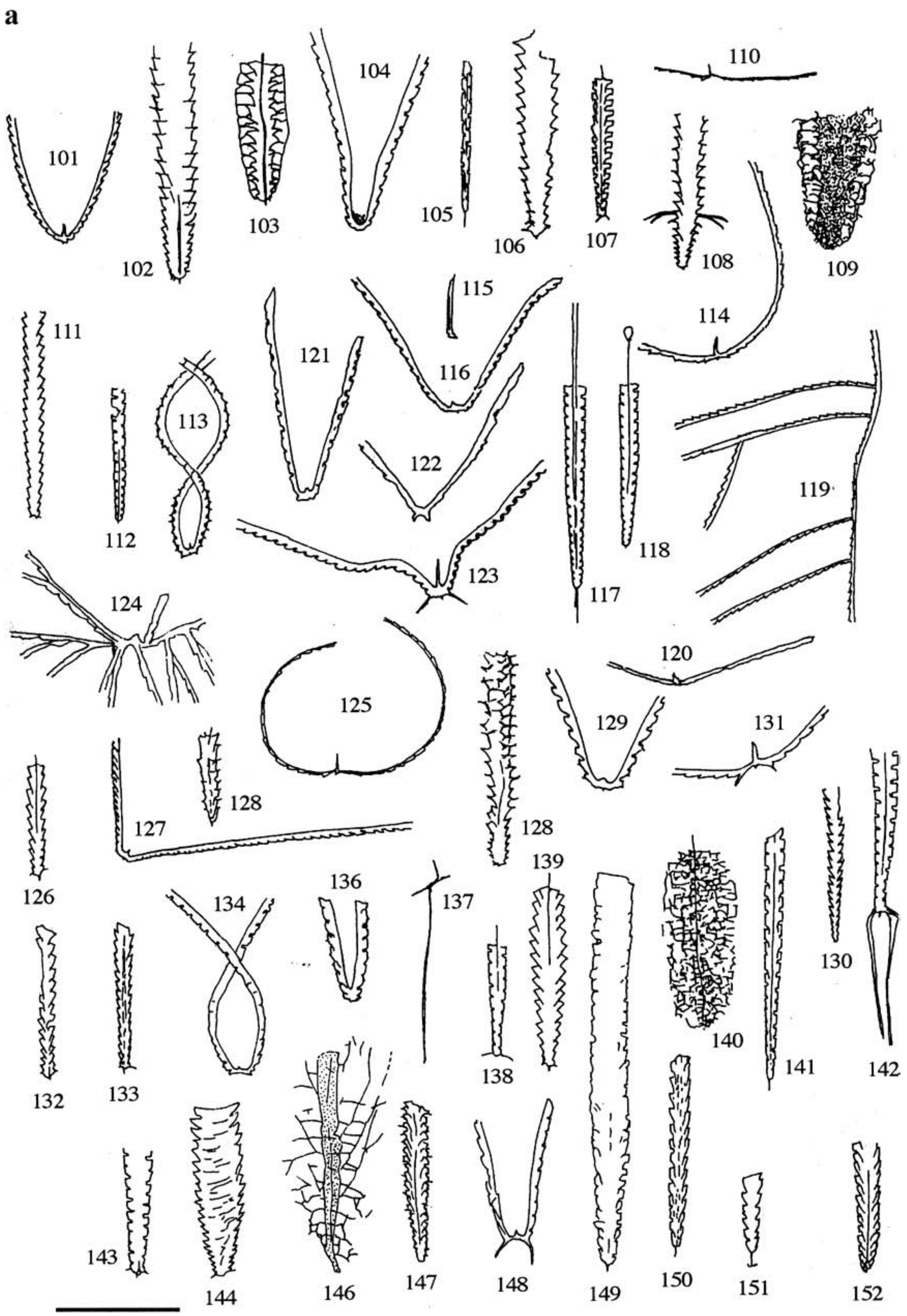

Figure 10. For legend see facing page.

8.f. *Corymbograptus varicosus* Biozone

Following recent revision of Skiddaw Group graptoloid biostratigraphy (Cooper *et al.* 1995), the *C. varicosus* Biozone has replaced the previously used *Corymbograptus deflexus* Biozone (Jackson, 1978; Fortey & Owens, 1990). Cooper *et al.* (1995, 2004) found *C. deflexus* to be rare in this interval, whereas *C. varicosus* is abundant. There is no clear definition for the base of the *varicosus* Biozone, due to the lack of

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b

No.	Taxa	caudatus	morrisi	linearis	complan.	complex.	pacificus	extraord.	persculp.	Sources
101	*Dicellograptus pumilus* Lapworth, 1876	X	X	X						6, 7, 11
102	*Orthograptus quadrimucronatus* (Hall, 1865)	X	X	X						6, 7, 10, 11, 14
103	*Neurograptus margaritatus* (Lapworth, 1876)	X	X	X						6, 7, 11, 13
104	*Dicellograptus moffatensis* (Carruthers, 1858)	X	?	X						6, 7
105	*N. angustus* (Perner, 1895) (= *C. miserabilis* E & W,1906)	X	X	X	X	?	?		>	6, 7, 9, 11, 14
106	*Orthograptus calcaratus basilicus* Elles & Wood, 1907	MU	X	L						6, 11
107	*Climacograptus dorotheus* Riva, 1976	U	X	X						6, 7, 11, 13, 16
108	*Orthograptus quadrimucronatus spinigerus* Lapworth, 1876b	U	X	X						6, 7, 11, 13, 14
109	*Plegmatograptus nebula* Elles & Wood, 1908	?	X	LM						6, 7, 11, 14
110	*Leptograptus flaccidus macer* Elles & Wood, 1903	?	X	LMcf.						7, 11, 16
111	*Orthograptus pauperatus* Elles & Wood, 1907	?	X	X						6, 7, 14
112	*Normalograptus mohawkensis* (Ruedemann, 1906)	?	X	X						6, 7, 13, 16
113	*Dicellograptus caduceus* Lapworth, 1876b		X							10
114	*Leptograptus flaccidus spinifer* Elles & Wood, 1903		X	X						6, 16
115	*Corynoides ultimus* Ruedemann, 1925		X							14
116	*Dicellograptus morrisi* Hopkinson, 1871		X	X						6, 7, 11, 13
117	*Climacograptus tubuliferus* Lapworth, 1876b		aff.	X						6, 7, 11, 14
118	*Climacograptus styloideus* Elles & Wood, 1906			X						6, 11
119	*Pleurograptus linearis* (Carruthers, 1858)			X						6, 7, 11, 14, 16
120	*Leptograptus flaccidus macilentus* Elles & Wood, 1903			X						11, 16
121	*Dicellograptus carruthersi* Toghill, 1970			X						6, 23
122	*Dicellograptus elegans rigens* Elles & Wood, 1904			?						11
123	*Dicellograptus elegans elegans* (Carruthers, 1876a)			M						7, 11, 13, 16
124	*Amphigraptus divergens divergens* (Hall, 1859)			M						7, 11
125	*Leptograptus capillaris* (Carruthers, 1868)			M						7, 11
126	*Orthograptus socialis* (Lapworth, 1880)			?M	X					8
127	*Dicellograptus complanatus* Lapworth, 1880				X					8
128	*Orthoretiolites pulcherrimus* (Keble & Harris, 1934)				X					8, 13
129	*Dicellograptus alector* Carter, 1972				X					8
130	*Glyptograptus occidentalis* Ruedemann, 1947				X					8
131	*Dicellograptus minor* Toghill, 1970				X	X	X	L		8, 9, 14
132	*Glyptograptus nicholsoni* Toghill, 1970					?	?			23
133	*Anticostia fastigata* (Davies, 1929)					X	L			9, 12, 14
134	*Dicellograptus complexus* Davies, 1929					X	LM			9, 12, 15, 16
135	*Dicellograptus* aff. *complexus* Davies, 1929					X	LM			9, 12
136	*Dicellograptus anceps* (Nicholson, 1867a)					X	X	L		9, 14, 15
137	*Pleurograptus lui* Mu, 1950					X	X	L		9, 12, 16
138	*Appendispinograptus supernus* (Elles & Wood, 1906)					X	X	L		9, 12, 15, 16
139	*Orthograptus abbreviatus* Elles & Wood, 1907					X	X	L		9, 12, 15, 16
140	*Plegmatograptus? craticulus* Williams, 1982b					X	X			9, 12, 14
141	*Normalograptus normalis* (Lapworth, 1877)					X	X	X	X>	9, 12, 14
142	*Appendispinograptus longispinus* (T.S. Hall, 1902)					U	L			15
143	*Amplexograptus latus* (Elles & Wood, 1906)					U	X	L		9, 12, 15, 16
144	*Orthoreteograptus denticulatus* Wang *et al.*, 1977					U	X	L		9, 12, 14
145	*Plegmatograptus lautus* Koren' & Tzaj, 1980			?			L			9, 12
146	*Nymphograptus velatus* Elles & Wood, 1908						L			9, 12, 14
147	*Paraorthograptus pacificus* (Ruedemann, 1947)						X	L		9, 12, 14, 15
148	*Dicellograptus ornatus* Elles & Wood, 1904						MU	L		9, 14, 15, 16
149	*Climacograptus? extraordinarius* (Sobolevskaya, 1974)							X		7, 9
150	*Glyptogr? pseudovenustus* cf. *pseudovenustus* (Legrand, 1976)								LM	6, 9, 14
151	*Glyptograptus avitus* Davies, 1929								MU>	6, 9, 14
152	*Normalograptus parvulus* (H. Lapworth, 1900)								MU>	6, 9

Figure 10. Ordovician graptolites (a) and their stratigraphical ranges (b) in Scotland, *caudatus* Subzone to *persculptus* Biozone. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

known suitable fossiliferous strata in the Lake District (Rushton *et al.* 1999, p. 266; Cooper *et al.* 2004, p. 13). This assemblage displays a marked increase in species and generic diversity. New appearances include *Baltograptus vacillans attenuatus*, *Didymograptus* aff. *balticus*, *Tetragraptus reclinatus*, *T.* (*P.*) *fruticosus*, *Expansograptus* cf. *decens* and *Acrograptus filiformis*. Some species are known only from the upper part

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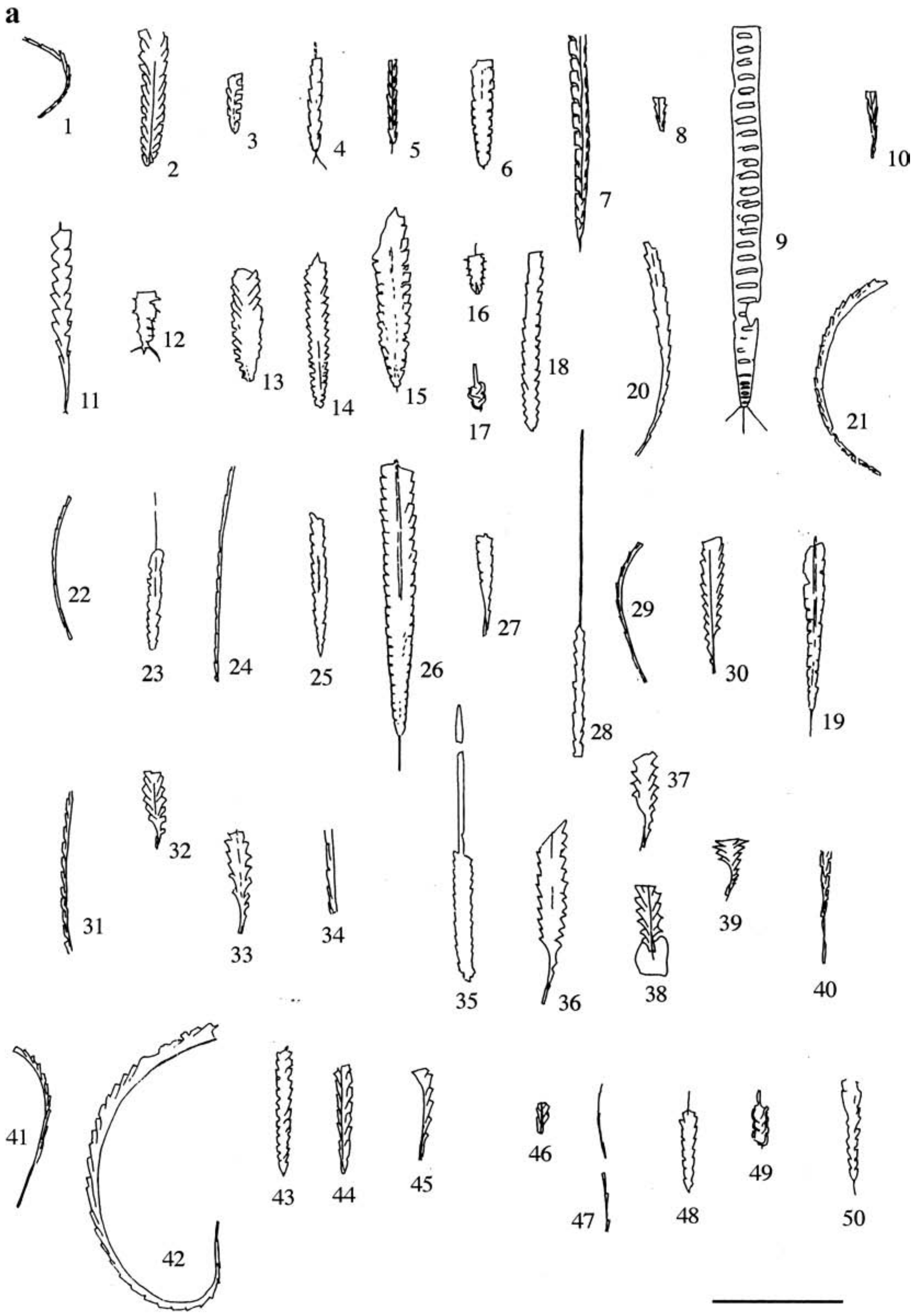

Figure 11. For legend see facing page.

of the biozone: *C. deflexus*, *Pseudophyllograptus angustifolius*, *Dichograptus octobrachiatus sedgwickii*, *Schizograptus tardifurcatus* and *Expansograptus* cf. *similis* (Fig. 3).

8.g. *Expansograptus simulans* Biozone

This biozone straddles the interval between the 'second' (Floian) and 'third' (Dapingian) stages of the Ordovician (Cooper & Sadler, 2004). The former *Didymograptus nitidus* Biozone was renamed on the basis that the former zone fossil does not occur in this interval in the Skiddaw Group (Cooper *et al.* 1995). The base of the biozone is defined on the incoming of *Expansograptus simulans* and *Acrograptus infrequens* (Cooper *et al.* 1995; Rushton *in* Cooper *et al.* 2004). A significant rise in graptolite diversity can be seen at this horizon, with about 33 taxa

b

No	Taxa	ascensus-acuminatus	atavus	acinaces	revolutus	triangulatus	magnus	leptotheca	convolutus	sedgwickii	Sources
1	*Atavograptus ceryx* (Rickards & Hutt, 1970)	<L									6, 14
2	*Normalograptus persculptus* (Elles & Wood, 1907)	<?									18, 26, 28
3	*Normalograptus parvulus* (H. Lapworth, 1900)	<X									18, 24, 28
4	*Glyptograptus avitus* Davies, 1929	<X									3, 18, 26, 27, 28
5	*N. angustus* (Perner, 1895) (=*C. miserabilis* E & W, 1906)	<X	X	X	X						6, 13, 16, 24, 25, 26, 27, 28
6	*Normalograptus medius* (Törnquist, 1897)	<X	A	X	X						1, 6, 16, 18, 24, 26, 27, 28
7	*Normalograptus normalis* (Lapworth, 1877)	<X	X	X	X	?	?	?			1, 6, 13, 16, 18, 24, 25, 26, 27, 28
8	*Parakidograptus acuminatus praematurus* (Davies, 1929)	L									6, 13
9	*Normalograptus trifilis* (Manck, 1923)	M									16, 24, 25, 26
10	*Akidograptus ascensus* Davies, 1929	X(LA)									6, 16, 18, 24, 26, 28
11	*Parakidogr. acuminatus acuminatus* (Nicholson, 1867)	MU									6, 13, 16, 18, 24, 25, 26, 27, 28
12	*'Climacograptus' tuberculatus* Nicholson, 1869	MU									4, 24
13	*Neodiplograptus* aff. *modestus primus* (Mikhailova, 1980)	X									18
14	*Neodiplograptus diminutus* (Elles & Wood, 1907)	X	X								6, 13, 14
15	*Neodiplograptus modestus modestus* (Lapworth, 1876)	X	X	X	L?						6, 13, 16, 24, 26
16	*Paraclimacograptus innotatus* (Nicholson, 1869) *s.l.*	<X	X	X	L						16, 24, 25, 26, 27
17	*Cystograptus vesiculosus* (Nicholson, 1868) *s.l.*	?	X(LA)	X	L						1, 6, 13, 16, 24, 25, 26
18	*'Orthograptus' cabanensis* Zalasiewicz & Tunnicliff, 1994	U									18, 28
19	*Normalograptus rectangularis* (M'Coy, 1850)	U	X	X	X	X					1, 6, 13, 16, 18, 24, 25, 26, 27, 28
20	*Dimorphograptus elongatus* Lapworth, 1876		L								6, 16, 25, 26, 27
21	*Huttagraptus? praematurus* (Toghill, 1968b)		L								16, 25, 26, 27
22	*Huttagraptus praestrachani* (Hutt, Rickards & Berry, 1977)		LM								7
23	*Diplograptus*? sp. of Rickards, 1970		X								13
24	*Atavograptus gracilis* Hutt, 1975		X								6, 18, 24, 25, 26, 27, 28
25	*Glyptograptus tenuis* (Rickards, 1970)		X								13, 25
26	*Neodiplograptus elongatus* (Churkin & Carter, 1970)		cf.								6, 27
27	*Rhaphidograptus extenuatus* (Elles & Wood, 1908)		X	L							6, 16, 24, 25, 26, 27
28	*Neodiplograptus? rarus* (Rickards, 1970)		X	X							13, 26
29	*Corono. gregarius minusculus* Obut & Sobolevskaya, 1968		X		aff.						26, 18, 28
30	*Dimorphograptus erectus* Elles & Wood, 1908 *s.l.*		X	X	LM						6, 13, 14, 16, 25, 26, 27
31	*Atavograptus atavus* (Jones, 1909)		X	X	X	X	X				1, 6, 13, 16, 18, 24, 25, 26, 27, 28
32	*Dimorphogr. decussatus decussatus* Elles & Wood, 1908		MU	L?							6, 16, 27
33	*Dimorphograptus decussatus partiliter* Elles & Wood, 1908		X?	X?							4, 16
34	*Pribylograptus* aff. *incommodus* sensu Hutt, 1975		U								6
35	*Diplograptus*? sp. of Hutt, 1974		U								6
36	*Dimorphograptus epilongissimus* Rickards, 1970		U	X	X						13, 14
37	*Dimorphograptus longissimus* (Kurck, 1882)		U	X	X						6, 14, 25, 27
38	*Dimorphograptus physophora* (Nicholson, 1868)		?U	X	X						6, 14, 16, 26, 27
39	*Dimorphograptus confertus confertus* (Nicholson, 1868)		U	A	X						1, 6, 13, 14, 16, 18, 26, 27, 28
40	*Rhaphidograptus toernquisti* (Elles & Wood, 1906)		U	X	X	X	X	X	X	L	1, 6, 13, 14, 16, 18, 24, 26, 27, 28
41	*Huttagraptus acinaces* (Törnquist, 1899)		?	A	X	L					1, 6, 16, 18, 24, 25. 26, 27, 28
42	*Coronograptus cyphus* (Lapworth, 1876)		??	X	X						1, 6, 13, 14, 16, 18, 24, 25, 26, 27, 28
43	*"Climacograptus"* sp. of Rickards, 1970			X							13
44	*Normalograptus* cf. *nikolayevi* Obut, 1965 *sensu* Hutt, 1974			X							6, 14
45	*Dimorphograptus confertus swanstoni* Lapworth, 1876			X	X						1, 14, 16
46	*Orthograptus* aff. *mutabilis* sensu Hutt, 1974			X	X						6
47	*Pristiograptus fragilis pristinus* Hutt, 1975			X	X						6, 18, 26, 28
48	*Glyptograptus attenuatus* (Rickards, 1970)			X	X						1, 13, 14
49	*Cystograptus penna* (Hopkinson, 1869)			X	X						4, 14, 25
50	*Glyptograptus* aff. *incertus* sensu Hutt, 1974			X	X	?					6, 18

Figure 11. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *ascensus–acuminatus* to *sedgwickii* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

recorded (Fig. 3). Several new forms are confined to this biozone, including *Didymograptus minutus*, *Tetragraptus postlethwaitei*, *Adelograptus*? *divergens* and *Tetragraptus* (*Pendeograptus*) *pendens*. Other noteworthy appearances are *Azygograptus eivionicus*, *Azygograptus lapworthi*, *Pseudobryograptus cumbrensis*, *Acrograptus*? *kurcki*, *Loganograptus logani* and *Tetragraptus crucifer*. Cooper *et al.* (1995) suggested that the presence of *Isograptus* cf. *primulus* in this interval indicates a correlation with the Chewtonian Stage (Ch 1–2).

The contemporaneous Scottish taxa differ markedly from those of England and Wales, with the exception of *Tetragraptus serra* and *Tetragraptus reclinatus*,

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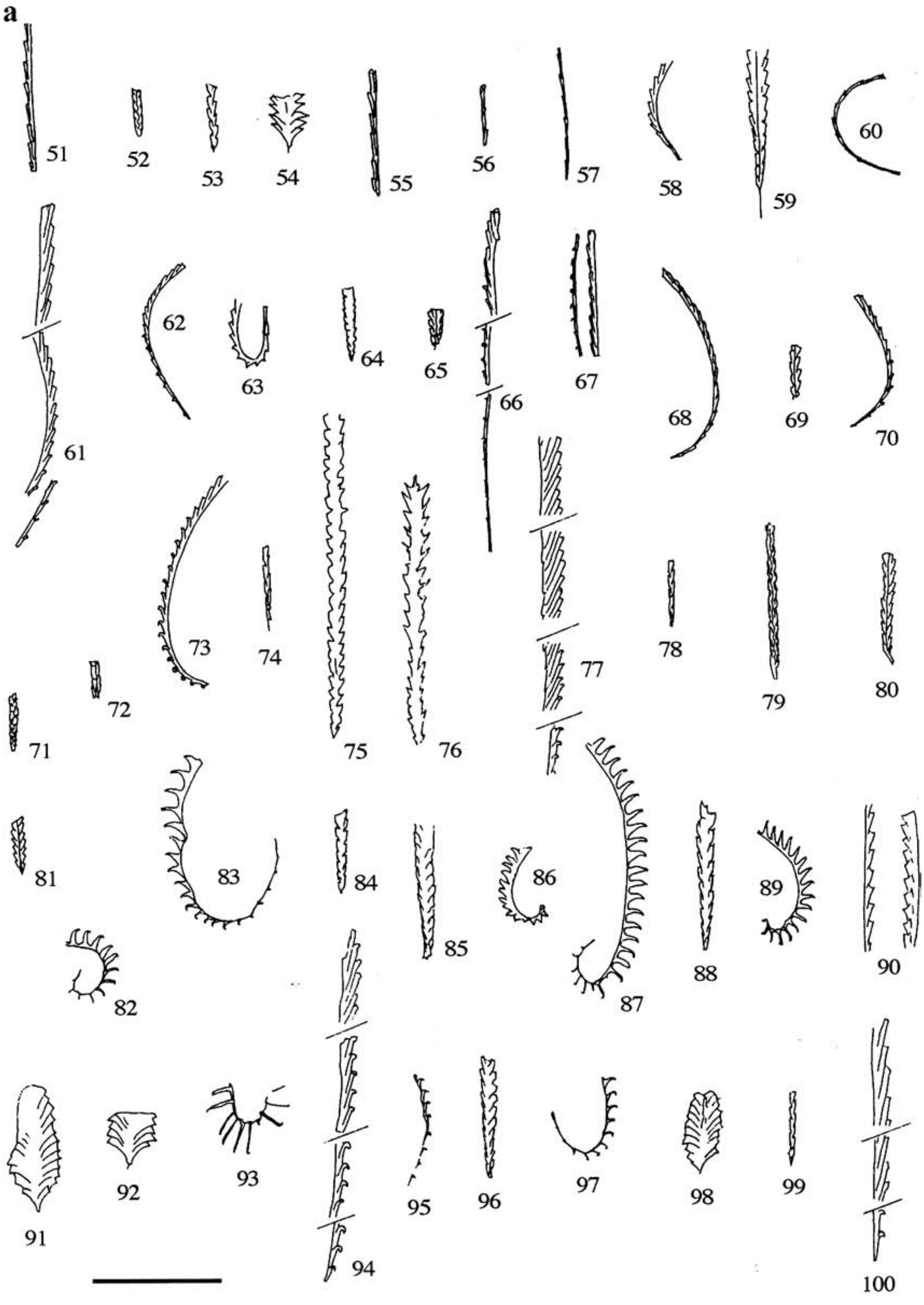

Figure 12. For legend see facing page.

which occur in both successions (Fig. 8). Stone & Rushton's (1983) work at Ballantrae revealed graptolite assemblages containing *Didymograptus* cf. *protomurchisoni*, *Tetragraptus bigsbyi* cf. *askerensis*, *Expansograptus*? aff. *geometricus*, *Didymograptus* cf. *protoindentus*, *Sigmagraptus praecursor*, *Paradelograptus* sp., *Tetragraptus* (*P.*) *fruticosus* and *Tetragraptus* cf. *kindlei*, which they found consistent with a Chewtonian age.

8.h. *Isograptus victoriae victoriae* Biozone

The recognition of distinct, biostratigraphically important graptolites within the old *Isograptus gibberulus*

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b

No	Taxa	atavus	acinaces	revolutus	triangulatus	magnus	leptotheca	convolutus	sedgwickii	halli	runcinatus	gemmatus	Sources
51	*Huttagraptus strachani* (Hutt & Rickards, 1970)		X	X	?								1, 6, 13, 14
52	*Me. slalom* Zalasiew., 1996 (=*'Me. hughesi'* pars)		X	X	X	X	?						21
53	*Glyptogr. tamariscus tamariscus* (Nicholson, 1868)		X	X	X	X	X	X	X	X		X	1, 6, 12, 14, 15, 16, 18, 26
54	*Pseudorthograptus mutabilis* (Elles & Wood, 1907)		U	X									1,6 18, 26, 27, 28
55	*Pribylograptus sandersoni* (Lapworth, 1876)		U	X	L?								1, 13, 14, 16, 18, 24, 25, 26, 27, 28
56	*Pribylograptus incommodus* (Törnquist, 1899)		U	X	X	X							1, 16, 18, 26, 27, 28
57	*Pristiograptus fragilis fragilis* (Rickards, 1970)		U?	X	X	X	X	X					1, 6, 13, 14
58	*Coronogr. gregarius gregarius* (Lapworth, 1876)		U?	X	X	X	X	X	?LM				6, 13, 14, 16, 18, 21, 24, 25, 26, 27, 28
59	*Glyptograptus sinuatus sinuatus* (Nicholson, 1869)		?	X	X	X	X						1, 6, 13, 14, 16, 21, 25, 27
60	*Coronograptus cirrus* Hutt, 1975	?		X									16, 24
61	*Monograptus austerus vulgaris* (Hutt, 1974)			X									6, 14
62	*Coronograptus leei* (Hsü, 1934)			X									26
63	*Coronograptus hipposideros* (Toghill, 1968b)			X									24, 33
64	*Glyptograptus cuneatus* Rickards, 1970			X									13, 14
65	*Normalogr. wyensis* Zalasiewicz & Tunnicliff, 1994			X									18, 28
66	*Monograptus austerus austerus* Törnquist, 1899			X	?								1, 6, 14, 18, 26, 27
67	*Monograptus revolutus revolutus* Kurck, 1882			X	?								1, 6, 14, 16, 18, 25, 27
68	*Pribylograptus argutus argutus* (Lapworth, 1876)			X	X	X	?						1, 6, 13, 14, 16, 18, 26
69	*Glyptograptus tamariscus varians* Packham, 1962			cf.	X	X	aff.						12, 13, 14, 18, 26
70	*Monograptus sudburiae* Hutt, 1974			X	X	X	X						1, 6, 14, 18
71	*Metaclimacograptus undulatus* (Kurck, 1882)			X	X	X	X	X	A	A		?	1, 6, 13, 14, 18, 26, 27
72	*"Climacograptus"* sp. 1 of Hutt, 1974			M									6, 14
73	*Monograptus difformis* Törnquist, 1899			MU	X								1, 6, 13, 14, 16, 26, 27
74	*Glyptograptus tamariscus distans* Packham, 1962			MU	X	X	aff.						1, 6, 12, 14, 15
75	*Glyptograptus tamariscus linearis* (Perner, 1897)			MU	X	X	X	X					12, 14, 24, 26
76	*Orthograptus* sp. nov. B (of Cocks & Toghill, 1973)			U									2
77	*Monograptus austerus bicornis* Hutt, 1974			U	X	X							6, 14
78	*Glyptograptus tamariscus angulatus* Packham, 1962			U	X	X	X						12, 14
79	*Clinoclimaco. retroversus* Bulman & Rickards, 1968			U	X	X	X	X	X				1, 6, 13, 14, 26
80	*Glyptograptus enodis enodis* Packham, 1962			?	X	X							6, 12, 14, 18, 27
81	*Rivagraptus cyperoides* (Törnquist, 1897)			?	X	X	X	X	X				1, 6, 13, 14, 16, 24, 26, 27
82	*Monogr. triangulatus predecipiens* Sudbury, 1958				LM								1, 14
83	*M. brevis walkerae* Rickards, Hutt & Berry, 1977				LM								34
84	*Normalogr. tangshanensis linearis* (Packham, 1962)				X								12
85	*Pseudogl. rhayaderensis* (Rickards & Koren', 1972)				X								14
86	*Monogr. triangulatus similis* Elles & Wood, 1913				?X								14
87	*Monogr. triangulatus triangulatus* (Harkness, 1851)				X	?							1, 6, 13, 14, 18, 24, 26, 27
88	*Glyptograptus enodis latus* Packham, 1962	?aff.			X	X							12, 26, 27
89	*Monograptus triangulatus separatus* Sudbury, 1958				X	X	?						1, 6, 13, 14
90	*Pristiograptus concinnus* (Lapworth, 1876)				X	X	X	X					1, 6, 13, 14, 16, 18, 26
91	*Petalolithus ovatoelongatus* (Kurck, 1882)				X	X	X	X	?				6, 13, 14, 16, 18, 21, 24, 26, 27
92	*'Petalolithus palmeus latus'* (Barrande, 1850)				?	?							1, 2, 14, 16, 26, 27
93	*Monograptus triangulatus extremus* Sudbury, 1958				M								14, 18, 26
94	*Monograptus austerus sequens* Hutt, 1974				M								6
95	*M. brevis rheidolensis* Rickards, Hutt & Berry, 1977				M								34
96	*Glyptograptus alternis* (Packham, 1962)				MU								12, 14, 18
97	*Monograptus brevis brevis* (Sudbury, 1958)				M	X							6, 35
98	*Petalolithus minor* (Elles, 1897)				MU	X	X	X					1, 14, 16, 21, 26
99	*Glyptograptus tamariscus acutus* Packham, 1962				U								12, 14
100	*Monogr. austerus praecursor* Elles & Wood, 1911				U	L							6, 14

Figure 12. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *atavus* Biozone to *gemmatus* Subzone. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

Biozone of the Skiddaw Group led to the proposal of a lower *I. victoriae victoriae* Biozone and an upper *I. gibberulus* Biozone (Rushton *in* Cooper *et al.* 2004, p. 17). The *I. v. victoriae* Biozone is characterized by the appearance of the zone fossil, which is confined to this interval. However, the index species is rare in the Lake District, leading to difficulties in identifying the biozonal boundaries. Horizontal didymograptids, such as *Expansograptus hirundo*, *E.* cf. *nitidus* and *E. extensus linearis* help to characterize the *victoriae* and *gibberulus* biozones. Other forms limited to the *victoriae* Biozone are *Phyllograptus densus* and *Isograptus victoriae* cf. *maximus*, while the appearance of *E. hirundo* and *E.* cf. *nitidus* (Figs 3, 4) is recorded in the Shelve area of Shropshire (Strachan, 1986).

No graptolite assemblage corresponding to this interval has been reported from Scotland (Fig. 8).

8.i. *Isograptus gibberulus* Biozone

This biozone, as restricted by Rushton (*in* Cooper *et al.* 2004, p. 17) in the Skiddaw Group of the

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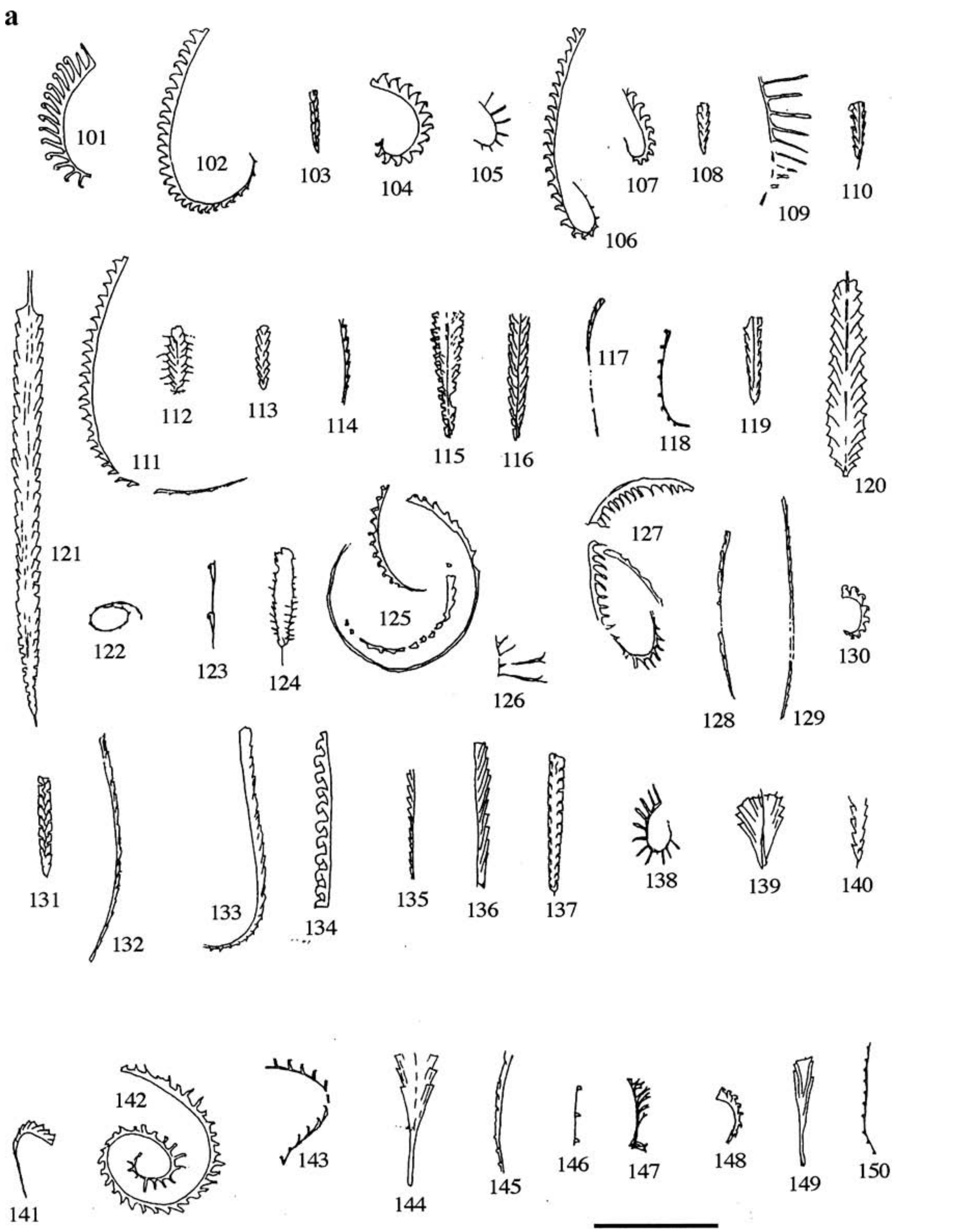

Figure 13. For legend see facing page.

English Lake District, is defined by the appearance of *I. gibberulus*. Cooper *et al.* (1995) suggested that the former *I. gibberulus* Biozone equated with the Australasian Castlemainian Stage (Ca 1–4), but, as now restricted, it represents the upper part of the Castlemainian (Ca 3–4) (Cooper *et al.* 2004). The identification of *Pseudisograptus dumosus* at this horizon from the Aberdaron area of Wales, and *Isograptus caduceus* cf. *imitatus* from Grisedale Pike in the Lake District (Jenkins, 1982) seems to confirm this. Other noteworthy appearances include *Pseudisograptus angel*, *Corymbograptus v-fractus volucer*, *Tetragraptus bigsbyi bigsbyi*, *Corymbograptus*? *uniformis* and *Xiphograptus svalbardensis* (Fig. 4).

In Scotland, an assemblage obtained from the North Ballaird Borehole in the Ballantrae ophiolite complex contained elements comparable to those for this interval in England and Wales (Stone & Strachan, 1981),

b

No	Taxon	triangulatus	magnus	leptotheca	convolutus	sedgwickii	halli	runcinatus	gemmatus	renaudi	utilis	Sources
101	*Monograptus triangulatus major* Elles & Wood, 1913	U	X									1, 6, 13, 14, 26
102	*Monograptus pseudoplanus* Sudbury, 1958	U	X									1, 6, 14, 18, 26, 27
103	*Normalograptus tamariscoides* (Packham, 1962)	U	?									12, 14
104	*Monograptus triangulatus fimbriatus* (Nicholson, 1868)	U	A	?								1, 6, 14, 16, 18, 26, 27
105	*Rastrites longispinus* Perner, 1897	U	X	?	??							1, 6, 13, 14, 16, 21, 26, 27
106	*Campograptus communis communis* (Lapworth, 1876)	U	X	?	??							1, 13, 14, 16, 18, 27, 28
107	*Campograptus communis rostratus* (E & W, 1913)	U	X	X	L?							1, 6, 14, 18, 27, 28
108	*Glyptograptus elegans* Packham, 1962	U	X	X	X	X	X		X			10, 12, 14, 26, 28
109	*Rastrites setiger* Elles & Wood, 1914	?U	?									4
110	*Pseudoglyptograptus vas* Bulman & Rickards, 1962	?U	X									6, 14, 18, 28
111	*'Monograptus' intermedius* (Carruthers, 1868)	?	?	?								14, 16
112	*Pseudorthograptus insectiformis* (Nicholson, 1869)	?	X	X	X							6, 14, 16, 21, 26, 27, 28
113	*Glyptograptus incertus* Elles & Wood, 1907	?	?		X	X	X	X	X			6, 10, 14, 16, 26, 27
114	*Monograptus* sp. (of Rickards, 1973)		LM									14
115	*Neodiplograptus magnus* (H. Lapworth, 1900)		A									1, 6, 13, 14, 16, 18, 28
116	*Neodiplograptus peggyae* Cullum & Loydell, 1997		X									38
117	*Monograptus chrysalis* Zalasiewicz, 1992		X									17, 28
118	*Monograptus tenuissimus* Obut & Sobolevskaya, 1968)		X									6, 14
119	*Pseudoglyptogr. barriei* Zalasiewicz & Tunnicliff, 1994		X									14, 18, 28
120	*Petalolithus primulus* Bouček & Přibyl, 1941		?									15
121	*Neodiplograptus thuringiacus* (Eisel, 1919)		X	?								2, 14
122	*Monograptus changyangensis* Sun, 1933		X	??								10
123	*'Monograptus' capis* Hutt, 1975		X	X	X	X	?	X				1, 6, 14, 25, 26, 27
124	*Rivagraptus bellulus* (Törnquist, 1890)		?	X	X	?						6, 14, 16, 21, 25, 26, 27
125	*Torquigraptus involutus* (Lapworth, 1876a)		?	X	X	X	X				U	1, 6, 14, 16, 21, 28
126	*Rastrites geinitzii* Törnquist, 1907		?	?	?							16, 27
127	*Monograptus cerastus* Hutt, 1975			X								1, 6, 14, 26
128	*Monoclimacis*? sp. of Hutt, 1974			X								6
129	*Pribylograptus*? *jonesi* (Rickards, 1970)			X	?							13, 27
130	*Campograptus millepeda* (M'Coy, 1850)			X	L?							1, 6, 14, 16, 21, 28
131	*Metaclimacograptus hughesi* (Nicholson, 1869)			X	L							1, 6, 13, 14, 16, 21, 28
132	*Monograptus imago* Zalasiewicz, 1992			X	L							17, 21, 28
133	*Monograptus argenteus* (Nicholson, 1869)			A	X							1, 6, 14, 16, 21, 26, 27, 28
134	*Campograptus lobiferus* (M'Coy, 1850)			X	A	?						1, 6, 13, 14, 16, 21, 25, 26, 27, 28
135	*Pristiograptus jaculum* (Lapworth, 1876)			X	X	?						1, 14, 16, 21, 26, 27, 28
136	*Pribylograptus leptotheca* (Lapworth, 1876)			X	X	?L						1, 6, 13, 14, 16, 18, 21, 26, 27, 28
137	*Normalograptus*? *scalaris* (Hisinger, 1837)			cf.	A	?				X	X	1, 13, 14, 16, 21, 26, 27, 28
138	*Rastrites peregrinus* Barrande, 1850			?	X							1, 6, 13, 14, 16, 21, 25, 26, 27
139	*Petalolithus folium* (Hisinger, 1837)			?	X							14, 16
140	*Glyptograptus serratus* Elles & Wood, 1907			?	X	L						14, 16, 25, 26, 27
141	*Monograptus limatulus* Törnquist, 1892			?U	X	?L						1, 6, 13, 14, 16, 21, 25, 26, 27, 28
142	*Lit.* aff. *convolutus* of Štorch, 1980 (=*L. richteri* (Pern.))				L							21, 28
143	*Torquigraptus urceolinus* (Stein, 1965)				L							21, 28
144	*Cephalograptus tubulariformis* (Nicholson, 1867)				L							14, 16, 26
145	*Monoclimacis crenularis* (Lapworth, 1880)				X							1, 6, 14, 16, 21, 26, 27, 28
146	*Rastrites spina sensu* Rickards, 1970				X							1, 6, 13, 14, 21
147	*Rastrites phleoides* Törnquist, 1887				X							6, 14
148	*Campograptus clingani* (Carruthers, 1867)				X							1, 6, 14, 16, 21, 25, 26, 27, 28
149	*Cephalograptus cometa cometa* (Geinitz, 1852)				X							6, 14, 16, 26
150	*Paradiversograptus capillaris* (Carruthers, 1867)				X							21, 28

Figure 13. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *triangulatus* Biozone to *utilis* Subzone. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

but also other taxa (*Arienigraptus gracilis, Isograptus caduceus australis, Tylograptus*? and *Yutagraptus v-deflexus*) that indicate a latest Castlemainian or early Yapeenian age (Stone & Rushton, 2003) (Fig. 8). In a review of this assemblage, Maletz (2004) referred the supposed *A. gracilis* to *Pseudisograptus initialis* Maletz, 2001 and the *Tylograptus*? to a species of *Meandrograptus.* However, although Stone & Rushton

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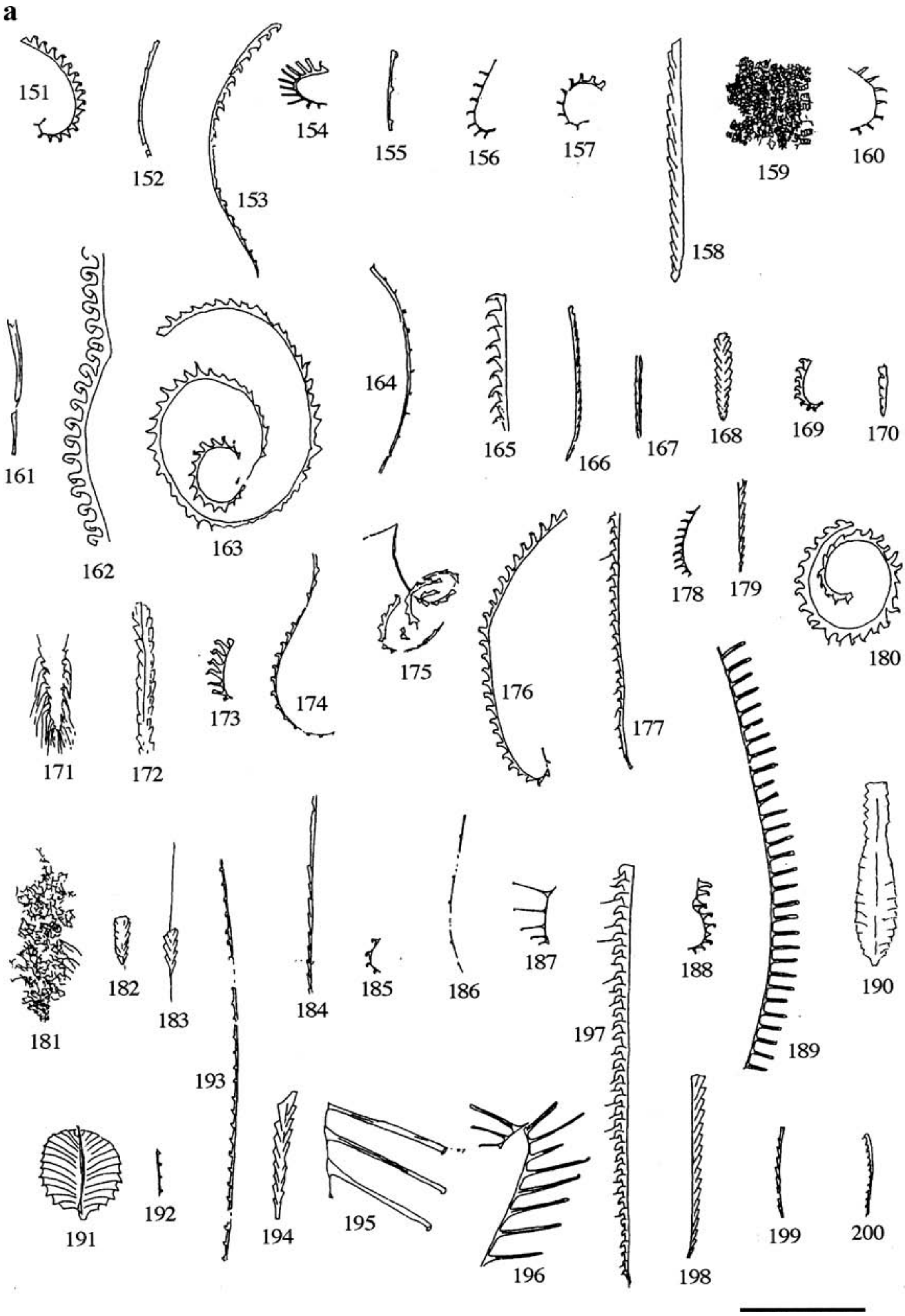

Figure 14. For legend see facing page.

(2004) gave reasons for rejecting the transfer of their specimens of *I. caduceus australis* to *Isograptus caduceus imitatus*, they accepted Maletz's suggestion that the North Ballaird assemblage is best restricted to the late Castlemainian (Ca4).

As yet, no graptolite assemblages have been reported from Scotland at a higher stratigraphical level, until the base of the *Nemagraptus gracilis* Biozone at the base of the Sandbian Stage (base of Upper Ordovician) (Fig. 8).

b

No	Taxon	convolutus	sedgwickii	halli	runcinatus	gemmatus	renaudi	utilis	johnsonae	proteus	carnicus	galaensis	Sources
151	*Torquigraptus denticulatus* (Törnquist, 1899)	X											1, 6, 14, 16, 21, 26, 27, 28
152	*Lagarograptus* sp. of Zalasiewicz, 1996	X											21
153	*Stimulograptus*? *undulatus* (Elles & Wood,1913)	X											4, 21, 28
154	*Lituigraptus convolutus* (Hisinger, 1837)	X	L?										1, 6, 14, 16, 21, 25, 26, 27, 28
155	*Streptograptus*? sp. of Zalasiewicz, 1996	X											21
156	*Rastrites hybridus erectus* of Hutt, 1975	X	?										6
157	*Torquigraptus*? *decipiens decipiens* (Törnquist, 1899)	X	X										1, 6, 14, 16, 21, 25, 26, 27, 28
158	*Pristiograptus regularis* (Törnquist, 1899)	X	X										1, 6, 13, 14, 16, 21, 25, 26, 28
159	*Pseudoretiolites perlatus* (Nicholson, 1868)	X		X									6, 10, 14, 21
160	*Rastrites hybridus hybridus* Lapworth, 1876	MU											15, 21, 26, 28
161	*Cephalograptus cometa extrema* Bouček & Přibyl, 1942	U	Laff.										6, 13, 14, 21, 28
162	*Campograptus harpago* (Törnquist, 1899)	U	?L										36
163	*Monograptus delicatulus* Elles & Wood, 1913	cf.	X										1, 6, 14, 21
164	*Neolagarograptus tenuis* (Portlock, 1843)		L										6, 14, 25, 26, 28
165	*Stimulograptus distans* (Portlock, 1843)		L										14
166	*Pribylograptus argutus sequens* (Rickards, 1970)		?L										13, 14
167	*Glyptograptus packhami* Rickards, 1970		LM										13, 14
168	*Parapetalolithus kurcki* (Rickards, 1970)		L	X		X	X	L				?aff.	10, 14, 28
169	*Campograptus obtusus* (Rickards, 1970)		M										13, 14
170	*'Climacograptus' simplex* Rickards, 1970		M										13, 14
171	*Comograptus barbatus* (Elles & Wood, 1907)		X										4
172	*Glyptograptus sinuatus crateriformis* Rickards, 1970		X										13, 14
173	*Monogr. urceolus* Richter, 1850 *sensu* Zalasiewicz, 1996												21
174	*Streptograptus nanshanensis minutus* Chen, 1984		cf										27
175	*Torquigraptus linterni* Williams *et al.*, 2003		X	X									37
176	*Torquigraptus magnificus* (Přibyl & Münch, 1942)		X	X									37
177	*Stimulograptus sedgwickii* (Portlock, 1843)		X	X	X	X	X	X					6, 13, 14, 16, 25, 26, 27, 28
178	*Rastrites gracilis* Přibyl, 1943b		?	X									10, 26, 37
179	*Pristiograptus variabilis* (Perner, 1897)		?	X	X	X							6, 10, 14, 15
180	*Oktavites contortus* (Perner, 1897)		?	X	X	X	X						10, 28
181	*Pseudoplegmatograptus obesus obesus* (Lapworth, 1877)		?	X	X	X	X	X	X	X	X	X	6, 10, 14
182	*Petalolithus* sp. 2 of Loydell, 1992			X									10
183	*Parapetalolithus praecedens* (Bouček & Přibyl, 1941a)			X									10
184	*Pristiograptus* sp. 1 of Loydell, 1993			X									10
185	*'Monograptus' admirabilis* (Přibyl & Münch, 1992)			X									10
186	*Paradiversograptus capillaris sensu* Loydell, 1993			X									10, 21, 28
187	*Rastrites schaueri* Štorch & Loydell, 1992			X									10
188	*Monograptus pulcherrimus* (Manck, 1928)			X									10
189	*Rastrites perfectus* Přibyl, 1943			X									10
190	*Parapetalolithus clavatus* (Bouček & Přibyl, 1941a)			?									10
191	*Parapetalolithus ovatus* (Barrande, 1850)			X	?								10, 15
192	*Streptograptus ansulosus* (Törnquist, 1892)			X	X								10, 28
193	*Paradiversograptus rectus* (Manck, 1923)			X	X								10
194	*Parapetalolithus conveniens* (Koren', 1967)			X	X	X							10
195	*Rastrites carnicus* Seelmeier, 1936			X		X	X						10
196	*Rastrites linnaei* Barrande, 1850			X	X	X	X	L					10
197	*Stimulograptus halli* (Barrande, 1850)			X	X	X	X	X					1, 10, 13, 15, 16, 28
198	*Pristiograptus pristinus* Přibyl, 1940a			X	X	X	X	X	X	X			10, 15
199	*Pristiograptus* sp. 2 of Loydell, 1993			U	X								10, 28
200	*Stimulograptus glanfredensis* Loydell, 1993			?	X	X							10

Figure 14. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *convolutus* Biozone to *galaensis* Subzone. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

8.j. *Aulograptus cucullus* Biozone

The base of the *cucullus* Biozone equates with that of the Darriwilian Stage (Cooper & Sadler, 2004). Rushton (*in* Cooper *et al.* 2004, p. 19) renamed the former *Didymograptus hirundo* Biozone the *Aulograptus cucullus* Biozone to take into account the fact that *Expansograptus hirundo* originates much earlier, in the *victoriae* Biozone. The base of the *cucullus* Biozone is characterized by the incoming of *A. cucullus*, and many other taxa originate in the biozone, among them the first cryptograptids, *Oelandograptus*

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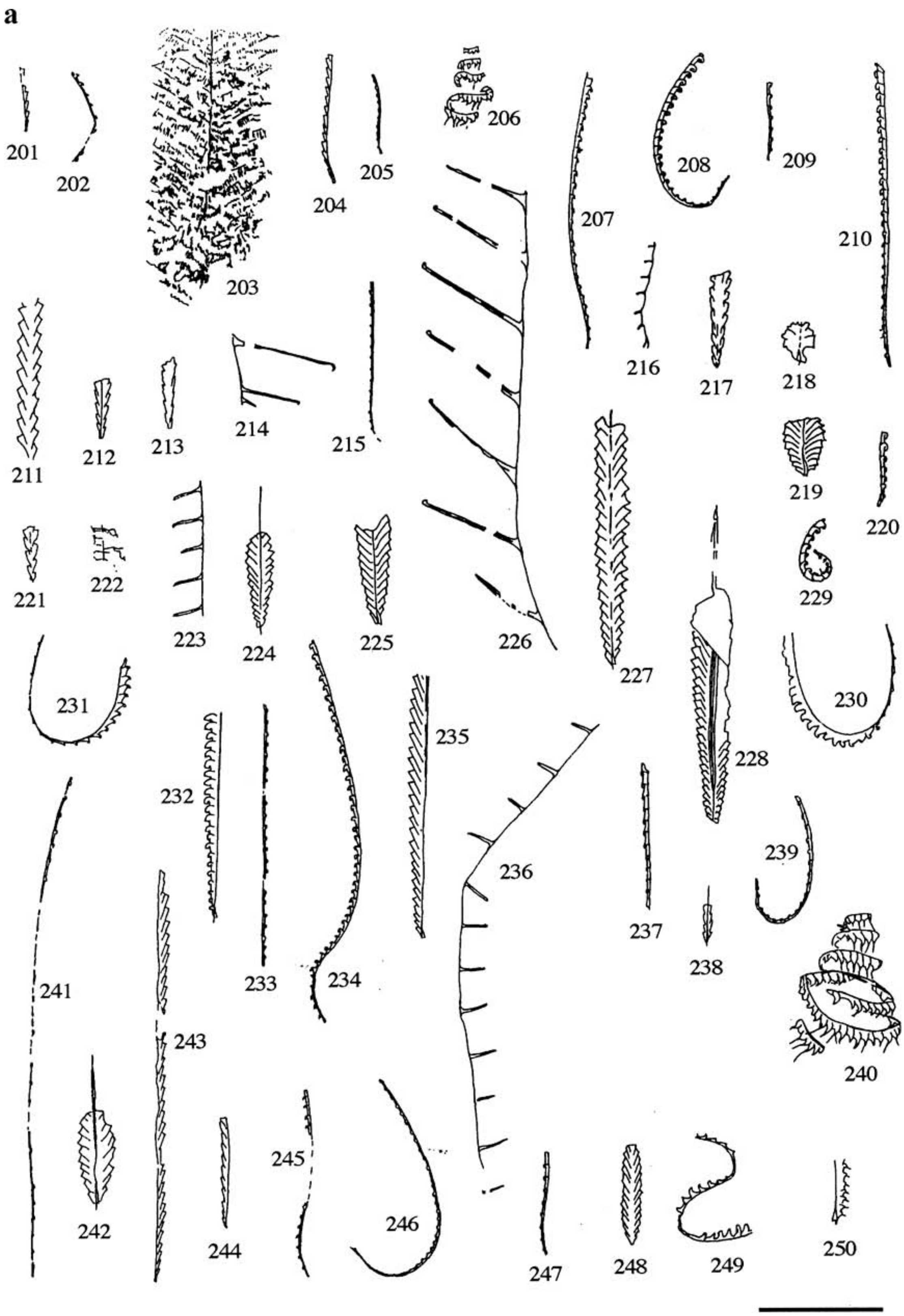

Figure 15. For legend see facing page.

austrodentatus anglicus, *Acrograptus nicholsoni planus*, *Didymograptus protobifidus, Expansograptus sparsus, Undulograptus cumbrensis, U. sinicus* and *Eoglyptograptus shelvensis*; these include the first biserial graptolites in the British Ordovician sequence (Fig. 4). Assemblages of the *A. cucullus* Biozone have also been recorded from the Shelve district of Shropshire (Strachan, 1986). The range chart shows a few taxa indicating the upper part of this biozone (Fig. 5); these are *Acrograptus acutidens*, and possibly *Amplexograptus confertus* and *Cryptograptus tricornis schaeferi*.

b

No	Taxon	runcinatus	gemmatus	renaudi	utilis	johnsonae	proteus	carnicus	galaensis	loydelli	sartorius	griestoniensis	crenulata	Sources
201	*Pristiograptus* sp. 3 of Loydell, 1993	X												10
202	*'Monograptus' gemmatus* (Barrande, 1850)	X	A											10, 13, 28
203	*Pseudoretiolites daironi* (Lapworth, 1877)	X	X											4
204	*Pristiograptus renaudi* (Phillipot, 1950)	X	X	A										10, 28
205	*Streptograptus strachani* Loydell, 1993	X	X	X										10
206	*Spirograptus guerichi* Loydell, Štorch & Melchin, 1993	X	X	X	X									10
207	*Paradiversograptus runcinatus* (Lapworth, 1876a)	A	?	X	L									10, 28
208	*Streptograptus plumosus* (Baily, 1871)	X	X	X	X									10, 28
209	*Streptograptus pseudoruncinatus* (Bjerreskov, 1975)	X	X	X	X									10, 28
210	*Monograptus bjerreskovae* Loydell, 1993b	X	X	X	X	X	X	X	X					10, 19, 28
211	*Parapetalolithus elongatus* Bouček & Přibyl, 1941a	?	X											10, 28
212	*Glyptograptus supernus* Fu, 1986	?	X											10
213	*Glyptograptus fastigatus* Haberfelner, 1931a	?	A	X										10, 28
214	*Rastrites maximus* Carruthers, 1867b	?	X	X										8, 10, 28
215	*Streptograptus filiformis* Chen, 1984a	?	X	X	X	?	X							10
216	*Rastrites fugax* Barrande, 1850		X											10, 28
217	*Glyptograptus auritus* Bjerreskov, 1975		X											10
218	*Parapetalolithus globosus* (Chen, 1984a)		X											10
219	*Parapetalolithus regius* (Hundt, 1957)		X											10
220	*Streptograptus* sp. of Loydell, 1993b		X											10, 28
221	*Glyptograptus* aff. *fastigatus* (broad form)		X											28
222	*Dabashanograptus dubius* Ge, 1990		X											10
223	*Rastrites abbreviatus* Lapworth, 1876		?											39
224	*Parapetalolithus hispanicus* (Haberfelner, 1931b)		X	X	L									10, 28
225	*Parapetalolithus palmeus palmeus* (Barrande, 1850)		X	?	X									10, 14
226	*Rastrites* sp. aff. *maximus* of Loydell, 1993		X			X	X							10
227	*Parapetalolithus altissimus* (Elles & Wood, 1908)		?		X	X								10, 14, 28
228	*'Parapetalolithus giganteus'* (Bouček & Přibyl, 1941a)			X				?						10
229	*Pseudostreptograptus williamsi* Loydell, 1991a			X	L									10
230	*Torquigraptus cavei* Loydell, 1993			X	X									10, 28
231	*Torquigraptus planus* Barrande, 1850			X	X									10, 28
232	*Monograptus marri* Perner, 1897			X	X	X	X	cf.	cf.	cf.		?		10, 19, 28, 29
233	*Streptograptus barrandei* (Suess, 1851)				X									10, 28
234	*Stimulograptus utilis* Loydell, 1991a				A									10, 28
235	*Pristiograptus bjerringus* (Bjerreskov, 1975)				X	X								10, 28
236	*Rastrites distans spengillensis* Rickards, 1970				L	X	X							10
237	*Streptograptus storchi* Loydell, 1991a				X	X	X	A						10, 19, 28
238	*Glyptograptus? nebula* Toghill & Strachan, 1970				X	?	X	X	?	?	?	X		14, 19, 28
239	*Streptograptus johnsonae* Loydell, 1991				U	A	X							10, 28
240	*Spirograptus turriculatus* (Barrande, 1850)				U	X	X	X	X	?				10, 19, 28
241	*Streptograptus tenuis* Loydell, 1993					X								10, 28
242	*Parapetalolithus schaueri* (Loydell, 1991a)					X	X							10
243	*Pristiograptus schucherti* Bjerreskov, 1981					X	X							10
244	*Pristiograptus huttae* Loydell, 1993						X							10
245	*Stimulograptus becki* (Barrande, 1850)						X							10, 28
246	*Streptograptus petilus* (Hutt, 1975)						X	X						6, 10
247	*Streptograptus pseudobecki* Bouček & Přibyl, 1942						X		X					19, 28, 41
248	*Parapetalolithus tenuis* (Barrande, 1850)				U		X	X	X					10, 19, 28
249	*Torquigraptus proteus* (Barrande, 1850)						X	X	?	?				6, 10, 19, 28
250	*Monograptus rickardsi* Hutt, 1975 (?=*M. priodon*)						?	?	?	?				6, 19, 28

Figure 15. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *runcinatus* Subzone to *crenulata* Biozone. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

8.k. *Didymograptus artus* Biozone

The base of the *D. artus* Biozone corresponds with that of the locally defined Llanvirn Series. The biozone was established by Fortey & Owens (1987) to replace the traditional *Didymograptus bifidus* Biozone, which was based on incorrect identifications. This interval displays a highly diverse and distinctive graptolite assemblage (Fig. 5), with the majority of taxa appearing at the base of the biozone, which is characterized by the zone fossil and *Didymograptus spinulosus* (Fortey & Owens, 1987; Fortey, Beckly

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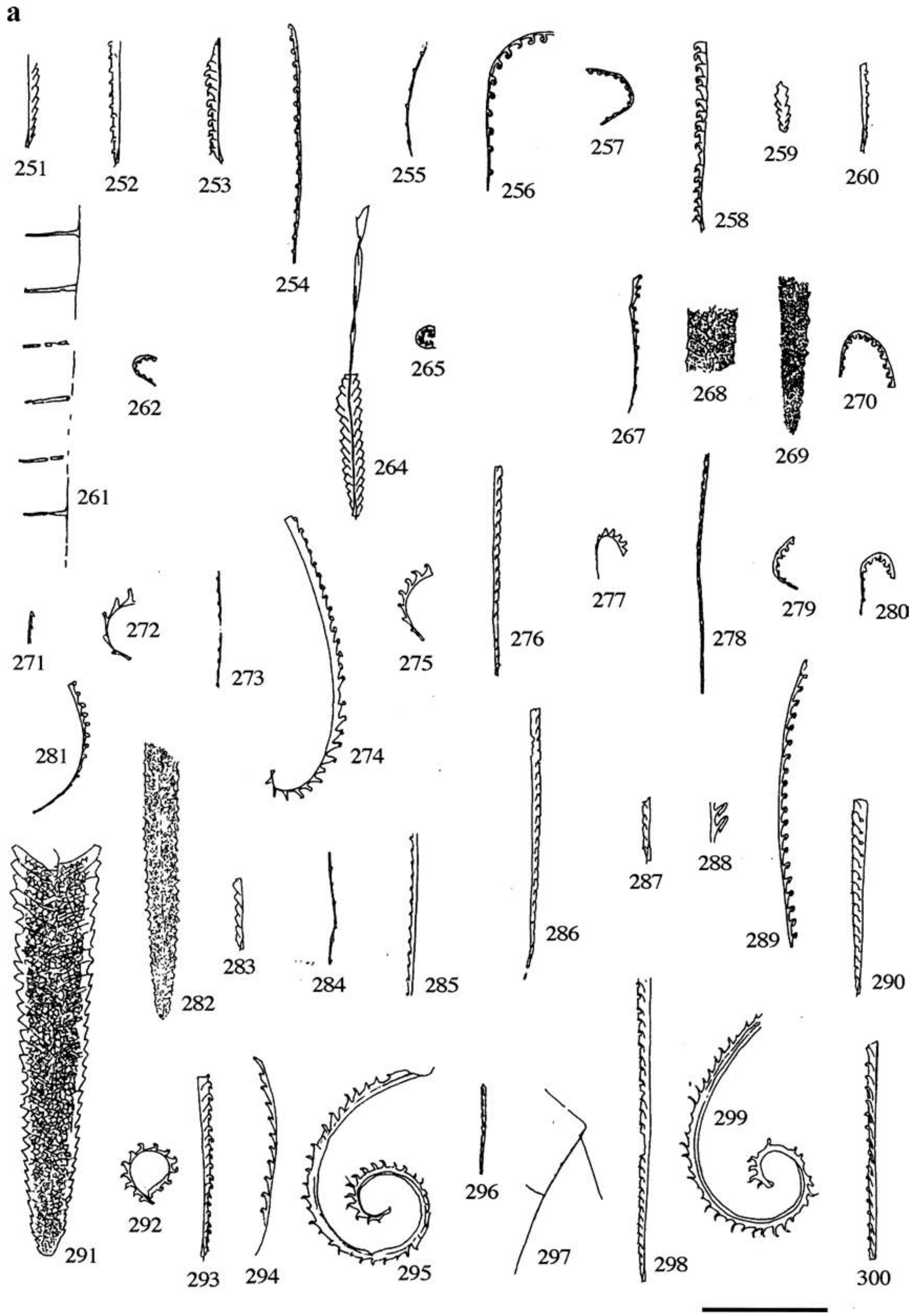

Figure 16. For legend see facing page.

& Rushton, 1990; Rushton *in* Cooper *et al.* 2004). Approximately 31 species originate in the biozone, 21 of which have ranges restricted to it. Several genera are recorded for the first time, notably *Glossograptus* and *Climacograptus*. The *artus* Biozone has good potential for further biostratigraphical subdivision. While most elements of the assemblage span the entire biozone, there is a distinguishable middle to upper biozonal assemblage containing *Pseudoclimacograptus scharenbergi*, *P. angulatus*, *Trichograptus fragilis*, *Diplograptus hollingworthi* and *Nicholsonograptus fasciculatus* (Fig. 5). A few taxa help differentiate the lower part of the biozone, such as *D. protobifidus* and *Expansograptus sparsus*, which originate in the

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b

No.	Taxon	proteus	carnicus	galaensis	loydelli	sartorius	griestoniensis	crenulata	spiralis	lapworthi	insectus	centrifugus	murchisoni	firmus	riccartonensis	Sources
251	*Pristiograptus nudus* (Lapworth, 1880) s.l.	?	X	X	X	X	X	X>								19, 28
252	*Monoclimacis*? *galaensis* (Lapworth, 1876)	?	X	X												19, 28
253	*Monograptus priodon* (Bronn, 1835)	?	?	?	?	?	X	X>								10, 11, 14, 19, 22, 28
254	*Streptograptus whitei* Zalasiewicz, 1994		X													19, 28
255	*Torquigraptus carnicus* (Gortani, 1923)		X	X	X											19, 28
256	*'Monograptus' crispus* Lapworth, 1876		aff.	X	A											19, 28, 29
257	*Streptograptus exiguus* (Lapworth, 1876)		X	X	X	X	L									19, 28, 29
258	*Stimulograptus clintonensis* (Hall, 1852)		?	X	X	X	L									19, 28
259	*Petalolithus* sp. 1 of Zalasiewicz, 1994			X												19
260	*Monoclimacis*? sp. A of Rickards 1970			X												13
261	*Rastrites distans* Lapworth, 1876			X												40
262	*Streptograptus*? sp. nov. Loydell, 1993b			X												10
263	*Pseudoplegm. reticulatus* (Bouček & Münch, 1944)			X	X											6
264	*Parapetalolithus wilsoni* (Hutt, 1974)			X	X	X										6, 42
265	*Cochl. veles* (Richter, 1871) (=*M. discus* Tqt, 1883)			X	X	X	X	L								19, 28, 29
266	*Pseudoplegm. elleswoodae* Bouček & Münch, 1944			?	?	?										
267	*Torquigraptus arcuatus* (Bouček, 1931)			?	?	?	?									9
268	*Retiolities geinitzianus* Barrande, 1850			?	?	X	X	X	X	X	X	X	L			11, 14, 19, 22 28, 29
269	*Stomatograptus longus* Obut, 1949				X											6, 43
270	*Streptograptus loydelli* Štorch & Serpagli, 1993				A	?										19, 28
271	*Streptograptus* aff. *sartorius* of Zalasiewicz, 1994					X										19, 28
272	*Torquigraptus pragensis ruzickai* (Přibyl, 1943)					?										19, 28
273	*Streptograptus sartorius* (Törnquist, 1881)					X	L									19, 28
274	*Torquigraptus pragensis pragensis* (Přibyl, 1943)					X	L									19, 28
275	*Torquigraptus tullbergi spiraloides* (Přibyl, 1945)					?	X									19, 28
276	*Mcl. directa* Zalasiewicz, Loydell & Štorch, 1995					?U	A									19, 20, 28, 29
277	*Monograptus pseudocommunis* Zalasiewicz, 1994						L									19, 28
278	*Monoclimacis griestoniensis* (Nicol, 1850)						A									19, 20, 28
279	*Streptograptus* aff. *loydelli* of Zalasiewicz, 1994						X									19, 28
280	*Monogr. drepanoformis* Toghill & Strachan, 1970						X									14
281	*Torquigraptus tullbergi tullbergi* (Bouček, 1931)						X	X								14, 19, 28
282	*Retiolites angustidens* Elles & Wood, 1908						X		X	X	X	X	L			4, 11, 29
283	*Pr. initialis* (Kirste, 1919) *sensu* Zalasiewicz, 1994						?	X								19, 28
284	*Torquigraptus pergracilis* (Bouček, 1931)						?			X						11, 19, 28
285	*Torquigr.* ex. gr. *pragensis?* of Zalasiewicz, 1994						U									19, 28
286	*Mcl. woodae* Zalasiewicz, Loydell & Štorch, 1995						?U	?L								20
287	*Monoclimacis crenulata* (Elles & Wood, 1911)							X	LM							11, 19, 28
288	*Lapworthograptus knockensis* (Elles & Wood, 1913)							X								23
289	*Lapworthograptus grayae* (Lapworth, 1876)							X	L			?				23, 29
290	*Monoclimacis vomerina vomerina* (Nicholson, 1872)							X	X	X	X	X	X	X	L	11, 19, 22, 28, 29, 30
291	*Stomatograptus grandis* (Suess, 1851)								L							2
292	*Oktavites*? *falx* (Suess, 1851)								L							9
293	*Monograptus parapriodon* Bouček, 1931								X							11, 19, 28, 30
294	*Diversograptus ramosus* Manck, 1923								X	L						11
295	*Oktavites spiralis* (Geinitz, 1842)								X	L						11, 19, 28
296	*Monoclimacis linnarssoni* (Tullberg, 1883)								X	X	L					11, 19, 28
297	*Barrandeograptus bornholmensis* (Laursen, 1940)								X	X	X	X	L			11, 29
298	*Monoclimacis geinitzi* (Bouček, 1932)								X	X	X	X	X			11, 30
299	*Oktavites excentricus* (Bjerreskov, 1975)								M							30
300	*Monoclimacis hemmanni* (Přibyl, 1941c)								M							11

Figure 16. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *proteus* Subzone to *riccartonensis* Biozone. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

cucullus Biozone but disappear in the lower part of the *artus* Biozone. The *D. artus* Biozone has been widely recognized in northern England and Wales (Elles, 1940; Strachan, 1986; Fortey & Owens, 1987; Fortey, Beckly & Rushton, 1990; Cooper *et al.* 1995, 2004).

8.l. *Didymograptus murchisoni* Biozone

Graptolite assemblages characteristic of this biozone have been recorded from the Builth–Llandrindod Wells district of central Wales (Elles, 1940; Hughes, 1989; Davies *et al.* 1997), the Shelve area of Shropshire

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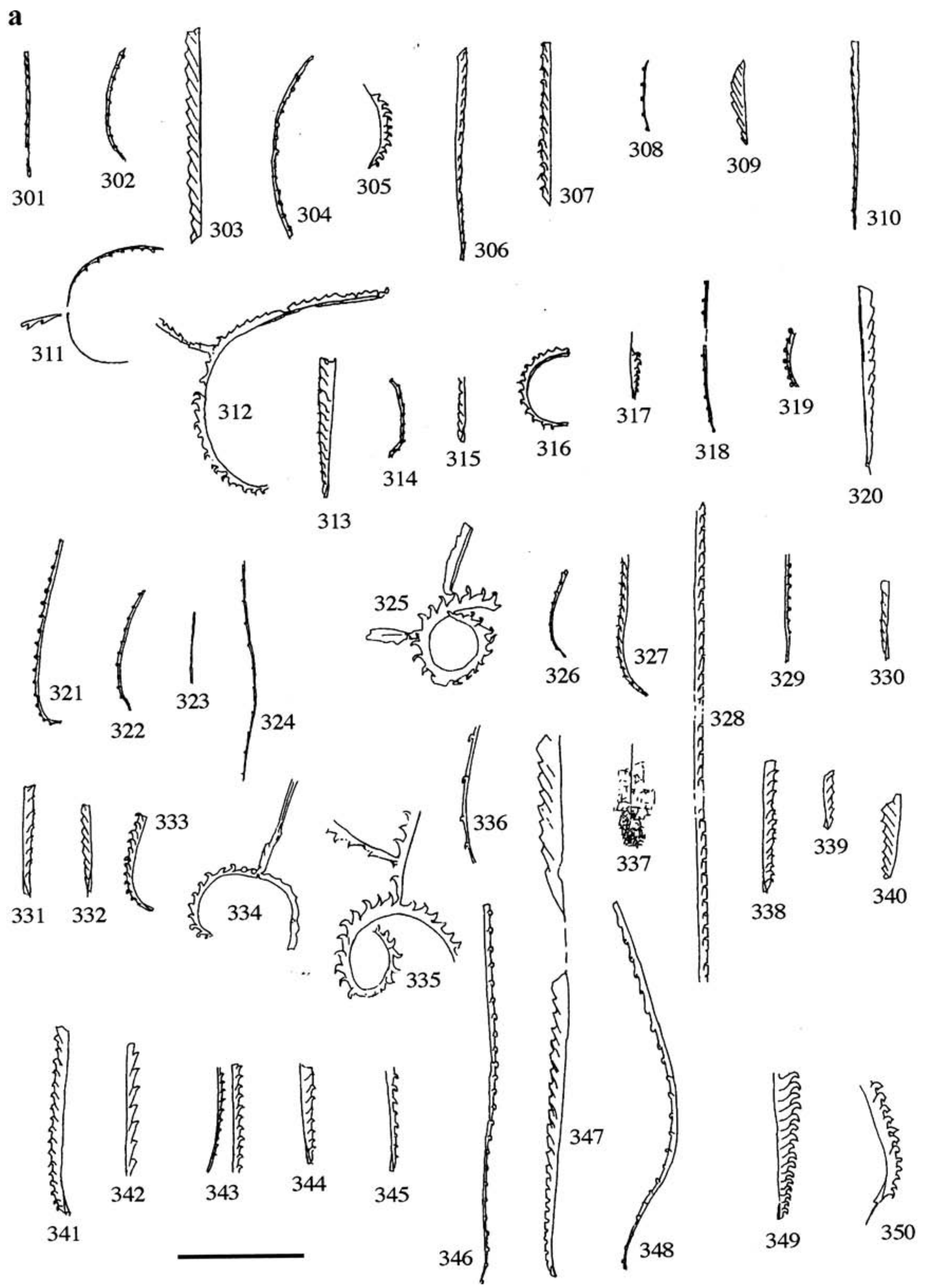

Figure 17. For legend see facing page.

(Strachan, 1986; Hughes, 1989), the Skiddaw Group strata of the Tarn Moor Tunnel in the Lake District (Wadge, Nutt & Skevington, 1972), the Fishguard area of South Wales (Davies *et al.* 2003) and Abereiddy Bay (Jenkins, 1987). The base of the *murchisoni* Biozone sees the incoming of the zone fossil, which is restricted to this biostratigraphical interval (Fig. 5). Other new appearances include *Diplograptus foliaceus*, *Cryptograptus tricornis tricornis*, *Pseudoclimacograptus angulatus magnus*, *P. angulatus micidus*? and *Didymograptus speciosus*? (Fig. 5). *Pterograptus elegans*?, *Lasiograptus retusus* and *Didymograptus nanus* are reported only from the lower part of the biozone, whereas *Diplograptus*? *decoratus*, *Amplexograptus caelatus* and *Normalograptus brevis* appear in its middle to upper part; this

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b

No.	Taxon	spiralis	lapworthi	insectus	centrifugus	murchisoni	firmus	riccartonensis	dubius	rigidus	lundgreni	nassa	ludensis	Sources
301	*Monoclimacis* n. sp. 1 of Loydell & Cave, 1996	M												11
302	*Streptograptus anguinus* (Přibyl, 1941)	M												11
303	*Pristiograptus prantli* Přibyl, 1940	MU												9
304	*Streptograptus nodifer* (Törnquist, 1881)	MU												6, 11, 14
305	*Stimulograptus vesiculosus* (Perner, 1899)	U												11
306	*Monoclimacis sublinnarssoni* (Tullberg, 1883)		L											11
307	*Streptograptus speciosus* (Tullberg, 1883)		L											11
308	*Streptograptus wimani* (Bouček, 1932)		L											11, 14
309	*Pristiograptus largus* Perner, 1899		L											11
310	*Monoclimacis vomerina* ssp. 1 of Loydell & Cave, 1996		L											11
311	*Barrandeograptus pulchellus* (Tullberg, 1883)		L											11
312	*Cyrtograptus lapworthi* Tullberg, 1883		X											11
313	*Monoclimacis basilica* (Lapworth, 1880)		M	X	X	X	?	X						11, 22, 29
314	*Mediograptus flittoni* Loydell & Cave, 1996			L										11
315	*Monoclimacis shottoni* Rickards, 1965			X	L									11, 29
316	*Cyrtograptus insectus* Bouček, 1931			X	?									11, 22
317	*Monograptus pseudocultellus* Bouček, 1932			L	X									11
318	*Mediograptus morleyae* Loydell & Cave, 1996			U										11
319	*Mediogr.* sp. aff. *inconspicuus* of Loydell & Cave, 1996			U	X									11
320	*Monoclimacis*? sp. 1 of Zalasiewicz & Williams, 1999				L									22
321	*Mediograptus danbyi* (Rickards, 1965)				L									22, 29
322	*Mediograptus cautleyensis* (Rickards, 1965)				X									14, 29
323	*Monoclimacis griestoniensis nicoli* Rickards, 1965				X									14
324	*Monograptus simulatus* Rickards, 1965				X									14
325	*Cyrtograptus centrifugus* Bouček, 1931b				X	L								11, 22, 29
326	*Mediograptus inconspicuus* (Bouček, 1931)				MU	L								11
327	*Monoclimacis adunca* (Bouček, 1931)				cf.	L								11, 22
328	*Monoclimacis kettneri* (Bouček, 1931)				cf.	X								11, 22
329	*Mediograptus flexuosus* (Tullberg, 1883)?				U									11
330	*Monoclimacis vikensis* Bassett & Rickards, 1971?					L								11
331	*Monoclimacis* n. sp. 2 of Loydell & Cave, 1996					L								11
332	*Pristiograptus praedubius* (Bouček, 1931)					L								11
333	*Monograptus radotinensis radotinensis* Bouček, 1931b					L								11
334	*Cyrtograptus bohemicus* Bouček, 1931					LM								11
335	*Cyrtograptus murchisoni* Carruthers, 1867					X								11, 22, 29
336	*Mediograptus remotus* (Elles & Wood, 1913)					X	?							4, 14, 29
337	*Pseudoplegmatograptus wenlockianus* Štorch, 1992					X	L							11
338	*Monograptus firmus firmus* Bouček, 1931					X	X	X						11, 14, 22
339	*Pristiograptus dubius dubius* (Suess, 1851)						X	X	X	X	X	X	X>	11, 14, 22
340	*Pristiograptus latus* Bouček, 1932							L						11
341	*Monograptus riccartonensis* Lapworth, 1876							X						11, 14, 22
342	*Barrandeograptus carruthersi* (Lapworth, 1876)							X						4, 14
343	*Monograptus radotinensis inclinatus* Rickards, 1965							X						14, 22, 28
344	*Monograptus firmus sedberghensis* Rickards, 1965							MU						14
345	*Monograptus instrenuus* Lenz & Melchin, 1991							?						22
346	*Monograptus antennularius* (Meneghini, 1857)							MU	X	LM				22, 29
347	*Monoclimacis flumendosae* (Gortani, 1923)							U?	X	X	X			14, 22, 28, 31
348	*Monograptus retroflexus* Tullberg, 1883 group								X	X	L			14, 22
349	*Monograptus priodon/flemingii* group								X	X	X			22
350	*Monograptus flexilis* Elles, 1900								MU	LM				14, 22, 28

Figure 17. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *spiralis* to *ludensis* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

suggests that refinement of the biostratigraphy may be possible.

8.m. *Hustedograptus teretiusculus* Biozone

The base of this biozone is delineated by the disappearance of *D. murchisoni* (Hughes, 1989), as the zone fossil originates in the middle part of the interval (Fig. 6). The lower part of the biozone therefore is an interregnum. The only taxa to appear at the basal boundary are *Dicellograptus divaricatus divaricatus*, *Climacograptus antiquus* and possibly *Normalograptus euglyphus*. Approximately half of the total species occurring at this biostratigraphical level appear in

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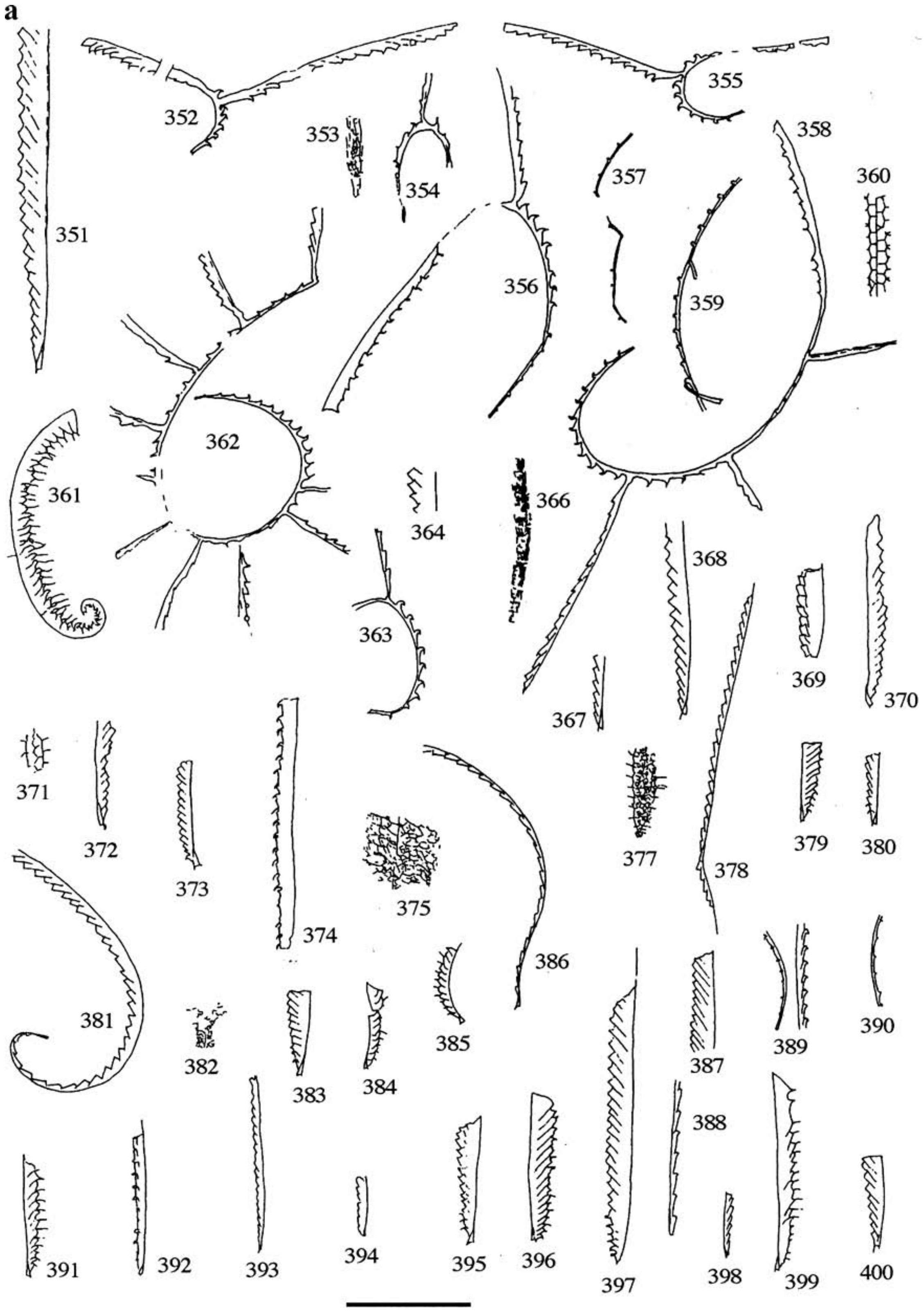

Figure 18. For legend see facing page.

the middle to upper part of the biozone. These data provide a strong case for a biostratigraphical review of the graptolite faunas found in this interval. However, Hughes (1989) remarked that Elles's (1940) attempt to subdivide the *teretiusculus* and *gracilis* biozones in the Builth area was incorrect, as her refinement was based on taxonomically unsound species and poorly preserved material. The *teretiusculus* Biozone, as it is presently understood, is recorded from Wales and Shropshire (Elles, 1940; Strachan, 1986; Hughes, 1989; Davies *et al.* 1997).

8.n. *Nemagraptus gracilis* Biozone

The base of this biozone equates with that of the Sandbian Stage of the Ordovician (Cooper & Sadler,

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b

		dubius	rigidus	lundgreni	nassa	ludensis	nilssoni	scanicus	incipiens	leintwardin.	bohemicus	
351	*Pristiograptus dubius pseudolatus* Rickards, 1965	MU	X	L?								22
352	*Cyrtograptus rigidus* Tullberg, 1883		X									14, 22
353	*Plect.? bouceki* Rickards, 1967 (=*Sok. textor*, Bouček & Munch, 1952)		X									14, 28, 29
354	*Cyrtograptus linnarssoni* Lapworth, 1880		M									22
355	*Cyrtograptus perneri* Bouček, 1933		??	X								14, 22
356	*Cyrtograptus ellesae* Gortani, 1923		??	X								14, 22
357	*Cyrtograptus* cf. *urbanekii* Teller, 1976			?L								22
358	*Cyrtograptus lundgreni lundgreni* Tullberg, 1883			X								14, 22
359	*Cyrtograptus lundgreni gracilis* Bouček, 1933			X								14
360	*Paraplectograptus eiseli* (Manck, 1918)			X								14
361	*Testograptus testis* (Barrande, 1850)			X								14
362	*Cyrtograptus ramosus* (Bouček, 1931)			U								14, 22
363	*Cyrtograptus hamatus* (Baily, 1862)			U								14, 22, 28, 31
364	*Pristiograptus* sp. 1 of Holland *et al.*, 1969			U								14
365	*Pristiograptus* aff. *jaegeri* of Warrren, 1971			U	X	LM						14
366	*Gothograptus nassa* Holm, 1890			?U	A	?X	?L					14, 22, 28
367	*Pristiograptus jaegeri* Holland *et al.*, 1969			cf.	U	X						14, 31
368	*Pristiograptus dubius ludlowiensis* (Bouček, 1936)				cf.			cf.				31
369	*Monograptus gerhardi* Kühne, 1955					X						31
370	*Monograptus ludensis* (Murchison, 1839)					X	L					14, 22, 31
371	*Holoretiolites* (*Balticograptus*) *lawsoni* Holland *et al.*, 1969					M						14, 31
372	*Pristiograptus auctus* Rickards, 1965					MU	LM					14, 31
373	*Monograptus deubeli* Jaeger, 1959					U						14, 31
374	*Monograptus uncinatus orbatus* Wood, 1900					aff.	LM					14, 31
375	*Plectograptus macilentus* (Törnquist, 1887)					cf.	LM					14, 31
376	*Monograptus* aff. *unguiferus*						L					31
377	*Spinograptus spinosus* (Wood, 1900)						L					14, 31
378	*Neodiversograptus nilssoni* (Barrande, 1850)						LM					14, 31
379	*Saetograptus* (*Colonograptus*) *colonus colonus* (Barrande, 1850)						X	LM				14, 31
380	*Saetograptus* (*Colonograptus*) *varians varians* (Wood, 1900)						X	X	L			14, 31
381	*Bohemograptus bohemicus s.l.* (Barrande, 1850)						X	X	X	?		14, 31
382	*Spinograptus clathrospinosus* (Eisenack, 1951)						MU					14
383	*Saetograptus* (*Colonograptus*) *roemeri* (Barrande, 1850)						MU	cf.				14, 31
384	*Saetograptus* (*Saetograptus?*) *wandalensis* (Watney & Welch, 1911)						MU					14
385	*Saetograptus fritschi fritschi s.l.* (Bouček, 1936)						MU					14
386	*Cucullograptus* (*Lobograptus*) *progenitor* Urbanek, 1966						MU					14
387	*Saetograptus* (*Colonograptus*) *colonus compactus* (Wood, 1900)						MU	LM				14, 31
388	*Lobograptus simplex* Urbanek, 1966						MU	LM				14
389	*Cucullograptus* (*Lobograptus*) *scanicus* (Tullberg, 1883)						MU	A				14
390	*Crinitograptus crinitus* (Wood, 1900)						MU	X				14, 31
391	*Saetograptus* (*Saetograptus*) *chimaera salweyi* (Lapworth, 1880)						MU	X				14, 31
392	*Monoclimacis micropoma* (Jaekel, 1889)						MU	X				14, 31
393	*Pristiograptus vicinus* (Perner, 1899)						MU	X	L			14, 31
394	*Monoclimacis haupti* (Kühne, 1955)						MU	X	LM			14, 31
395	*Saetograptus* (*Saetograptus*) *leintwardinensis incipiens* (Wood, 1900)						MU	X	A	?		14, 31
396	*Saetograptus* (*Saetograptus*) *chimaera chimaera* (Barrande, 1850)						U	X				14
397	*Saetogr.* (*Saetograptus*) *chimaera semispinosus* (Elles & Wood, 1911)						U	X	X			14
398	*Pristiograptus welchae* Rickards, 1965							M				14
399	*Saetograptus clunensis* (Earp, 1944)							MU	LM			14, 31
400	*Pristiograptus tumescens* (Wood, 1900)							MU	A	?		14

Figure 18. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *dubius* to *bohemicus* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

2004), or with that of the Caradoc of British usage. This biostratigraphic interval was first described by Lapworth (1879–1880) and defined by the incoming of the dicellograptids and nemagraptids. Subsequent work led to a revised definition of the base of the biozone, which is now taken at the incoming of *N. gracilis* (Finney & Bergström, 1986). Assemblages representing this biozone have been recorded from the Builth region of Wales and the Shelve area of the Welsh Borderland (Elles, 1940; Strachan, 1986; Hughes, 1989; Davies *et al.* 1997). However, although the position of the base of the *gracilis* Biozone at Builth Wells is unclear (Hughes, 1989; Davies *et al.* 1997), Bettley, Fortey & Siveter (2001) have identified a correlatable base to the biozone west of Shelve and at Meidrim, south Wales. The Anglo-Welsh *N. gracilis* assemblage is diverse,

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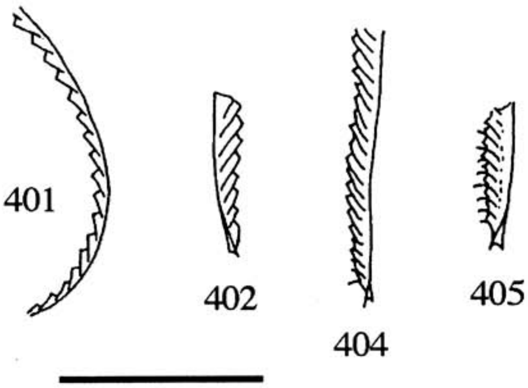
a



b

No	Taxon	scanicus	incipiens	leintwardinen	bohemicus	Sources
401	*Bohemograptus bohemicus tenuis* (Bouček, 1936)	MU	X		X	14, 31
402	*Pristiograptus minor* (M'Coy, 1851)		cf.			31
403	*Saetograptus* aff. *incipiens* (Wood, 1900)		X	LM		14, 31
404	*Saetograptus* (*Saetograptus*) *leintwardinensis primus* (Bouček, 1936)			LM		14, 31
405	*Saetograptus* (*Saetograptus*) *leintwardinensis leintwardinensis* (Lapworth, 1880)			X		14, 31

Figure 19. Silurian graptolites (a) and their stratigraphical ranges (b) in Great Britain, *scanicus* to *bohemicus* biozones. Scale bar represents 10 mm. For key to symbols in range charts, see Figure 3.

containing some 26 incoming species, as well as many longer-ranging forms from underlying zones (Fig. 6). Several species appear in the upper part of the biozone, and although only one of these, *Lasiograptus pusillus*, seems limited to this level, this assemblage may potentially be biostratigraphically useful. Incoming upper zonal taxa include *Climacograptus bicornis, Dicranograptus nicholsoni nicholsoni*, *Amplexograptus perexcavatus* and *Glossograptus hincksii hincksii*.

Graptolites reappear dramatically in the Ordovician sequence of Scotland in the *gracilis* Biozone. Following the sparse, low-diversity assemblages of the Scottish lower to middle Arenig interval of British usage, and the absence of Llanvirn biozones, a varied and abundant graptolite assemblage of *N. gracilis* age (about 75 taxa) has been recorded from southern Scotland (Stone, 1995; Rushton, Tunnicliff & Tripp, 1996; Armstrong *et al.* 1998; Williams *et al.* 2004), including the Girvan district (Rushton, 2001*b*). From this biozone upwards, the Scottish graptolite succession is more directly comparable to that of England and Wales than in the Lower Ordovician, although the two biostratigraphical schemes still reflect significant assemblage differences (Fig. 1), making precise correlation difficult (Zalasiewicz, Rushton & Owen, 1995; Williams *et al.* 2004). In Scotland, the *gracilis* Biozone is similarly defined as in England and Wales, although Stone (1995) commented on the importance of *Expansograptus*? *superstes* and *Dicellograptus intortus* to the characteristic *gracilis* assemblage (Figs 8, 9). *D. intortus* appears lower in the Anglo-Welsh sequence, however, and the exact position of the base of the *gracilis* interval cannot be clearly recognized in Scotland (Rushton, 1990; see also Williams *et al.* 2004). Recent work by Williams *et al.* (2004) has restricted the *gracilis* Biozone as outlined in the next section.

8.o. *Diplograptus foliaceus* Biozone

The *D. foliaceus* Biozone is an Anglo-Welsh biostratigraphical unit, traditionally employed for the graptolite assemblages found between those of the underlying *gracilis* Biozone, and the *Dicranograptus clingani* Biozone above (Fig. 1). It was formerly known as the *Diplograptus multidens* Biozone; however, the taxonomic validity of *D. multidens* has been questioned (Hughes, 1989), and we follow Bettley, Fortey & Siveter (2001) in naming the biozone after its suggested senior synonym, *D. foliaceus*. Much of Elles & Wood's (1901–1918) and Elles's (1940) earlier work on this biozone from the Shelve inlier and the type sections of the Caradoc area of Wales must be treated with caution, as many of the original taxa have not been found following recent studies (Hughes, 1989). Nonetheless, work carried out by the BGS in central Wales has confirmed the existence of a distinct and stratigraphically useful *foliaceus* Biozone assemblage (Figs 6, 7) with several newly occurring taxa (Davies *et al.* 1997; Williams *et al.* 2003*a*). An upper biozonal

This paper		Earlier usage	
Biozone	Subzone	Biozone	Subzone
clingani	morrisi	clingani	morrisi
	caudatus		caudatus
biocornis	wilsoni	wilsoni	
	apiculatus-ziczac	peltifer	
gracilis		gracilis	

Figure 20. Comparison of presently adopted and earlier Scottish zonal schemes for the *gracilis* to *clingani* biozonal interval.

assemblage with biostratigraphical potential has been identified (Fig. 7), including *Dicranograptus nicholsoni minor* and *Dicellograptus patulosus*.

8.p. *Climacograptus bicornis* Biozone (in Scotland)

Williams *et al*. (2004) recently formalized the use of this zone for Scottish strata, having reviewed all the Scottish early Caradoc graptolite assemblages preserved from the 19th century geological survey of southern Scotland (Peach & Horne, 1899) and from the work of the British Geological Survey during the 1980s and 1990s. The *bicornis* Biozone corresponds to the range of *Climacograptus bicornis*, commencing with its appearance in the *N. gracilis–C. bicornis* faunas from the Glenkiln Shales (in beds that were formerly assigned to the *gracilis* Biozone) and ranging up almost to the base of the *Dicranograptus clingani* Biozone in the lower Hartfell Shales (S. H. Williams, 1994). M. Williams *et al*. (2004) divided the *bicornis* Biozone into two subzones, the *apiculatus–ziczac* Subzone and the *wilsoni* Subzone (Fig. 20), as described below.

Formerly, two zones were recognized in the Scottish strata that follow the last appearance of *Nemagraptus gracilis* and precede the advent of the *Dicranograptus clingani* Biozone; these were known as the *Climacograptus peltifer* and *C. wilsoni* biozones. There are problems with the recognition of the *C. peltifer* Biozone, partly because the validity of the index species is doubtful (Strachan, 1971; Riva, 1976), and also because the original, supposedly diagnostic, *peltifer* assemblage (Elles, 1925) is much less diverse than the underlying *N. gracilis*-bearing assemblages and contains few elements that do not occur in the *gracilis* Biozone (Rushton, 1990; Williams *et al.* 2004). The long-recognized *wilsoni* Biozone is more distinctive where it is found, but is of relatively local occurrence and is not widely recorded. Williams *et al*. (2004) reduced it to a subzone of the *bicornis* Zone.

The correlation of the zonal units in the *gracilis* to *clingani* interval is not a simple one-to-one correlation, because in the new arrangement, the *gracilis* Biozone has a reduced stratigraphical range, characterized by the range of *N. gracilis* below the first appearance of *C. bicornis*. The upper and better-known assemblages (e.g. from the Glenkiln Shale) that were formerly assigned to the *gracilis* Biozone are now referred to the lower part of the *bicornis* Subzone, namely the *apiculatus–ziczac* Subzone (see Figs 8, 9).

8.p.1. Orthograptus apiculatus–Dicranograptus ziczac *Subzone (in Scotland)*

This subzone is recognized by the first appearances (FADs) of a large number of taxa; Williams *et al.* (2004, fig. 2) listed about 40 that first appear at about this level, though because good measured sections are lacking, the FADs are not claimed to be precisely synchronous. The subzone is named after two distinctive species that are fairly widely recorded (Williams *et al.* 2004, p. 101) and have similar ranges. The *apiculatus–ziczac* Subzone differs significantly from the *peltifer* Zone as previously used because *N. gracilis* is present in its lower part, together with such taxa as *Dicranograptus furcatus minimus, Expansograptus*? *superstes* and *Hallograptus* spp. The assemblages in the lower part of the *apiculatus–ziczac* Subzone, in which the range of *N. gracilis* overlaps with those of *C. bicornis* and the taxa named above, are well known from the Glenkiln Shales of southern Scotland, and were formerly assigned to the extended concept of the *N. gracilis* Biozone. The upper part of the *apiculatus–ziczac* Subzone, above the range of *N. gracilis*, is a weakly characterized interval that may, at least in part, correspond to the *peltifer* Biozone (Williams *et al.* 2004, p. 105), and such faunas have been recorded in the higher Glenkiln Shales.

8.p.2. Climacograptus wilsoni *Subzone (in Scotland)*

Lapworth (1878, p. 308) established the *C. wilsoni* Biozone during his work on the Moffat Series of the Southern Uplands, and it remains a recognizable part of the Scottish biostratigraphical scheme (Williams, 1994) although it has not been recognized elsewhere in Great Britain (Elles & Wood, 1901–1918; Elles, 1925, 1937). However, a taxonomic and biostratigraphical review of the *wilsoni* Biozone by Williams (1994) confirmed the value of this graptolite assemblage in southern Scotland. A type section was designated at Hartfell Spa (Williams, 1994) and the biozone has been recognized elsewhere (Stone, 1995; Williams, 1994). The *wilsoni* assemblage has fewer taxa than the '*peltifer* assemblage', and many of them continue from the lower biozone (Fig. 9). The base of the *C. wilsoni* Biozone is defined by the appearance of the index species; other incoming taxa are *Orthograptus calcaratus vulgatus*, *Corynoides curtus*, *C. calicularis*, *Dicellograptus angulatus* and *Orthograptus* of the *amplexicaulis* group.

8.q. *Dicranograptus clingani* Biozone

The *D. clingani* Biozone was established in the Moffat area by Lapworth (1878, p. 308) and has been widely recognized in Scotland (Williams, 1982*a*; Stone, 1995; Floyd, 1999) and also in Wales (Davies *et al.* 1997; Howells & Smith, 1997; Young, Gibbons & McCarroll, 2002; Williams *et al.* 2003*a*). Work at Hartfell Score in the Southern Uplands of Scotland and Whitland in south Wales led Zalasiewicz, Rushton & Owen (1995)

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to erect two subzones within the *clingani* interval, clearly defined by distinct graptolite assemblages and recognizable in both regions (Fig. 1), although there is some variation in assemblage composition (Zalasiewicz, Rushton & Owen, 1995). The potential for subdivision of the biozone in the Southern Uplands had previously been remarked on by Williams (1982*a*).

8.q.1. Ensigraptus caudatus *Subzone*

The base of this subzone is defined by the incoming of the index species at Hartfell Score with a large assemblage of other forms (Zalasiewicz, Rushton & Owen, 1995). The base of this subzone also defines that of the Katian Stage of the Ordovician (Cooper & Sadler, 2004). *D. clingani* is restricted to the *caudatus* Subzone in both Wales and Scotland (Zalasiewicz, Rushton & Owen, 1995; Davies *et al.* 1997; Figs 7, 9). In North Wales the *caudatus* Subzone is present in the Nod Glas Formation (Pratt, Woodhall & Howells, 1995, p. 49; Young, Gibbons & McCarroll, 2002, p. 53). In South Wales the assemblage contains similar elements to those found in the Southern Uplands, such as *Orthograptus quadrimucronatus* and *Climacograptus spiniferus*. However, *E. caudatus* itself has been recognized in this region only in the Llanilar–Rhayader area (Davies *et al.* 1997) and doubtfully from Cardigan (Williams *et al.* 2003*a*). Overall, the *caudatus* Subzone assemblages of Wales, with about 28 taxa present, are less diverse than those of Scotland, in which about 46 taxa are known.

8.q.2. Dicellograptus morrisi *Subzone*

In Wales and Scotland, the *D. morrisi* Subzone has a large and diverse graptolite assemblage, but fewer incoming species than the underlying *E. caudatus* Subzone (Figs 7, 10). At Hartfell Score, southern Scotland, Zalasiewicz, Rushton & Owen (1995) described this interval as a partial-range subzone, the base being defined by the appearance of *D. morrisi* and the top by the incoming of the *linearis* Biozone assemblage. At Whitland, South Wales, the base of the subzone was delineated by the incoming of *Normalograptus angustus* (Perner, 1895) (likely a senior synonym of *Climacograptus miserabilis*: Loydell, 2007) and possibly *D. morrisi*, the range of which is limited to this subzone (Zalasiewicz, Rushton & Owen, 1995). '*Glyptograptus*' *daviesi* is the only incoming species definitely reported from the base of the *morrisi* Subzone in Wales (Fig. 7), but in Scotland several taxa (besides the zone fossil) appear, including *Normalograptus mohawkensis*, *Climacograptus dorotheus*, *Dicellograptus caduceus* and *Leptograptus flaccidus spinifer* (Fig. 10). Davies *et al.* (1997) did not identify a discrete upper *clingani* Biozone assemblage in central Wales, but it is present in the Nod Glas of North Wales (Pratt, Woodhall & Howells, 1995, p. 49) and in coastal sections west of Cardigan, Williams *et al.* (2003*a*) found that the *morrisi* Subzone was better represented than the underlying *caudatus* Subzone.

8.r. *Pleurograptus linearis* Biozone

The original work on the graptolite assemblage of this interval was carried out by Lapworth (1878) on the upper part of the Lower Hartfell Shales in the Southern Uplands. Williams (1982*a*) has undertaken the only comprehensive study of the *P. linearis* Biozone in this area since Elles & Wood's (1901–1918) review of British graptolites, though Toghill (1970*b*) redescribed some of the fauna. Williams (1982*a*) was able to delineate the base of the biozone for the first time in the North Cliff section of Dob's Linn, and designated it as the type section for the interval base. Taxa diagnostic of the base include the zone fossil, with *Climacograptus tubuliferus*, possibly *Climacograptus styloideus* and *Leptograptus flaccidus macilentus*; however, several forms appear mid-biozone including: *Amphigraptus divergens divergens*, *Leptograptus capillaris* and *Dicellograptus elegans elegans* (Fig. 10). The overall assemblage is quite diverse in Scotland, most species continuing from underlying biozones. Graptolites characteristic of this biostratigraphical interval have been reported in the Rhins of Galloway, southwest Scotland (Stone, 1995) and at many sites along-strike to the NE (Floyd, 1999; McMillan, 2002), including Hartfell Score in the Moffat district (Zalasiewicz, Rushton & Owen, 1995). Floyd (1999) recorded the *linearis* Biozone in the Girvan succession.

At Whitland in south Wales, a low-diversity graptolite assemblage, possibly equating (at least in part) with the *P. linearis* Biozone, was recognized by Zalasiewicz, Rushton & Owen (1995), the base of which marks the appearance of large normalograptids. They referred to this biozone as the '*Normalograptus* proliferation interval'. Davies *et al.* (1997) did not record any *linearis* Biozone assemblages from the Llanilar–Rhayader area, but Williams *et al.* (2003*a*) recognized equivalents of the *linearis* Biozone at Frongoch, southwest of Cardigan, and records of *Climacograptus styloideus* at Llanystumdwy suggest that the *linearis* Biozone may be present in North Wales (Harper, 1956). Exact correlation between the base of the Ashgill Series as defined in the UK, and the British graptolite biostratigraphical sequence cannot as yet be made, as the Welsh record is poor, and the Lower Ashgill of Scotland is rarely graptolitic (Rushton, 1990). The *linearis* Biozone currently spans the British Caradoc–Ashgill boundary, as the lower part of the biozone is believed to correlate with the uppermost Caradoc Onnian Substage (see Fig. 1; Ingham, 1966; Ingham & Wright, 1970). Rickards (2002) described several species referable to the *linearis* Biozone from strata as high as the upper Rawtheyan (shelly zone 6) in the typical Ashgill succession of the Cautley district, northern England (see below).

8.s. *Dicellograptus complanatus* Biozone

The *D. complanatus* Biozone is another graptolite assemblage biozone initally recognized in the Southern

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Uplands of Scotland (Dob's Linn) by Lapworth (1879–1880*a*), but rarely recognized since. The work of Williams (1987) on strata representing this interval from the Moffat and Girvan areas has resulted in a greater understanding of the *complanatus* Biozone assemblage, although the upper and lower limits of the biozone cannot be precisely delineated as the fossiliferous beds lie within strata barren of graptolites. The assemblage is of low diversity and consists mainly of species confined to this level, including the zone fossil and *Dicellograptus alector*, *Orthoretiolites*? *pulcherrimus*, *Dicellograptus minor* and *Glyptograptus occidentalis*. Longer-ranging species occur, such as *Normalograptus angustus* (= *Climacograptus miserabilis* of older literature) and *C. tubuliferus* (Fig. 10).

The *complanatus* Biozone has not been conclusively proven to occur in Wales (Rushton, 1990), and no diagnostic *complanatus* Biozone species have been recovered. There is no graptolitic evidence for the *complanatus* Biozone in northern England; indeed there is scarcely space to accommodate it: Rickards (2002, 2004) placed graptolites from shelly zone 6 (upper Rawtheyan) of the type Ashgill section, Backside Beck, Cautley, northern England (Ingham, 1966; Ingham & Wright, 1970) in the *linearis* Biozone and recorded graptolites from shelly zone 7 that could represent the *complanatus* or the *anceps* graptolite Biozone. In the Girvan area, however, beds that are correlated with shelly zone 7 have yielded *Paraorthograptus pacificus*, the index species of the upper subzone of the *anceps* Biozone (Floyd, Williams & Rushton, 1999). The suggestion by Elles (1925, p. 343) that the *complanatus* Biozone was 'a sub-zone of the *P. linearis* zone...', possibly representing special environmental conditions, might bear renewed examination.

8.t. *Dicellograptus anceps* Biozone

Lapworth introduced the *D. anceps* Biozone for the graptolite assemblages of the uppermost Hartfell strata in the Moffat area (Lapworth, 1878, p. 316). A taxonomic and stratigraphical review of this interval was undertaken by Williams (1982*b*), who was able to subdivide the biozone into two subzones: a lower *Dicellograptus complexus* Subzone and an upper *Paraorthograptus pacificus* Subzone. The base of the *D. complexus* interval is marked by the incoming of *D. complexus* and *D. anceps*. The subzone possesses a relatively small but distinct graptolite assemblage with *Dicellograptus minor* and *Normalograptus angustus* (= *N. miserabilis*) continuing from the previous biozone. New appearances include *Anticostia fastigata*, *Appendispinograptus supernus*, *Normalograptus normalis* and *Pleurograptus lui* (Fig. 10) while *Orthograptus abbreviatus* is abundant. The upper part of the *complexus* Subzone is characterized by the incoming of *Amplexograptus latus* and *Orthoretiograptus denticulatus*. The overlying *P. pacificus* Subzone has a slightly more diverse assemblage, consisting of the same taxa from the underlying *complexus* Subzone with the addition, at the base, of *P. pacificus*, *Nymphograptus velatus* and *Plegmatograptus lautus* (Fig. 10). Stone (1995) noted *anceps* Biozone assemblages in southwest Scotland and there are several records along-strike to the NE (McMillan, 2002).

Graptolites of probable *D. anceps* Biozone age have been recorded in Wales, although no potential for subdivision has been reported (Davies *et al.* 1997). Taxa present include *App. supernus*, *N. normalis* and *O. abbreviatus* (Fig. 7), while *D. anceps* itself has been recorded at Nant-y-môch (Jones, 1909; Cave & Hains, 1986). The *anceps* Biozone may be present in the north of England, but is not proved.

8.u. *Normalograptus extraordinarius* Biozone

This biozone, recognized in Scotland but not in England and Wales because of a lack of graptolitic (anoxic) strata, sees the incoming of *Normalograptus extraordinarius* and *Normalograptus*? *pseudovenustus* cf. *pseudovenustus*. At Dob's Linn this appears in Band E, formerly placed in the *anceps* Biozone (Williams, 1986), where it overlaps with the latest appearances of taxa such as *Dicellograptus anceps*, *D. ornatus*, *Appendispinograptus supernus* and *Paraorthograptus pacificus*. Above this, a very thin black bed, between the highest bed of the *anceps* Biozone and the base of the *persculptus* Biozone, was termed the *Climacograptus*? *extraordinarius* Band (Ingham, 1979; Williams, 1983, 1986, 1988); the graptolite assemblage in this is small, comprising only the zonal fossil with *Climacograptus* sp. indet. and *Glyptograptus*? sp. indet.

8.v. *Normalograptus persculptus* Biozone

This biozonal assemblage was originally subdivided from the lower part of the *acuminatus* Biozone by Jones (1909) at Pont Erwyd, central Wales. The interval has since been recognized throughout the UK (Davies, 1929; Toghill, 1968*a*; Rickards, 1970, 1976; Hutt, 1974–1975; Williams, 1988; Stone, 1995, p. 11; McMillan, 2002, p. 24), where it equates to the local Hirnantian. The *persculptus* Biozone is now accepted as the highest graptolite assemblage biozone of the Ordovician in the UK biostratigraphical scheme. Indeed, work on the synonymy of *N. persculptus* and '*Glyptograptus*' *bohemicus* led Štorch & Loydell (1996) to recommend that the base of the *persculptus* Biozone could be further extended to include an *extraordinarius* Subzone. The base of the interval is taken at the appearance of *N. persculptus*; other incoming species include *Glyptograptus avitus*, *Atavograptus ceryx*, *N. parvulus*, *N. medius* and '*Climacograptus*' *tuberculatus* (Figs 7, 10).

9. Silurian

9.a. *Akidograptus ascensus*–*Parakidograptus acuminatus* Biozone

This is the basal Silurian graptolite biozone of the British succession. Charles Lapworth (1878, p. 318)

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originally recognized it as such, and named it the *Diplograptus acuminatus* Zone, although Lapworth's (and Elles & Wood's 1901–1918) concept of this biozone embraced also the underlying *persculptus* Biozone. It is the lowest of six biozones that Lapworth based on the Birkhill Shale Formation succession at Dob's Linn in southern Scotland.

The base of the biozone is marked by the incoming of *Akidograptus ascensus* and *Parakidograptus acuminatus praematurus* and, 1.6 m higher, of *Parakidograptus acuminatus acuminatus* (Melchin, Cooper & Sadler, 2004). The assemblage as a whole is dominated by biserial graptolites (Fig. 11). Some of the commonest taxa (*Normalograptus normalis*, *N. medius*, *N. angustus*) range up from the *persculptus* Biozone, and these are joined by newcomers such as *Neodiplograptus modestus s.l.* and *Ne. diminutus*. Records of typically Ordovician taxa, most notably those of orthograptids of the *truncatus* group (Hutt, 1974–1975; Rickards, 1976) have not been substantiated by later work.

The only monograptid known is *Atavograptus ceryx*, reported as coming up from the *persculptus* Biozone and rarely recorded (in Scotland) from this interval (Hutt, 1974–1975; Rickards, 1976), though reported by Harper & Williams (2002) as appearing in the *ascensus* Biozone. *Normalograptus persculptus* has been recorded into the upper part of the biozone (Davies, 1929; Zalasiewicz & Tunnicliff, 1994; Davies *et al.* 1997; but see Loydell, 2007).

Informal subdivision of the *ascensus–acuminatus* Biozone has been made (Rickards, 1976; Zalasiewicz & Tunnicliff, 1994; Davies *et al.* 1997), and in some studies a formal distinction has been made (e.g. Rong *et al.* 2007). *A. ascensus* is generally more abundant in, and *P. acuminatus praematurus* is confined to, the lower part of the biozone, with *P. a. acuminatus* appearing higher and being more common in the upper part (Toghill, 1968*a*; Hutt, 1974–1975; see also Loydell, 2007). *Atavograptus ceryx* has been recorded only in the lower part (though presumably there must be some link between *A. ceryx* and later atavograptids which appear in the succeeding *atavus* Biozone). The middle of the biozone has been recognized by the presence of the distinctive short-ranged species *Normalograptus trifilis*. Although *Cystograptus vesiculosus* has also been recorded as low as the middle of the biozone (e.g. Rickards, 1976; McMillan, 2002, appendix 1, loc. 48), these records seem to represent *C. ancestralis* (Štorch, 1996), at least in part (M. Melchin, pers. comm.). The first record of *N. rectangularis* is in the upper part of the biozone.

9.b. *Atavograptus atavus* Biozone

Herbert Lapworth (1900) originally referred to this unit as the *Monograptus tenuis* 'Zone', from the Rhayader District of Central Wales. He recorded the assemblage of '*M. tenuis*', *Climacograptus scalaris normalis* and *C. rectangularis*. However, Lapworth's zonal species had been misidentified, and Jones (1909) renamed the zone the *Monograptus atavus* Zone.

From 19 taxa recorded in the *ascensus–acuminatus* Biozone, the number in the *atavus* Biozone increases to approximately 30 (Fig. 11). The essential feature of this biozone is the radiation of monograptid and dimorphograptid taxa. The incoming of *Atavograptus atavus* defines the base of the biozone, and *A. gracilis* and *Huttagraptus*? *praematurus* appear at more or less the same level. *Pribylograptus* cf. *incommodus* appears higher in the biozone. The dimorphograptids appear to form a useful temporal succession; thus *Rhaphidograptus extenuatus* and *Dimorphograptus elongatus* appear at or near the base of the biozone, while later newcomers include *Dimorphograptus confertus confertus*, *Dimorphograptus decussatus decussatus*, *Dimorphograptus longissimus* and *Dimorphograptus epilongissimus* (see Hutt, 1974–1975); the common and long-ranging *Rhaphidograptus toernquisti* originates near the top of the biozone. This suggests the possibility of informal subdivision, as noted by Rickards (1976), a possibility reinforced by the seeming restriction of *Huttagraptus*? *praematurus* to the lower part of the biozone (Zalasiewicz, Williams & Akhurst, 2003).

Biserial graptolites continue to be important. Most of the common normalograptids from the *ascensus–acuminatus* Biozone range up into the *atavus* Biozone and beyond; these include *N. normalis, N. angustus*, *N. medius* and *N. rectangularis*.

Toghill (1968*a*) described a *vesiculosus* Biozone assemblage from Dob's Linn which equates with that of the *atavus* Biozone recorded elsewhere (Rickards, 1976). Elles & Wood (1901–1918**)** recorded a zone of '*Mesograptus modestus* and *Orthograptus vesiculosus*' to account for the assemblage between the *acuminatus* and *cyphus* biozones, and many of the taxa that they recorded clearly indicate an *Atavograptus atavus* Biozone assemblage.

9.c. *Huttagraptus acinaces* Biozone

Jones's (1909) initial description of the *Monograptus rheidolensis* Biozone assemblage from the Pont Erwyd district, central Wales, was based on the appearance of *M. rheidolensis* (= *Huttagraptus acinaces*), *M.* (= *Pribylograptus) sandersoni*, *Dimorphograptus confertus swanstoni*, '*Climacograptus hughesi*' (= *Metaclimacograptus slalom*) and *Glyptograptus tamariscus*. Jones's (1909) original definition of the biozone adequately describes the core *acinaces* Biozone assemblage. Many of the earlier Rhuddanian normalograptids and dimorphograptids range up into the biozone (Figs 11, 12).

Although Toghill (1968*a*) recorded *H. acinaces* and *G. tamariscus s.l.* from his *vesiculosus* Biozone (= *atavus* Biozone), both Rickards (1970) and Hutt (1974–1975) placed these as key taxa defining the base of the *acinaces* Biozone, along with '*M. hughesi*' (= *M. slalom*). Rickards (1976) correlated the upper part

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of Toghill's *vesiculosus* Biozone with the *acinaces* Biozone, and suggested an origin for *acinaces* in the late *atavus* Biozone, though this has not been substantiated by further work (e.g. Davies *et al.* 1997).

The biozone as a whole is less easy to recognize than the *atavus* Biozone below or the *revolutus* Biozone above. Subdivision of this interval is not easy, but *Pribylograptus incommodus*, *Huttagraptus strachani*, *Pristiograptus fragilis pristinus* and *Pseudorthograptus mutabilis* (and questionably *Coronograptus gregarius*) seem to appear in the upper part of the biozone. In Central Wales (Zalasiewicz & Tunnicliff, 1994; Davies *et al.* 1997), the zone fossil and associated normalograptids represent the lower part of the biozone, and a more diverse assemblage occurs in the upper part, with the incoming of several species, including *Metaclimacograptus slalom* and *Glyptograptus tamariscus tamariscus*, that are commonly recorded at stratigraphically lower levels in other areas.

Toghill (1968*a*) did not recognize an *acinaces* assemblage in the Birkhill Shale at Dob's Linn; the *acinaces* Biozone appears to be represented by the lower part of his *cyphus* Biozone (see discussion in Hutt, 1974–1975; Rickards, 1976), as well as part of his underlying *vesiculosus* Biozone. The *acinaces* Biozone and the sub- and superjacent biozones are recognized in the Birkhill Shales southwest of Dob's Linn to the Rhins of Galloway (Stone, 1995; McMillan, 2002).

9.d. *Monograptus revolutus* Biozone

The biozone traditionally placed at this level is that of *Coronograptus cyphus* (e.g. Elles & Wood, 1901–1918; Rickards, 1970; Hutt, 1974–1975; Rickards, 1976). This latter assemblage, originally recognized by H. Lapworth (1900) from the Wye Valley sequence of Rhayader, consisted of *Coronograptus cyphus cyphus*, *Monograptus revolutus*?, *'Monograptus' attenuatus*, *Pribylograptus sandersoni*?, *Normalograptus rectangularis* and *N. normalis*.

As *C. c. cyphus* has been recorded in assemblages broadly referable to the underlying *acinaces* Biozone (e.g. Zalasiewicz & Tunnicliff, 1994; see also Rickards, 1976), its appearance cannot define the base of the *cyphus* Biozone without altering the concept of the overall assemblage and also attenuating the underlying *acinaces* Biozone.

M. revolutus and *C. gregarius gregarius* appear in the middle of Toghill's (1968*a*) *cyphus* Biozone at Dob's Linn. This, combined with an increase in numbers of *C. cyphus cyphus* at about the same level, suggested to Rickards (1976) and Hutt (1974–1975) that only the upper part of Toghill's biozone represents the *cyphus* Biozone recognized in other parts of Britain. Elles & Wood (1901–1918) included a *cyphus* Biozone in their zonal scheme, containing *C. c. cyphus* and *C. g. gregarius*. Both these forms have been recorded from the underlying *acinaces* Biozone (Rickards, 1976; Zalasiewicz & Tunnicliff, 1994), and the appearance of *Rhaphidograptus toernquisti*, *Glyptograptus tamariscus tamariscus*, *Huttagraptus acinaces* and *Pribylograptus incommodus* in their *cyphus* Biozone suggests that at least the lower part of it is equivalent to the *acinaces* Biozone.

Given this rather complicated state of affairs, we consider that the *revolutus/austerus* group of graptolites provides a more useful delineation, and their appearance at the base of the biozone is noted by most authors (H. Lapworth, 1900; Jones, 1909; Elles & Wood, 1901–1918; Rickards, 1970, 1976; Hutt, 1974–1975; Baker, 1981; Zalasiewicz & Tunnicliff, 1994; Davies *et al.* 1997). We therefore propose renaming the zone after *M. revolutus*, following Bjerreskov (1975).

Other newly appearing species are *Coronograptus gregarius gregarius* (although this species possibly originates in the upper *acinaces* Biozone), *Pribylograptus argutus argutus* and *Metaclimacograptus undulatus* (Fig. 12). Some taxa continue from the previous biozone, notably *Atavograptus atavus*, *Huttagraptus acinaces*, *Normalograptus medius*, *N. rectangularis*, *Rhaphidograptus toernquisti*, cf. *Pseudorthograptus mutabilis*, *Cystograptus vesiculosus* and *Metaclimacograptus slalom*, but they are mostly in decline and are not recorded from all areas.

A distinct middle to upper part to this biozone can sometimes be recognized, mainly based on the appearance of several glyptograptids, such as *G. tamariscus distans*, *G. t. varians*, *G. t. linearis* and *G. t. angulatus*. A probable forerunner to the triangulate monograptids, *M. difformis*, also appears midway through the biozone.

9.e. *Monograptus triangulatus* Biozone

The *Monograptus triangulatus* Biozone represents the lowest part of a broad interval formerly known as the *Monograptus gregarius* Zone (Lapworth, 1878; Elles & Wood, 1901–1918). The *gregarius* Biozone was still used in the Britain until the 1960s (Toghill, 1968*a*). Elles & Wood (1901–1918) divided the zone into three subzones. The lowest of these, the *fimbriatus* Subzone, equates with the current *triangulatus* Biozone. Toghill (1968*a*) described the distribution of graptolites in the Birkhill Shales at Dob's Linn, and horizons 33–31 of his *gregarius* Biozone contain a typical *triangulatus* zonal assemblage. Sudbury's (1958) detailed work on triangulate monograptids from the Rheidol Gorge in central Wales contributed greatly to the concept of the existing *triangulatus* Biozone. Despite using the *gregarius* Biozone herself, she also acknowledged a possible three-fold subdivision based on her reassessment of the morphologies and ranges of the triangulate monograptids as a stratigraphically important group. This enabled Rickards (1976) to outline the distinctive assemblages comprising the *triangulatus*, *magnus* and *leptotheca* biozones.

The base of the *triangulatus* Biozone is marked by the appearance of several triangulate monograptids including *Monograptus triangulatus triangulatus*, *M. t. separatus* and *M. t. predecipiens*. Other new

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appearances include *Pristiograptus concinnus*. Diversity is high at this stratigraphical level, with many taxa continuing from the previous biozone in addition to the new appearances. Some 60 taxa are currently recognized (Figs 12, 13).

Locally, biostratigraphically barren strata are found at the base of the biozone. For example, in the Lake District (Hutt, 1974–1975), central Wales (Zalasiewicz & Tunnicliff, 1994; Davies *et al.* 1997) and at Llanystumdwy, North Wales (Baker, 1981), taxa suggesting the middle of the biozone are the first to appear appear above the *cyphus* Biozone as recognized by those authors (and in this account referred to the *revolutus* Biozone).

Subdivision of the *triangulatus* Biozone is possible: the middle to upper parts of the biozone are marked by the incoming of distinctive taxa such as *M. triangulatus major, M. t. fimbriatus*, *Petalolithus minor*, *Rastrites longispinus, Glyptograptus tamariscus acutus*, *Campograptus communis communis* and *Ca. c. rostratus*.

9.f. *Neodiplograptus magnus* Biozone

Jones (1909) originally recognized a '*magnus* band' from the Rheidol Gorge section. Later studies revealed a *magnus* Biozone assemblage from the Machynlleth area, Wales (Jones & Pugh, 1916). The biozone is defined by the appearance of *Neodiplograptus magnus*. Other new appearances include *Pseudoglyptograptus vas* (Hutt, 1974–1975), *P. barriei*, *Monograptus chrysalis* and *Neodiplograptus peggyae*. *Monograptus triangulatus fimbriatus* (that may be a junior synonym of *Monograptus pectinatus* Richter: Bjerreskov, 1975), *M. t. major* and *M. pseudoplanus* are common associates, while *M. t. triangulatus* may persist into the lower part of the biozone (Baker, 1981) (Fig. 13). This biozone has also been recognized in Scotland (Toghill, 1968*a*).

Many taxa continue from previous biozones. The upper part of the *magnus* Biozone is poorly represented in Britain, commonly being represented by barren (bioturbated) strata (e.g. Baker, 1981; Davies *et al.* 1997).

9.g. *Pribylograptus leptotheca* Biozone

Marr & Nicholson (1888) first identified this biozone in the Skelgill Beds of northern England, where it was named the *Monograptus argenteus* Zone. Elles & Wood (1901–1918) termed it the *M. argenteus* Subzone of the *gregarius* Zone, and recorded the incoming of *Pribylograptus leptotheca*, *Monograptus argenteus*, *Pristiograptus regularis* and *P. jaculum* at this level (although their overall list of species appearances contains a mixture of forms recorded from both higher and lower levels by other authors). Later, Jones & Pugh (1916) recorded a similar assemblage from the same stratigraphical interval at Machynlleth in Wales, and they referred to it as the *leptotheca* Biozone; this has been more widely adopted as the name for the biozone.

Both *Monograptus argenteus* and *Pribylograptus leptotheca* have been recorded in Scotland, northern England and Wales (e.g. Hutt, 1974–1975; Baker, 1981; Davies *et al.* 1997), and although there are variations in relative abundance, the presence of either may characterize the base of this biozone (Fig. 13). Other newly appearing taxa recorded include *Pristiograptus regularis* (see Toghill, 1968*a*), and *Pristiograptus jaculum*, *Glyptograptus serratus* and *Monograptus cerastus*. Rickards (1976) suggested that *Pr. leptotheca* originated in the *magnus* Biozone, although this has not been substantiated by further work (e.g. Davies *et al.* 1997). Hutt (1974–1975) and Zalasiewicz (1992*b*) identified the incoming of the monoclimacid thecal morphology (e.g. *M. imago*) at this level in Britain.

A major feature of the *leptotheca* Biozone is the marked increase in monograptids with hooked thecae, which include *Campograptus millepeda* and *Ca. lobiferus*. Several species continue from the previous biozone, and *Coronograptus gregarius gregarius* was singled out by Hutt (1974–1975) as being very common.

In many regions, for example, central Wales (Zalasiewicz, 1990; Davies *et al.* 1997), *leptotheca* Biozone assemblages occur in thin fossiliferous levels within a generally barren sequence. This makes subdivision of this interval difficult in Britain, although more continuously fossiliferous sequences are found outside Britain (e.g. Štorch, 1998).

9.h. *Lituigraptus convolutus* Biozone

This biozone was initially described at Skelgill by Marr & Nicholson (1888). At Dob's Linn, this biozone represents Lapworth's (1878) original *clingani* band (lower part of *convolutus* Biozone) and *cometa* Zone (upper part of *convolutus* Biozone).

The broad features of the biozone have been agreed upon by subsequent authors (Toghill, 1968*a*; Hutt, 1974–1975; Rickards, 1976; Baker, 1981). A number of taxa appear at or around the base of the biozone, including *L. convolutus* itself, *Campograptus clingani*, *Monograptus limatulus*, *Torquigraptus? decipiens*, *Cephalograptus cometa cometa*, *C. tubulariformis*, *Glyptograptus incertus s.l.* and *Torquigraptus urceolinus* (which Štorch, 1998, suggested might be a junior synonym of *M. decipiens*) (Figs 13, 14). Other distinctive and useful forms characterizing this biozone include *Rastrites spina* of Rickards, 1970, *Paradiversograptus capillaris, Monoclimacis crenularis* and *Rastrites peregrinus*. *Normalograptus scalaris, Metaclimacograptus hughesi, Pristiograptus jaculum* and *Campograptus lobiferus* have been commonly reported, though they extend beyond the biozone. A probable first occurrence of *Streptograptus* has been noted at this level (Zalasiewicz, 1996).

Subdivision of this biozone seems achievable, especially given the faunal diversity at this level, but is hampered by the dominance of bioturbated, non-graptolitic strata, particularly at low stratigraphical levels in England and Wales. Several workers (Toghill, 1968*a*; Hutt, 1974–1975; Rickards, 1976; Davies *et al.* 1997) record the incoming of *Cephalograptus cometa extrema* as a reliable indicator of the upper part of the *convolutus* Biozone, and the usefulness of the cephalograptid lineage was further emphasized by Štorch (1998) in his thorough review of the *convolutus* Biozone in Bohemia. Zalasiewicz (1996; see also Davies *et al.* 1997) identified a possible lower subdivision of the *convolutus* Biozone that contains a narrow form of *L. convolutus* (= *Lituigraptus richteri* of Štorch, 1998). At least part of this division might now, however, be considered to represent the upper part of the *leptotheca* Biozone (cf. Štorch, 1998).

9.i. *Stimulograptus sedgwickii* Biozone

This biozonal assemblage was originally identified from the upper Birkhill Shale Formation of Dob's Linn by Lapworth (1878) and he named it the *M. spinigerus* Biozone (it is now named after the senior synonym *St. sedgwickii*). He recorded a diverse fauna, and distinguished an upper and lower subdivision within the biozone.

The base is defined by the appearance of *Stimulograptus sedgwickii*, which appears together with *Neolagarograptus tenuis* (Hutt, 1974–1975). Suggestions of a slightly earlier origin for *St. sedgwickii* (Rickards, 1976) have not been substantiated by further work (Davies *et al.* 1997). Other incoming taxa include *Glyptograptus sinuatus crateriformis*, *Pribylograptus argutus sequens*, *Glyptograptus packhami* and *Parapetalolithus kurcki* (Rickards, 1970, 1976; Hutt, 1974–1975), together with *Torquigraptus linterni* and questionably *Rastrites gracilis* (Williams *et al.* 2003*b*). Hutt (1974–1975) also referred to the characteristic abundance of *Glyptograptus incertus* at the base of the biozone (see Loydell, 1992–1993*a* for discussion), while *Oktavites contortus, Streptograptus ansulosus, Torquigraptus involutus* and *Metaclimacograptus undulatus* are common in, though not confined to, this biozone (Fig. 14).

L. tenuis seems to be restricted to the lower part of the biozone (Rickards, 1976; Davies *et al.*. 1997) and thus appears to form a useful basis for subdivision (cf. Štorch, 2001; Štorch & Massa, 2006; Melchin, 2007). At Dob's Linn this species shows marked stratigraphical variations in abundance within its range (Pannell, Clarkson & Zalasiewicz, 2006).

9.j. *Stimulograptus halli* Biozone

Jones & Pugh (1916) first recognized the *Stimulograptus halli* Biozone in the Machynlleth–Llyfnant area of central Wales, as an upper part of the *sedgwickii* Biozone. Rickards (1976) considered that the *halli* and *sedgwickii* Biozone assemblages were not sufficiently distinctive to be separately recognizable and, owing to difficulties in distinguishing between *Stimulograptus sedgwickii* and *S. halli*, recommended that the *halli* Biozone be removed from the UK biostratigraphical scheme. Subsequently, however, Loydell (1991*a*) was able to differentiate *halli* Biozone assemblages in the Cwmsymlog Formation of western mid-Wales, and reinstated the biozone. Loydell (1992–1993*a*) recorded that species defining the base of the biozone are *Stimulograptus halli*, *Pristiograptus pristinus* and *Rastrites linnaei* (Fig. 14). Other incoming species are *Rastrites schaueri*, *Paradiversograptus capillaris sensu* Loydell, *'Monograptus' admirabilis* and *Parapetalolithus praecedens*. A number of relatively long-ranging species also occur, including *'Monograptus' capis*, *Torquigraptus involutus*, *Stimulograptus sedgwickii* and *Oktavites contortus*. Loydell (1991*b*) recognized a *halli* Biozone assemblage similar to that found in Wales in the upper Birkhill Shales in Dob's Linn, southern Scotland.

9.k. *Spirograptus guerichi* Biozone

This biozone was formerly a part of the *turriculatus* Biozone, as recorded by Elles & Wood (1901–1918) and others. Formerly, the lower part of the *turriculatus* Biozone was separated off as the *Rastrites maximus* Subzone; this subzone was first postulated at Dob's Linn (Lapworth, 1878), but Loydell (1991*b*) found that *R. maximus* does not appear to occur there, and the Upper Birkhill Shales at Dob's Linn are now assigned to the *halli* Biozone (see above). Rickards (1976) remarked that the *maximus* Subzone did not occur at the type locality of the *turriculatus* Biozone at Browgill, in the English Lake District (Marr & Nicholson, 1888), but he (Rickards, 1970, 1976) identified the *maximus* Subzone in the Howgill Fells and considered it to be an important part of the *turriculatus* Biozone, although the subzone itself was defined only on the presence of *R. maximus* itself. Toghill (1968*a*) described a *maximus* Subzone assemblage from the upper Birkhill Shales, and Hutt (1974–1975) recorded one locality containing *R. maximus* in the Lake District.

Loydell (1991*a*,*b*) did not use the *maximus* Subzone for the Anglo-Welsh sequence (although he did record the species), and he divided the *turriculatus* Biozone into six subzones based on his work in western mid-Wales (Fig. 2). This biostratigraphical subdivision was enhanced when the former *turriculatus* Biozone was divided into two, creating a lower *Spirograptus guerichi* Biozone, followed by an upper *Spirograptus turriculatus* Biozone (Loydell, 1992–1993*a*; Loydell, Štorch & Melchin, 1993). His six subzones remained in place, with the *guerichi–turriculatus* biozonal boundary occurring in the middle of the *utilis* Subzone. Loydell, Štorch & Melchin (1993), having observed that *Spirograptus turriculatus* itself does not appear until the middle of the *turriculatus* Biozone as formerly understood, defined the *guerichi* Biozone as 'the interval from the first appearance of *Spirograptus guerichi* to that of *Spirograptus turriculatus*'. Davies *et al.* (1997) employed the new biozones and their subdivisions in the Llanilar–Rhayader district, but noted that not all of

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Loydell's subzones could be consistently recognized. McMillan (2002) likewise adopted subdivision into the *guerichi* and *turriculatus* biozones. Loydell's (1992–1993*a*) *guerichi* and *turriculatus* biozones and their component subzones are defined by the appearance or relative abundance of their index species.

9.k.1. Paradiversograptus runcinatus *Subzone*

The base is delineated by the appearance of *Paradiversograptus runcinatus* and *Spirograptus guerichi*, with the eponym being abundant (Loydell, 1991*a*, 1992–1993*a*). The numbers of *P. runcinatus* have been enhanced by current sorting, but this does not reduce the usefulness of the subzone, as it can be recognized in Scandinavia (Loydell, 1992–1993*a*). Davies *et al.* (1997) did not recognize the subzone in the Llanilar–Rhayader district, and assigned some localities to a *runcinatus* to *renaudi* interval. *'Monograptus' gemmatus*, *Pristiograptus renaudi*, *Streptograptus plumosus* and *Str. pseudoruncinatus* appear in this subzone (Fig. 15).

9.k.2. 'Monograptus' gemmatus *Subzone*

Loydell (1991a, 1992–1993a) described a diverse, distinctive assemblage including *Streptograptus pseudoruncinatus*, *Spirograptus guerichi*, *Rastrites fugax*, *Glyptograptus fastigatus*, *G. tamariscus tamariscus* and '*Monograptus*' *gemmatus*. In addition to these, several species appear at the base of the subzone and are confined to it, for example, the parapetalolithids, *Parapetalolithus elongatus*, *P. globosus* and *P. regius*, with *Glyptograptus auritus* (Fig. 15). This subzone has been recognized by Davies *et al.* (1997).

9.k.3. Pristiograptus renaudi *Subzone*

This subzone is characterized by abundant *Pristiograptus renaudi* and *Streptograptus strachani* (Loydell, 1991*a*, 1992–1993*a*), although neither of these taxa originate at the base of this subzone. However, Loydell recorded that *Torquigraptus planus* and *T. cavei* first appear here, and they are useful indicators of the *renaudi* to *utilis* subzone interval. Other newly appearing species include *Monograptus marri* and *Parapetalolithus hispanicus* (Fig. 15). Both Loydell (1991*a*) and Davies *et al.* (1997) noted that the transition from the *gemmatus* Subzone into this subzone has not yet been recognized in a continuous section, and only one faunal assemblage from the Llanilar–Rhayader district has been assigned to this interval (Davies *et al.* 1997).

9.l. *Spirograptus turriculatus* Biozone

In its current, more biostratigraphically restricted usage, the *turriculatus* Biozone is defined as lying between 'the first appearance of *Spirograptus turriculatus* to that of '*Monograptus*' *crispus*, or other species indicative of the *crispus* Biozone' (Loydell, 1992–1993*a*). *Spirograptus turriculatus* is taxonomically distinct from *Spirograptus guerichi* (Loydell, Štorch & Melchin, 1993), which characterizes the underlying biozone. As a result, older definitions for the base of the *turriculatus* biozone (Rickards, 1970, 1976; Hutt, 1974–1975) are no longer applicable, since these now refer to the base of the *guerichi* Biozone. Loydell's (1992–1993*a*) definition of the base of the *turriculatus* Biozone placed it in the middle of the *Stimulograptus utilis* Subzone (Fig. 2). One means of avoiding the situation of placing a zonal boundary *within* a subzone might be to place the base of the *turriculatus* Biozone at the base of a slightly extended *johnsonae* Biozone, to be defined by the first appearance, rather than acme, of *johnsonae*, which coincides with the first appearance of *Sp. turriculatus* (M. Melchin, pers. comm.); the current definition of the *johnsonae* Subzone, however, has been found to work well in practice (e.g. Davies *et al.* 1997).

9.l.1. Stimulograptus utilis *Subzone*

Loydell (1991*a*) erected this subzone as the fourth subdivision of the old *turriculatus* Biozone. Subsequently, Loydell (1992–1993*a*) divided the *utilis* Subzone into two parts, marking the boundary between the *guerichi* and *turriculatus* biozones. This was based on the incoming of *Parapetalolithus tenuis*, *Spirograptus turriculatus* and *Streptograptus johnsonae*, and an abundance of *Monograptus marri* and *Streptograptus plumosus*, in the middle of the subzone (Fig. 15). Several species seem to disappear mid-subzone, including *Parapetalolithus kurcki*, *Rastrites linnaei*, *Paradiversograptus runcinatus*, *Parapetalolithus conicus (= Pa. hispanicus)* and *Pseudostreptograptus williamsi*. Davies *et al.* (1997) recorded the *utilis* Subzone widely in the Llanilar–Rhayader district.

9.l.2. Streptograptus johnsonae *Subzone*

This subzone is defined on the abundance of *Streptograptus johnsonae* and common *Monograptus bjerreskovae* and *M. marri* (Loydell, 1991*a*, 1992–1993*a*), and has been recognized in the Llanilar–Rhayader area (Davies *et al.* 1997). Appearances at the base of the subzone are rare, including only *Parapetalolithus schaueri* and *Pristiograptus schucherti* (Loydell, 1992–1993*a*). As the range charts demonstrate (Fig. 15), a significant proportion of the low-diversity *johnsonae* Subzone assemblage is composed of relatively long-ranging species.

9.l.3. Torquigraptus proteus *Subzone*

Torquigraptus proteus appears at the base of this subzone, and its presence and abundance characterizes this interval (Loydell, 1991*a*, 1992–1993*a*). As other authors record (Zalasiewicz, 1994; Davies *et al.* 1997), appearances also include *Monograptus rickardsi* (which may be a junior synonym of *M. priodon*: Loydell, 1992–1993*a*) and *Monoclimacis*? *galaensis*, as well as *Pristiograptus huttae* (see Loydell, 1992–1993*a*) and *Streptograptus pseudobecki* (Zalasiewicz, 1994; Loydell, 1990). The bulk of this relatively small assemblage (Figs 15, 16) contains taxa from underlying biozones and subzones.

9.l.4. Torquigraptus carnicus *Subzone*

Zalasiewicz (1994) and Davies *et al.* (1997) recognized a further subzone in central Wales, representing the highest part of the *turriculatus* Biozone. The base of this subzone is characterized by the appearance of *T. carnicus*, while *Streptograptus whitei*, *S. exiguus* and possibly *Stimulograptus clintonensis* also appear in this interval, as does *Monograptus* aff. *crispus*, a narrow precursor to the eponym of the succeeding biozone (Fig. 16). *Streptograptus storchi* is noted as abundant in the *carnicus* Subzone (Zalasiewicz, 1994; Davies *et al.* 1997).

9.m. *'Monograptus' crispus* Biozone

Initially described from the Lake District (Marr & Nicholson, 1888), this biozone is defined by the incoming of *'Monograptus' crispus* (assigned to *Streptograptus* by Loydell & Maletz, 2004), while the distinctive and useful *Cochlograptus veles* (= *M. discus* of some authors) appears at about the same level (Fig. 16). In central Wales, the boundary between the *crispus* Biozone and the underlying *turriculatus* Biozone was not easily resolved (Zalasiewicz, 1994; Davies *et al.* 1997), as both these characteristic species are rare at the base of the biozone. Loydell (1991*a*, 1992–1993*a*) noted also the incoming of *Streptograptus*? sp. nov. of Howe (M. P. A. Howe, unpub. Ph.D. thesis, Univ. Cambridge, 1982) at or near the base of the biozone. Zalasiewicz (1994; see also Davies *et al.* 1997) divided the *crispus* Biozone into three subzones based on sections in central Wales. As *S. crispus* does not range into the highest of these either in Britain or elsewhere, the *sartorius* Subzone is here elevated to biozonal status.

9.m.1. Monoclimacis? galaensis *Subzone*

Zalasiewicz (1994) and Davies *et al.* (1997) recognized this interval as a partial-range subzone, characterized by the overlap of *Monoclimacis*? *galaensis* and *Torquigraptus carnicus* with *'Monograptus' crispus* and *Cochlograptus veles* (= *Monograptus discus*). *Stimulograptus clintonensis* and *Streptograptus exiguus* are also common at this level (Fig. 16).

9.m.2. Streptograptus loydelli *Subzone*

Zalasiewicz (1994) described this subzone as a partial-range subzone, defined by the overlap of *'Monograptus' crispus* and *Streptograptus loydelli*. He termed it the *'Monograptus' crispus* Subzone, the name being changed here to reflect the taxon whose incoming defines its base. *'Monograptus' crispus* is abundant in this subzone, disappearing at its top (Fig. 16). This subzone is well exposed in the Cwm Ystwyth section in central Wales (Davies *et al.* 1997).

9.n. *Streptograptus sartorius* Biozone

The base of this biozone is represented by the incoming of *Streptograptus sartorius*, together with *Torquigraptus pragensis pragensis* and *Torquigraptus pragensis ruzickai*?, and the disappearance of *'Monograptus' crispus* (Zalasiewicz, 1994) (Fig. 16). Davies *et al.* (1997) also recorded this biozone at Cwm Ystwyth and described the interval as akin to an interregnum, with low faunal diversity.

9.o. *Monoclimacis griestoniensis* Biozone

First recognized by Wood (1906) in the Talerddig Grits of Trannon, Wales, this biozone has an assemblage characterized by an incoming of monoclimacids. Its base is defined by the incoming of the zone fossil, *Monoclimacis griestoniensis*. It has been more usually recognized in central Wales by the incoming of *Monoclimacis directa* (= *Monograptus* cf. *griestoniensis* of Elles & Wood: see Zalasiewicz, Loydell & Štorch, 1995), which there seemed to appear at about the same level (Zalasiewicz, 1994; Davies *et al.* 1997); Wilson's (D. R. Wilson, unpub. Ph.D. thesis, Univ. Birmingham, 1954) work suggests that it might appear at a slightly lower level in the Howgill Fells.

In central Wales the *griestoniensis* Biozone can be informally subdivided. A lower interval is characterized by abundant *Monoclimacis directa*, co-occurring with *Monograptus pseudocommunis*, *Streptograptus* aff. *loydelli* of Zalasiewicz, 1994 and *Torquigraptus pergracilis* of Zalasiewicz, 1994 (Fig. 16). *Monoclimacis griestoniensis s.s.* dominates the upper part of the biozone (Zalasiewicz, 1990, 1994). *Monograptus priodon, C. veles* (= *M. discus*) and *Pristiograptus nudus* range through the biozone.

9.p. *Monoclimacis crenulata* Biozone

Initially referred to as the *Monograptus crenulatus* Biozone by Wood (1906) in the Trannon area, the biozone was originally defined on the appearance of the zone fossil (= *Monoclimacis crenulata*), associated with an undistinctive assemblage, generally of low diversity. More recent work in central Wales has suggested that the incoming of *Monoclimacis vomerina* may be a more useful indicator of the base of this biozone (Zalasiewicz, 1994; Davies *et al.* 1997). The assemblage includes taxa from underlying biozones including *C. veles* (= *M. discus*) and *M. priodon* (Fig. 16). The *Monoclimacis crenulata* Biozone formerly included all British strata from the top of the *Monoclimacis griestoniensis* Biozone to the base of

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the Wenlock Series. Rickards (1976) noted that this biozone was rarely found abroad, where a more refined biostratigraphical subdivision could be recognized (Bouček, 1953; Bjerreskov, 1975). Since then, work by Loydell & Cave (1993, 1996) has led to the recognition of more biozones within the upper Telychian of Wales, and the current *crenulata* Biozone now represents only the lowest part the original biozone.

9.q. *Oktavites spiralis* Biozone

Graptolite assemblages representing the *Oktavites spiralis* Biozone were recognized relatively recently in the UK by Loydell & Cave (1993, 1996). Initial biostratigraphical work at Buttington Brick Pit, central Wales (Loydell & Cave, 1993) and subsequent studies in eastern mid-Wales (Loydell & Cave, 1996) resulted in division of the long-established *crenulata* Biozone, and allowed direct comparison with the graptolite biozonation of Bohemia (Bouček, 1953) and Scandinavia (Bjerreskov, 1975). The *Oktavites spiralis* Biozone has a distinctive faunal assemblage, and Loydell & Cave (1993, 1996) recorded the introduction of several taxa through the biozone. These include the zone fossil (previously commonly given a longer range in the UK (e.g. Rickards, 1976), prior to closer scrutiny of the Telychian spiraliform monograptids, many of which are superficially similar) and *Monoclimacis hemmanni*, *Streptograptus anguinus*, *Monoclimacis geinitzi*, *Streptograptus nodifer* (referred to *Awarograptus* by Zalasiewicz & Howe, 2003), *Barrandeograptus bornholmensis* and *Stimulograptus vesiculosus* (Figs 16, 17).

9.r. *Cyrtograptus lapworthi* Biozone

The *Cyrtograptus lapworthi* Biozone was first recorded in Britain by Loydell & Cave (1996) from the Banwy River section, central Wales. It equates roughly with the upper part of the *spiralis* Biozone and the *Stomatograptus grandis* Biozone of the Czech Republic. Loydell & Cave (1996) described a relatively diverse and characteristic graptolite assemblage. Several new species appear at the base of the biozone, including the zone fossil (Fig. 17). Some are confined to its lower and middle parts, suggesting a potential for subdivision; these include *Monoclimacis sublinnarssoni*, *Streptograptus speciosus*, *Streptograptus wimani* and *Pristiograptus largus*. A number of taxa continue from the previous biozone, and a few appear in the middle of the biozone, notably *Monoclimacis basilica* and *Barrandeograptus pulchellus*. *C. lapworthi* itself marks the first appearance of *Cyrtograptus* in Britain. In the Llanilar–Rhayader district of central Wales, Davies *et al.* (1997) assigned strata overlying the *spiralis* Biozone to a '*spiralis/centrifugus* interregnum', the assemblage being dominated by long-ranging graptolites such as the members of the *Monoclimacis vomerina* and *Monograptus priodon* groups and *Retiolites geinitzianus*.

9.s. *Cyrtograptus insectus* Biozone

The biostratigraphical succession outlined by Loydell & Cave (1996) in the Banwy River section included the first record of the *Cyrtograptus insectus* Biozone in Britain. The biozone contains a number of taxa whose ranges are limited to the lower–middle or middle–upper parts of this interval, indicating the possibility of further biostratigraphical subdivision (Fig. 17). This biozone is notable for the introduction of *Mediograptus*: *Mediograptus flittoni* appears at the base, together with *Monoclimacis shottoni*, *C. insectus* and *Cyrtograptus* sp. of Loydell & Cave; *Monoclimacis linnarssoni* disappears in the lower part of the biozone. Species defining the middle and upper parts of the biozone in the Banwy section include *Monograptus pseudocultellus*, *Mediograptus morleyae* and *Mediograptus* sp. aff. *inconspicuus* of Loydell & Cave.

9.t. *Cyrtograptus centrifugus* Biozone

The *Cyrtograptus centrifugus* Biozone was first identified in Britain in the Howgill Fells, northern England (Rickards, 1967). Rickards (1967, 1976) described an assemblage containing *C. centrifugus*, monoclimacids and monograptids. The base of this biozone has long been equated with the base of the Wenlock Series in the UK, although more recent micropalaeontological evaluation at Hughley Brook suggests that this level actually equates to a horizon within the upper *centrifugus* or succeeding *murchisoni* graptolite Biozone (Mullins & Aldridge, 2004). The incoming of the zone fossil defines the biozonal base, although several other species also appear for the first time (Rickards, 1976; Loydell & Cave, 1996; Davies *et al.* 1997; Zalasiewicz & Williams, 1999). These include *Mediograptus danbyi*, *Med. cautleyensis*, *Monograptus simulatus* and *Monoclimacis*? sp. 1 (*sensu* Zalasiewicz & Williams, 1999) (Fig. 17). *Mediograptus inconspicuus* and questionably *Mediograptus flexuosus* appear in the middle to upper part of the biozone. These are accompanied by relatively long-lived taxa ranging from previous zones (Loydell & Cave, 1996; Zalasiewicz & Williams, 1999; Davies *et al.* 1997).

9.u. *Cyrtograptus murchisoni* Biozone

In many areas of Britain, the *murchisoni* Biozone assemblage is often indistinguishable from the underlying *centrifugus* Biozone where the eponym is absent (Rickards, 1967, 1976; Zalasiewicz & Williams, 1999; Davies *et al.* 1997). The biozone was initially recognized by Lapworth (1879–1880) from Builth Wells, and contains the index species together with *Monograptus priodon* and *Monoclimacis vomerina*. In

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central Wales, Loydell & Cave (1996) and Zalasiewicz & Williams (1999) have recognized taxa such as *Monoclimacis vikensis*?, *Mcl. adunca*, *Pristiograptus praedubius*, *Monograptus radotinensis radotinensis*, *Cyrtograptus bohemicus* and *Pseudoplegmatograptus*? *wenlockianus*? (Fig. 17). Loydell & Cave (1996) noted that species diversity drops markedly in the upper part of the biozone, indicating a potential for future subdivision.

9.v. *Monograptus firmus* Biozone

The rapid decline in diversity in the upper part of the *murchisoni* Biozone, coupled with the incoming of *M. firmus* in the Banwy River section, central Wales, resulted in Loydell & Cave (1996) establishing the *firmus* Biozone in Britain for the first time. Approximately seven species, most of which have long biostratigraphical ranges, are found at this level; these include *Monograptus priodon*, *Monoclimacis vomerina* and possibly *M. basilica* (Fig. 17). Loydell & Cave (1996) identified the long-ranging *Pristiograptus dubius* as appearing in the biozone. Zalasiewicz & Williams (1999) reported the appearance of *M. firmus s.l.* from strata which they assigned to the upper part of the *murchisoni* Biozone at Builth Wells in Wales, but they did not recognize a discrete *firmus* Biozone.

9.w. *Monograptus riccartonensis* Biozone

The *riccartonensis* Biozone was first recognized in the UK by Elles (1900) at Builth Wells, south-central Wales. It has since been recognized in many areas of Britain, and notable studies include Rickards's (1967, 1969) work in northern England, that of Davies *et al.* (1997) in the Llanilar–Rhayader district of central Wales, and Zalasiewicz & Williams's (1999) re-examination of the sequence at Builth Wells. The base of the biozone is generally taken at the incoming of *Monograptus riccartonensis*, the stratigraphical range of which defines the biozone (Fig. 17); this taxon dominates most assemblages.

Several authors have noted stratigraphical variations in specific composition and diversity in this generally impoverished interval, and this might form the basis of future two- or three-fold subdivision (Rickards, 1967, 1976; White *et al.* 1992; Zalasiewicz & Williams, 1999). The middle to upper parts of this biozone are generally more diverse, and include *Pristiograptus dubius s.l.*, *Monograptus firmus s.l., M. radotinensis inclinatus* and the first appearance of *Monograptus antennularius* and possibly of *Monoclimacis flumendosae*.

9.x. Note on middle Wenlock graptolite biostratigraphy

The interval from the upper part of the *riccartonensis* Biozone through to the *lundgreni* Biozone is problematical in the British Isles, and a number of biozonal schemes have been proposed. This account (Fig. 2) uses the most recent of these (Zalasiewicz & Williams, 1999), which is based upon a re-examination of the historically important (Elles, 1900; Jones, 1947) Builth district of south-central Wales. The problems, and suggested correlations with earlier schemes and those used elsewhere in the world, are outlined in that paper. The most important difference from widely used earlier biozonations (e.g. Rickards, 1976) is that separate *flexilis* and *ellesae* biozones are not recognized, because *Monograptus flexilis* appears earlier than, and then largely co-exists with, *Cyrtograptus rigidus* at Builth, while *C. ellesae* appears later than *C. lundgreni* (Zalasiewicz & Williams, 1999; Williams & Zalasiewicz, 2004). The biostratigraphical problems in part reflect imperfect taxonomy and in part originate from, and continue to be exacerbated by, biofacies control. Most UK middle Wenlock sequences (including Builth) are dominated by a few morphologically variable and long-ranging monograptid, monoclimacid and pristiograptid taxa, while the biostratigraphically useful cyrtograptids are rare in comparison to successions such as those of Bohemia (e.g. Štorch, 1994).

9.y. *Pristiograptus dubius* Biozone

The *dubius* Biozone was originally defined in the Czech Republic (Bouček, 1960; also Štorch, 1994), and Zalasiewicz & Williams (1999) recognized the biozone in the UK for the first time at Builth Wells. This interval is an interregnum, with recognition largely reliant on identification of the biozones directly above and below. The biozone is typified by variable, long-lived taxa of the *Pristiograptus dubius* group, as well as by *Monograptus priodon/flemingii* and *Monoclimacis flumendosae* (Figs 17, 18). Rare first occurrences recorded at Builth include *Mediograptus* ex. gr. *retroflexus* and *M. flexilis*, the latter first being found midway up the biozone. The *dubius* Biozone is approximately equivalent to the *antennularius* Biozone of Rickards (1965, 1967, 1969) and White *et al.* (1992).

9.z. *Cyrtograptus rigidus* Biozone

The *rigidus* Biozone was originally defined at Builth by Elles (1900) as her *symmetricus* Zone. Her species *C. symmetricus* was, however, a misidentification of *C. rigidus*, and the name of the biozone was subsequently changed. The base of the *rigidus* Biozone is defined by the appearance of the index fossil, which is limited to the biozone. The *rigidus* Biozone, as defined herein, extends to the base of the *lundgreni* Biozone and therefore equates with Elles's (1900) *linnarssoni* Zone (= *flexilis* Biozone: Rickards, 1976) as well as her *symmetricus* (= *rigidus*) Zone (see Zalasiewicz & Williams, 1999).

Other elements of the assemblage include taxa ranging up from the *dubius* Biozone such as

Monograptus flexilis, M. priodon/flemingii, Mediograptus ex. gr. *retroflexus*, *Monoclimacis flumendosae* and graptolites of the *Pristiograptus dubius* group including the distinctively broad *P. pseudolatus* (Fig. 18).

At Builth (Zalasiewicz & Williams, 1999), this unit could not be subdivided, because (1) *Monograptus flexilis*, one index species of the formerly recognized *flexilis/linnarssoni* Biozone, in fact appears below *C. rigidus*, and then has a range largely that overlaps with it; (2) the other index species, *Cyrtograptus linnarssoni*, seems to be based on an unusually narrow and/or deformed example of *C. rigidus s.l.*; this taxon has accordingly been widely misidentified, most attributed specimens being referable to *C. rigidus*; and (3) temporal subspecies of *C. rigidus* could not be distinguished at Builth. *C. rigidus cautleyensis* Rickards, 1967 has been interpreted as a late, slender subspecies indicative of the *flexilis/linnarssoni* Biozone (e.g. Rickards, 1976). The type material of this taxon from the Howgill Fells does seem to be a recognizable slender morphotype (Williams & Zalasiewicz, 2004), but it could not be recognized as distinct at Builth; on present evidence it may be a true geographical subspecies restricted to northern England. Finally, the remainder of the assemblage, consisting of abundant pristiograptid, monograptid and monoclimacid graptolites that belong to a few variable, long-ranging taxa, are of limited biostratigraphical use.

9.aa. *Cyrtograptus lundgreni* Biozone

This biozone was first defined at Builth by Elles (1900). The base of the biozone is recognized by the incoming of the index species. However, re-examination of the Builth succession (Zalasiewicz & Williams, 1999) has shown that it overlies the *rigidus* Biozone directly without the intervening *linnarssoni* or *ellesae* biozones that Elles had recognized. Zalasiewicz & Williams (1999; see also Williams & Zalasiewicz, 2004) found that *C. ellesae*, the zonal index species of the *ellesae* Biozone, in fact appears higher than *C. lundgreni*, and the ranges of *C. ellesae* and *C. lundgreni* overlap (see also Warren, 1971; Rickards, 1976); thus we do not recognize the *ellesae* Biozone in this account. This causes problems regarding the links between biostratigraphy and chronostratigraphy, because the boundary between the Sheinwoodian and Homerian stages was placed at the base of the *ellesae* Biozone as recognized in the Welsh Borders (Bassett, Rickards & Warren, 1975; see discussion in Zalasiewicz & Williams, 1999 and Melchin, Cooper & Sadler, 2004).

There is some potential for finer subdivision. At the base of the biozone, *C. lundgreni* was found to overlap with the latest occurrences of *Mediograptus* ex. gr. *retroflexus*. There might be also a discrete middle to upper biozonal assemblage including *Cyrtograptus ramosus*, *C. hamatus*, *C. ellesae* and *Testograptus testis*, although its recognition may be hampered in practice because such taxa are rare in comparison with the more long-ranging pristiograptids, monoclimacids and monograptids (Fig. 18). Davies *et al.* (1997) and Bassett, Rickards & Warren (1975) recorded this biozone from central Wales, and Warren *et al.* (1984) used it in north Wales.

9.bb. *Gothograptus nassa* Biozone

The *nassa* Biozone was first adopted for use in Britain by Warren (1971) working in north Wales. It succeeds a major graptolite extinction event, with most of the graptolites characteristic of the preceding *lundgreni* Biozone not surviving into this interval (Rickards, 1976; Jaeger, 1991). Indeed, only four taxa have been recorded (Fig. 18), one of which is a first appearance. The assemblage consists of *Pristiograptus dubius* (and its subspecies *ludlowiensis*) and *Gothograptus nassa*, which dominate most assemblages, with *P.* aff. *jaegeri* of Holland, Rickards & Warren, 1969; reliable records of *Pristiograptus jaegeri* appear in the upper part of the biozone. *G. nassa* has been reported beyond its biozone in Britain (Fig. 18), although subsequent detailed work in Arctic Canada, Baltica and the Czech Republic (Porębska, Kozłowska-Dawidziuk & Masiak, 2004) suggests that it is confined there to its biozone and the overlying *praedeubeli* Biozone (not recognized in Britain) of that region; this suggests that careful reassessment of UK material of *nassa* is needed. Zalasiewicz & Williams (1999) referred only to a *nassa–ludensis* Biozone representing the uppermost interval of Wenlock strata at Builth Wells; both indicator species are rare in this area and their biostratigraphical ranges cannot be clearly constrained. In general, the low abundance and diversity of graptolites in upper Wenlock strata in the British Isles make it difficult to apply the fine upper Wenlock graptolite biostratigraphy recognized elsewhere in the world (e.g. Lenz *et al.* 2006).

9.cc. *Monograptus ludensis* Biozone

Originally recognized as the *vulgaris* Zone by Wood (1900) at Builth and Long Mountain, this biozone was redefined and renamed by Holland, Rickards & Warren (1969; see also Rickards, 1976).

The base of the *ludensis* Biozone is taken at the incoming of the biozonal species (Fig. 18) which, in the lower part of the interval, co-occurs with taxa from the preceding *G. nassa* Biozone. This biozonal assemblage indicates the possibility of a more refined biostratigraphic subdivision (see Rickards, 1976), as the first occurrences of other species range from the middle to upper part of the biozone. These include *Holoretiolites* (*Balticograptus*) *lawsoni*, *Pristiograptus auctus*, *Monograptus deubeli* and *M.* aff. *uncinatus orbatus*. The loss of *P.* aff. *jaegeri* of Holland, Rickards & Warren (1969) midway through the biozone

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reinforces the distinction between a lower and an upper assemblage within the *ludensis* Biozone.

9.dd. *Neodiversograptus nilssoni* Biozone

In recent years, much biostratigraphical work has been undertaken on British strata of Ludlow age by the British Geological Survey on Ludlow successions in central Wales (Schofield *et al.* 2004; Barclay *et al.* 2005). Nevertheless, the biozonal criteria for the series have not changed significantly since Rickards's (1976) review of Silurian graptolite biostratigraphy. The base of the *N. nilssoni* Biozone coincides only approximately (Melchin, Cooper & Sadler, 2004) with the base of the Ludlow Series. Many Lower Ludlow taxa had been identified in Britain, notably from the Lake District and Ludlow itself (Nicholson, 1868; Hopkinson, 1873), before Lapworth (1879–1880), working in central Wales and the Welsh Borderlands, designated the 'zone of *Monograptus nilssoni*', which included the whole Lower Ludlow. Further studies, most importantly those of Wood (1900), led to refinement and subdivision of this broad biostratigraphical unit (Rickards, 1967, 1969; Warren, 1971).

The *nilssoni* Biozone shows a much greater specific diversity than the preceding Wenlock biozones, with the appearance and diversification of *Saetograptus* being especially characteristic. The appearance of the zone fossil defines its base, and taxa such as *Monograptus uncinatus orbatus*, *Plectograptus macilentus*, *Spinograptus spinosus*, *Saetograptus colonus colonus*, *S. varians varians* and *Bohemograptus bohemicus s.l.* also appear at about this level (Fig. 18).

In north Wales, Warren (*in* Warren *et al.* 1984, p. 54) divided the *nilssoni* Biozone into lower and upper divisions, and there is potential for further subdivision (see discussion in Rickards, 1976). There is a distinct lower to middle zonal assemblage, with *M. ludensis* and *P. auctus*, which disappears in the mid-*nilssoni* Biozone. A distinct assemblage appears in the middle to upper part of the biozone and contains many new genera and species of Monograptidae, notably *Cucullograptus* (*Lobograptus*) *progenitor*, *C.* (*L.*) *scanicus*, *C.* (*L.*) *simplex, Monoclimacis micropoma*, *Mcl. haupti*, *Pristiograptus vicinus* and *Crinitograptus crinitus*. The saetograptids diversify rapidly in this upper interval with the incoming of *Saetograptus roemeri*, *S. fritschi fritschi*, *S. leintwardinensis incipiens*, *S. wandalensis*, *S. chimaera chimaera*, *S. chimaera salweyi* and *S. chimaera semispinosus*. This biostratigraphical refinement has been expressed in Poland and the Czech Republic in terms of a lower *nilssoni* Biozone succeeded by an upper *progenitor* Biozone (Urbanek, 1966; Teller, 1969; Přibyl, 1983); Melchin, Cooper & Sadler (2004) and Koren' *et al.* (1996) indeed used this assemblage (and the incoming of *C.* (*L.*) *scanicus*) to define the base of the *scanicus* Biozone, and this resolution might ultimately prove optimal also for the British succession.

9.ee. *Cucullograptus (Lobograptus) scanicus* Biozone

Wood (1900) established the *scanicus* Biozone in the Builth and Ludlow areas, and, while widely employed, this interval remains problematical in the British Isles. Rickards's (1976) range chart showed no appearances at the base of this interval, and it was characterized by extinctions of many *nilssoni* Biozone taxa and an increase in the abundance of *Cucullograptus* (*Lobograptus*) *scanicus* and *Saetograptus chimaera chimaera* (Wood, 1900; Rickards, 1976) (Figs 18, 19). Recent work in the Montgomery district of central Wales (White *in* Cave & Hains, 2001, p. 69) showed a number of appearances there at this level, including most of the subspecies of *S. chimaera*. The incoming of *Pristiograptus tumescens tumescens*, *Saetograptus clunensis*, *Pristiograptus welchae* and *Bohemograptus bohemicus tenuis* was shown in the middle part of the *scanicus* interval by Rickards (1976).

9.ff. *Saetograptus incipiens* or *Pristiograptus tumescens* Biozone

Wood (1900) established this biozone in Wales and the Welsh Borderland and employed both zonal terms. As with the preceding *scanicus* Biozone, it is somewhat ill-defined and approximates to an interregnum. The biozonal name varies locally according to the relative abundance and/or the presence or absence of *Saetograptus incipiens* and *Pristiograptus tumescens*, both of which originate in earlier biozones (see discussion in Rickards, 1976). Graptolite species diversity is reduced in the *incipiens/tumescens* Biozone compared with previous Ludlow biozones, with approximately ten confirmed taxa (Figs 18, 19), most of them ranging from the preceding biozones. Only one new form appears: *Saetograptus*? aff. *incipiens* (Wood, 1900). A number of species have been recorded as disappearing in the lower to middle part of the interval (Rickards, 1976), perhaps indicating the possibility of subdivision; these include *Monoclimacis haupti*, *Pristiograptus vicinus*, *Saetograptus clunensis* and *S. varians varians*. In practice, though, this interval, sharing so many taxa with the *scanicus* Biozone, is hard to recognize, particularly in spot localities.

9.gg. *Saetograptus leintwardinensis leintwardinensis* Biozone

This biozone was initially defined by Marr (1892) in the Lake District and has been widely recognized in the UK (Wood, 1900; Holland, Lawson & Walmsley, 1963; Rickards, 1967), largely on the incoming of *S. l. leintwardinensis* (Fig. 19). Only two other taxa are confirmed in this biozone, namely *Saetograptus*? aff. *incipiens*, which continues from the previous biozone, and *Saetograptus leintwardinensis primus*, which is confined to the lower–middle part of the biozone (Shergold & Shirley, 1968). Such a low-diversity

Table 1. Ordovician range chart sources (England & Wales) (for Figs 3–7)

Source number	Reference
1	Baker, 1981
2	Beckly & Maletz, 1991
3	Beckly, 1988
4	Rickards, 2002
5	Davies *et al*. 1997
6	Bulman, 1963
7	Cooper *et al*. 2004
8	Gibbons & McCarroll, 1993
9	Rushton & Zalasiewicz, 1999
10	Cooper *et al*. 1995
11	Davies, 1929
12	Elles, 1933
13	Elles, 1940
14	Elles & Wood, 1901–1918
15	Fortey & Owens, 1987
16	Fortey, Beckly & Rushton, 1990
17	Hughes, 1989
18	Hutt & Rickards, 1970
19	Jenkins, 1982
20	Jenkins, 1983
21	Maletz, Rushton & Lindholm, 1991
22	Molyneux & Rushton, 1988
23	Rickards, 1970
24	Rushton & Molyneux, 1989
25	Skevington, 1966
26	Skevington, 1970
27	Skevington, 1973
28	Strachan, 1986
29	Strahan *et al*. 1914
30	Toghill, 1968*a*
31	Toghill, 1970*a*
32	Wadge, Nutt & Skevington, 1972
33	Zalasiewicz, 1986
34	Zalasiewicz, 1992*a*
35	Zalasiewicz & Tunnicliff, 1994
36	Zalasiewicz, Rushton & Owen, 1995
37	Young, Gibbons & McCarroll, 2002
38	Williams *et al*. 2003*a*
39	Skevington & Jackson, 1976
40	Cocks *et al*. 1984
41	Legrand *in* Rushton, 1982
42	Stubblefield & Bulman, 1927
43	Howells & Smith, 1997
44	Pratt, Woodhall & Howells, 1995
45	Bulman & Rushton, 1973
46	Old, Sumbler & Ambrose, 1987
47	Owens *et al*. 1982
48	Rushton, 2006
49	Rickards, 2004

assemblage may reflect a deteriorating environment or a deepening evolutionary crisis amongst British graptolites at this time.

9.hh. *Bohemograptus* proliferation Biozone

This biozone was originally described in the UK by Holland & Palmer (1974), when they identified *Bohemograptus bohemicus tenuis* from strata overlying the *leintwardinensis* Biozone in the Welsh Borderlands (see also White *in* Cave & Hains, 2001). This taxon is the youngest graptolite in the UK biostratigraphical sequence, and the sole representative in this biozone (Fig. 19). *B. bohemicus tenuis* has not been reported from the immediately underlying *leintwardinensis* Biozone, despite its origination earlier in the Ludlow, in the *scanicus* Biozone (Rickards, 1976).

Table 2. Ordovician range chart sources (Scotland) (for Figs 8–10)

Source number	Reference
1	Rushton, 2001*b*
2	Rushton *et al*. 1986
3	Rushton, Tunnicliff & Tripp, 1996
4	Stone & Rushton, 1983
5	Stone & Strachan, 1981
6	Stone, 1995
7	Williams, 1982*a*
8	Williams, 1987
9	Williams, 1988
10	Williams, 1994
11	Zalasiewicz, Rushton & Owen, 1995
12	Williams, 1982*b*
13	Floyd, 1999
14	McMillan, 2002
15	Floyd & Rushton, 1993
16	Barnes, 2008
17	Stone & Rushton, 2003
18	Armstrong *et al*. 1998
19	Rushton, 2003*a*
20	Rushton, 2003*b*
21	Zalasiewicz *et al*. 2000
22	Elles & Wood, 1901–1918
23	Toghill, 1970*b*
24	Williams *et al*. 2004

Table 3. Silurian range chart sources (for Figs 11–19)

Source number	Reference
1	Baker, 1981
2	Cocks & Toghill, 1973
3	Davies, 1929
4	Elles & Wood, 1901–1918
5	Harris, J. H., unpub. Ph.D. thesis, Univ. Cambridge, 1987
6	Hutt, 1974–1975
7	Hutt & Rickards, 1970
8	Loydell, 1991*b*
9	Loydell & Cave, 1993
10	Loydell, 1992–1993*a*
11	Loydell & Cave, 1996
12	Packham, 1962
13	Rickards, 1970
14	Rickards, 1976
15	Strachan, 1997
16	Toghill, 1968*a*
17	Zalasiewicz, 1992*b*
18	Zalasiewicz & Tunnicliff, 1994
19	Zalasiewicz, 1994
20	Zalasiewicz, Loydell & Štorch, 1995
21	Zalasiewicz, 1996
22	Zalasiewicz & Williams, 1999
23	Zalasiewicz, 1995
24	BGS Scottish Sheet Memoir 4 (Kirkowan)
25	BGS Scottish Sheet Memoir 5 (Kirkcudbright)
26	BGS Scottish Sheet Memoir 9 (Thornhill)
27	Stone, 1995
28	Davies *et al*. 1997
29	White *et al*. 1992
30	Bull & Loydell, 1995
31	BGS Sheet Memoir 165 (Montgomery)
32	Zalasiewicz, Williams & Akhurst, 2003
33	Toghill, 1968*b*
34	Rickards, Hutt & Berry, 1977
35	Sudbury, 1958
36	Chopey-Jones, Williams & Zalasiewicz, 2003
37	Williams *et al*. 2003*b*
38	Cullum & Loydell, 1996
39	Štorch & Loydell, 1992
40	Štorch & Serpagli, 1993
41	Loydell, 1990
42	Wilson, D. R., unpub. Ph.D. thesis, Univ. Birmingham, 1954
43	Loydell, 1993*b*

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Table 4. Index to taxa; O/EW/no. = Ordovician/England and Wales/taxon number in range chart (Figs 3–7); O/Sc/no. = Ordovician/Scotland/taxon number in range chart (Figs 8–10); S/no. = Silurian/taxon number in range chart (Figs 11–19)

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Table 4. (*Cont.*)

cyperoides, *Rivagraptus* S/81
cyphus, *Coronograptus* S/42

daironi, *Pseudoretiolites* S/203
danbyi, *Mediograptus* S/321
davidensis, *Isograptus ovatus* O/EW/145
daviesi, '*Glyptograptus*' O/Sc/95; O/EW/224
deani, *Holograptus* O/EW/48
decens, *Didymograptus* O/EW/31
decipiens, *Torquigraptus*? *decipiens* S/157
decipiens, *Tetragraptus* O/Sc/2
decoratus, *Diplograptus*? O/EW/152
decussatus, *Dimorphograptus decussatus* S/32
deflexus, *Corymbograptus* O/EW/36
delicatulus, '*Monograptus*' S/163
densus, *Dichograptus maccoyi* O/Sc/21
densus, *Phyllograptus* O/EW/65
dentatus, *Eoglyptograptus* O/EW/102
denticulatus, *Torquigraptus* S/151
denticulatus, *Orthoretiograptus* O/Sc/144
desmograptoides, *Rhabd. flabelliformis* O/EW/2
deubeli, *Monograptus* S/373
difformis, *Monograptus* S/73
diffusus, *Trochograptus* O/EW/28
diminutus, *Neodiplograptus* S/14
directa, *Monoclimacis* S/276
discus, *Monograptus* (=*Cochlogr. veles*) S/265
distans, *Glyptograptus tamariscus* S/74
distans, *Rastrites* S/261
distans, *Stimulograptus* S/165
distinctus, *Expansograptus* O/EW/78
divaricatus, *Dicellogr. divaricatus* O/Sc/47; O/EW/155
divergens, *Adelograptus*? O/EW/40
divergens, *Amphigraptus divergens* O/Sc/124
divergens, *Isograptus victoriae* O/EW/74
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Table 4. (*Cont.*)

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speciosus, *Streptograptus* S/307
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strachani, *Huttagraptus* S/51
strachani, *Streptograptus* S/205
styloideus, *Climacograptus* O/Sc/118; O/EW/232
sublinnarssoni, *Monoclimacis* S/306
subtilis, *Nemagraptus* O/EW/162; O/Sc/31A
sudburiae, *Monograptus* S/70
suecicus, *Expansograptus* O/EW/85
supernus, *Appendispinograptus* O/Sc/138; O/EW/239
supernus, *Glyptograptus* S/212
superstes, *Expansograptus*? O/Sc/52; O/EW/170
svalbardensis, *Xiphograptus* O/EW/83
swanstoni, *Dimorphograptus confertus* S/45

tailbertensis, *Climacograptus* O/EW/118
tamariscoides, *Normalograptus* S/103
tamariscus, *Glyptograptus tamariscus* S/53
tardifurcatus, *Schizograptus* O/EW/53
tardiusculus, *Dicranograptus* O/Sc/75A
tenellus, *Adelograptus* O/EW/9
tenuicornis, *Orthograptus calcaratus* O/Sc/90; O/EW/202
tenuis, *Bohemograptus bohemicus* S/401
tenuis, *Glyptograptus* S/24
tenuis, *Neolagarograptus* S/164
tenuis, *Parapetalolithus* S/248
tenuis, *Streptograptus* S/241
tenuissimus, '*Monograptus*' S/118
teretiusculus, *Hustedograptus* O/Sc/51; O/EW/160
testis, *Testograptus* S/361
textor, *Sokolovograptus* S/353
thuringiacus, *Neodiplograptus* S/121
toernquisti, *Rhaphidograptus* S/40
triangulatus, *Monograptus triangulatus* S/87
tricornis, *Cryptograptus tricornis* O/Sc/65; O/EW/150
trifilis, *Normalograptus* S/9
tuberculatus, *Climacograptus* O/EW/240; S/12
tubulariformis, *Cephalograptus* S/144
tubuliferus, *Climacograptus* O/Sc/117; O/EW/227
tullbergi, *Torquigraptus tullbergi* S/281
tumescens, *Pristiograptus* S/400
turriculatus, *Spirograptus* S/240
typus, *Phyllograptus* O/EW/73

ultimus, *Corynoides* O/Sc/115; O/EW/225
undulatus, *Metaclimacograptus* S/71
undulatus, *Stimulograptus*? S/153
unguiferus, *Monograptus* S/376
uniformis, *Corymbograptus*? O/EW/80
uplandicus, *Orthograptus* O/EW/169
urbanekii, *Cyrtograptus* S/357
urceolinus, *Torquigraptus* S/143
urceolus, *Monograptus* S/173
utilis, *Stimulograptus* S/234

validus, *Azygograptus* O/EW/21
validus, *Leptograptus validus* O/EW/175; O/Sc/36A (s.l.)
variabilis, *Pristiograptus* S/179
varians, *Glyptograptus tamariscus* S/69
varians, *Saetograptus varians* S/380
varicosus, *Corymbograptus* O/EW/30
vas, *Pseudoglyptograptus* S/110
v-deflexus, *Yutagraptus*? O/Sc/24
velatus, *Nymphograptus* O/Sc/146
veles, *Cochlograptus* (=*M. discus*) S/265
vesiculosus, *Cystograptus* S/17
vesiculosus, *Stimulograptus* S/305
v-fractus, *Corymbograptus v-fractus* O/EW/47
vicinus, *Pristiograptus* S/393
victoriae, *Isograptus victoriae* O/Sc/18; O/EW/66
vikensis, *Monoclimacis* S/330
volucer, *Corymbograptus v-fractus* O/EW/84
vomerina, *Monoclimacis vomerina* S/290
vulgaris, *Monograptus austerus* S/61
vulgatus, *Orthograptus calcaratus* O/Sc/82; O/EW/203

walkerae, *Monograptus brevis* S/83
wandalensis, *Saetograptus* S/384
welchae, *Pristiograptus* S/398
wenlockianus, *Pseudoplegmatograptus* S/337
whitei, *Streptograptus* S/254
whitfieldi, *Orthograptus* O/Sc/58; O/EW/171
williamsi, *Pseudostreptograptus* S/229
wilsoni, *Climacograptus* O/Sc/81
wilsoni, *Parapetalolithus* S/264
wimani, *Streptograptus* S/308
woodae, *Monoclimacis* S/286
wyensis, *Normalograptus* S/65

ziczac, Dicranograptus O/Sc/71; O/EW/195

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