

A refined graptolite biostratigraphy for the late Ordovician-early Silurian of central Wales

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Morphometric analysis of graptolites from the *persculptus* and *acuminatus* biozones of central Wales identifies four successive morphospecies of normalograptids. These graptolites can be used for biostratigraphical subdivision of these strata as follows: (a) an early *persculptus* Biozone interval containing broad forms with geniculate thecae that have the morphology of *Persculptograptus persculptus* with an early insertion point for the full median septum (theca 1¹); (b) an supradjacent level of early *persculptus* Biozone age, with narrower, parallel-sided forms that have been referred to as *Normalograptus?* cf. *parvulus* and a slightly later insertion point for the full median septum (theca 1²); (c) a third interval, encompassing the later part of the *persculptus* Biozone to the early *acuminatus* Biozone, with *?Normalograptus parvulus*, which has the full median septum delayed to the level of theca 3-7; and (d) a younger interval, in the mid-*acuminatus* Biozone with *Persculptograptus persculptus?* specimens which do not display the median septum on its reverse side. These taxa can be used for refined biostratigraphy and correlation in the late Ordovician and early Silurian of central Wales. The progressive delay in the insertion of the median septum in these taxa may have wider application for the correlation of the interval immediately after the Hirnantian glacial maximum.

Stratigraphy, Hirnantian, Rhuddanian, evolution, graptolites.

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The latest Ordovician graptolite assemblages are of generally very low diversity (e.g. Koren' & Bjerreskov 1999; Chen *et al.* 2000). Though more diverse assemblages occur on the Yangtze Platform, China, where high-resolution biostratigraphic correlation is possible (e.g. Chen *et al.* 2005b), such high-resolution graptolite biostratigraphy has not previously been achieved in low-diversity faunas (cf. Chen *et al.* 2000). However, we use graptolites from central Wales to define four intervals in the latest Ordovician and earliest Silurian allowing high-resolution correlation within individual graptolite biozones.

The low-diversity late Ordovician graptolite fauna of central Wales contains abundant normalograptids including *Persculptograptus persculptus* (Elles & Wood 1907) and *Normalograptus? parvulus* (Lapworth 1900). These taxa are commonly used for worldwide correlation of this interval (e.g. Koren' & Bjerreskov 1999; Chen *et al.* 2000; Armstrong *et al.* 2005) when they flourished following the climatically-related end-Ordovician mass extinction (Chen *et al.* 2005a, b). '*Diplograpsus persculptus*' was first recognised by Salter (1865), but was formally described and figured by Elles and Wood (1907, p. 257) to whom the species has been ascribed (Williams 1983; Zalasiewicz & Tunnicliff 1994; Štorch & Loydell 1996; Strachan 1997). Like *P. persculptus*, *N? parvulus* is also based on material from central Wales (Lapworth 1900; Zalasiewicz & Tunnicliff 1994; Strachan 1997).

In central Wales, these graptolites show a progressive delay in the insertion of their median septum, first reported by K.A. Davies (1929) in assemblages of '*Glyptograptus persculptus*'. The median septum is the partition between thecae on the left-side and right-side of the rhabdosome. The delay in its insertion is apparent on the reverse side of the rhabdosome (i.e. the opposite side to that which reveals the sicula), with the median septum being inserted proximally in stratigraphically early forms and more distally in stratigraphically later forms (K.A. Davies 1929). The obverse side of the rhabdosome, meanwhile, shows a complete median septum in all cases except rare, pathological specimens (e.g. Zalasiewicz & Tunnicliff 1994, text-fig. 5c); in stratigraphically late specimens the median septum forms a partial internal wall, not reaching the reverse side of the rhabdosome. K.A. Davies' (1929) observations were later corroborated by Zalasiewicz & Tunnicliff (1994),

albeit on the basis of limited material. Such a delay in the insertion of the median septum has also been noted in other normalograptids (Waern 1948) and in *Rhaphidograptus toernquisti* (Hutt, 1974).

In this paper we describe how: (a) the insertion point of the medium septum in certain normalograptids can be used to define four successive intervals in the *persculptus* to mid *acuminatus* biozone strata in central Wales; and (b) how these can be used for refined correlation in sequences deposited in the aftermath of the Hirnantian glacial maximum. This glaciation reached its peak in the *extraordinarius* Biozone and continued into the early part of the *persculptus* Biozone (Sutcliffe *et al.* 2000; Chen *et al.* 2005b; Page *et al.* 2007).

Geological setting

The Late Ordovician (Hirnantian) to Early Silurian (Rhuddanian) succession of central Wales (Fig. 1A) consists of a lower, unfossiliferous sequence of slumped and disturbed strata, which is abruptly overlain by a bedded sequence in which graptolites are abundant. The disturbed rocks are included in the Yr Allt Formation; the bedded sequence constitutes the mudstone-dominated Cwmere Formation and the laterally equivalent sandstone-rich units that replace it in some sections (see J.R. Davies *et al.* 1997 for definitions and synonyms). Hirnantian *persculptus* Biozone graptolites characterise the lower part of the Cwmere Formation (and its equivalents) with Silurian graptolite assemblages occurring above them at higher levels (*acuminatus* and younger biozones). The base of the Cwmere Formation includes a distinctive and widely recognised unit of burrow-mottled strata, called the Mottled Mudstone Member. Earliest *persculptus* Biozone graptolites occur close to the base of this member. They are preserved within thin beds of graptolitic mudstone known collectively as the '*persculptus* Band' (Jones & Pugh, 1916; J.R. Davies *et al.* 1997), which can be traced across central Wales. The succession and its faunas are widely acknowledged to reflect eustatic changes in sea level linked to the end of the Hirnantian glacial maximum (e.g. Woodcock *et al.* 1996; Cherns *et al.* 2006; Page *et al.* 2007);

the sharp base of the graptolite-bearing Mottled Mudstone Member is viewed as marking an abrupt post-glacial deepening event (Schofield *et al.* 2004) that continued during the deposition of the Cwmere Formation, when almost continuous sea floor anoxia was established (Woodcock *et al.* 1996; J.R. Davies *et al.* 1997).

Graptolite assemblages have been recovered from the Mottled Mudstone Member of the Cwmere Formation as well as overlying parts of this Formation and from laterally equivalent facies (such as the Cerig Gwynion Grits and Dyffryn Flags). These strata are well exposed in Cerig Gwynion Quarry near Rhayader (see Tunnicliff 1989; J.R. Davies *et al.* 1997; Zalasiewicz & Tunnicliff 1994; Fig. 1D) and the associated Prysog stream section (Lapworth 1900; J.R. Davies *et al.* 1997; Fig. 1B); the succession is also exposed at the Ystradffin section some 30 km to the south (K.A. Davies 1929). At the latter locality, the Mottled Mudstone Member is overlain by the Cwmere Formation in normal sequence (Fig 1C). However, at Cerig Gwynion Quarry and in the Prysog stream section the succession is more complex: the lower part of the Cwmere Formation, above the Mottled Mudstone Member, is replaced by sandstone-rich facies of the Caban Conglomerate Formation. The Caban Conglomerate Formation has variable vertical and lateral extent (J.R. Davies *et al.* 1997); and in this area the Cerig Gwynion Grits facies of the Caban Conglomerate Formation is overlain by the Dyffryn Flags facies though the boundary between these two facies is gradational (Fig. 3). The biostratigraphic succession for this locality was studied in detail by Zalasiewicz & Tunnicliff (1994). At all the localities, the graptolite-bearing strata comprise turbiditic mudstones and/or sandstones interbedded with subordinate hemipelagic layers (or hemipelagites). Hemipelagic layers have not been recognised in the underlying Yr Allt Formation.

Collections

At both Ystradffin and Cerig Gwynion, collections were obtained from two thin, closely-spaced laminated graptolite-bearing levels located close to the base of the Mottled Mudstone Member. These represent the local '*persculptus* Band'

(Fig. 2). At Cerig Gwynion Quarry and in the Prysgr stream section, additional younger assemblages were also collected from facies of the Caban Conglomerate Formation (Fig. 3). Faunas from hemipelagites preserved between the thick sandstones of the Cerig Gwynion Grits are of *persculptus* Biozone age. The overlying, thinner-bedded Dyffryn Flags range from the *persculptus* Biozone into the basal Silurian *acuminatus* Biozone. Details of the exposures are as follows.

Cerig Gwynion Quarry and Prysgr stream section

Cerig Gwynion Quarry is situated to the north of the A470 trunk road, west of Rhayader (Fig. 1B, D). Within the quarry six graptolite-bearing levels yielded hundreds of graptolites, including *P. persculptus*, *P. persculptus?*, *?N. parvulus* and *N? cf. parvulus*. The exposures are located along a series of tracks and minor excavations through the quarry (Fig. 1D). *Normalograptus medius*, *N. miserabilis* and *N. normalis* have also been recorded from the quarry (see Tunnicliff 1989), but these are not treated further here. The two oldest graptolite-bearing levels are located at the base of the quarry, close to the main entrance (horizons C1 and C2; Figs 2A, 3); these correspond to the '*persculptus* Band' of the Mottled Mudstone Member (J.R. Davies *et al.* 1997). These levels have a far greater abundance of graptolites than younger levels in the succession and the graptolites are often current-aligned within them. Younger levels (C3-C6; Fig. 3) are interspersed throughout a thick succession of turbidite sandstone and mudstone units; here, graptolite-bearing hemipelagic layers are difficult to locate and are individually thinner (because their vertical continuity is interrupted by turbiditic input) than the anoxic intervals of the '*persculptus* band'. These horizons correspond to those identified in locality A of Zalasiewicz & Tunnicliff (1994).

Adjacent to the A470, approximately 1.5 km to the north-east of Cerig Gwynion Quarry, is the Prysgr stream section (Fig. 1B). The stream section locally exposes turbidite sandstones and mudstones with sporadic layers of laminated hemipelagite. This horizon (C7; Fig. 3) represents the mid to late *acuminatus* Biozone. It was collected by Lapworth (1900) and more recently

by Zalasiewicz & Tunnicliff (1994). No new material from this site was located in this study.

Ystradffin

Approximately 30 km to the southwest along the strike of the Ordovician/Silurian boundary is the remote section of Ystradffin, also referred to as Nant Y Caw (K.A. Davies 1929; see Fig. 1A). On a steep hillside, 1.5 km south of the Llyn Brienne reservoir, lies a large slate waste heap from which a small steeply-incised stream runs towards the road (Fig. 2). The exposure within the stream section is poor and sporadic. To the southeast, behind the waste heap, a small stream flows into a small, deep quarry, which is partly water-filled. The main section through the *persculptus* Biozone is on the north-east face of the quarry.

K.A. Davies (1929) placed the Ordovician/Silurian boundary at Ystradffin using lithological criteria; however, more recent biostratigraphic study has more accurately relocated the boundary in this section (see J.R. Davies *et al.* 1997). K.A. Davies (1929) placed the Ordovician/Silurian boundary at the change from “doubly cleaved” shales of the Bala to the regularly cleaved shales of the Silurian. The Bala shales identified by K.A. Davies (1929) have subsequently been referred to the top of the Yr Allt Formation (J.R. Davies *et al.* 1997, table 6), and the overlying “regularly cleaved” shales, that K.A. Davies (1929) held to be Silurian, have since been referred to the Mottled Mudstone Member of the lowermost Cwmere Formation, which is nowadays regarded as of late Ordovician age (J.R. Davies *et al.* 1997). K.A. Davies (1929) observed that, approximately 3 feet (0.90m) above the base of the “regularly cleaved” strata, ‘*G. persculptus*’ was present within a thin layer (the *persculptus* band). He stated that, some 7 feet (2.3 m) above this layer, there was a second thin layer with high concentrations of a more “robust” and longer morphotype of ‘*G. persculptus*’.

We have re-examined this locality (Fig. 2) and located both of the graptolite-bearing layers identified by K.A. Davies (1929). However, our field observations show that the layer with “robust” *persculptus* (Y1) occurs stratigraphically below rather than above the layer with narrow specimens

(Y2). We ascribe the discrepancy between our observations and those of K.A. Davies (1929) to his misidentification of bedding and cleavage at this locality (hence “doubly cleaved”), combined with minor slumping of the exposed rock mass. We consider that levels Y1 and Y2 are direct correlatives of levels C1 and C2 respectively.

Material and Preservation

Our field-collections yielded over 450 specimens, representing an unbiased sample of these graptolites. These specimens were typically part-observed by rock when recovered; they have subsequently been excavated using needles. This is a painstaking process, but altogether over 300 suitably preserved specimens were prepared for analysis (see Table 2). These were dominantly near-proximal fragments or complete specimens with short stipes. For comparison we have also examined the specimens of K.A. Davies (1929). We also compared the lectotypes of *P. persculptus* and *N? parvulus*, which come from localities in central Wales and were designated by Williams (1983, p. 622) and Zalasiewicz & Tunnicliff (1994, p. 705) respectively. All this material is held in the collections of the British Geological Survey at Keyworth, Nottingham.

The graptolites are preserved in laminated hemipelagites, mostly as partial- to full-relief pyrite steinkerns surrounded by denatured periderm (Fig. 4A-C, E-F). Pyritized specimens show well-preserved morphological detail, particularly fusellar banding (Fig. 4C, G) and the insertion of the median septum (Fig. 4D). In contrast, flattened specimens do not clearly show the median septum or fusellar banding (Fig. 4H). All graptolites in this study have undergone conditions of deep burial diagenesis (J.R. Davies *et al.* 1997; Schofield *et al.* 2004), during which their preservation altered significantly (e.g. Page *et al.* 2005). Though periderm may undergo a considerable volume loss in maturation (AAP, unpublished observations), this has a negligible effect on any measurements taken here. Whilst pyritized graptolites may remain relatively undeformed during tectonism (e.g. Fig. 4F; Sudbury 1958) flattened graptolites may undergo significant distortion due to both collapse

and tectonism (e.g. Sudbury 1958; Underwood 1992) and may not clearly preserve morphological features such as the insertion of the median septum (cf. Fig. 4G). Thus, only undeformed, pyritized specimens (e.g. Fig. 4A, C-D, F) were included in the morphometric analysis.

To allow accurate measurement, the coating of phyllosilicate minerals that encases all the graptolites considered in this study was removed in preparation (see Fig 4A-B, H). The material from Cerig Gwynion Quarry is preserved in a weakly cleaved facies of high diagenetic grade (J.R. Davies *et al.* 1997) with only a slight tectonic distortion. However, the material from Ystradffin is preserved in a strongly cleaved facies of highest anchizone grade (J.R. Davies *et al.* 1997), and graptolites may show evidence of tectonic strain. At Ystradffin we only considered fully intact specimens in full relief (e.g. Fig 4F, cf. Fig. 4E), as diagenetic flattening may result in distortion (e.g. Sudbury 1958; Underwood 1992; Koren' & Rickards 1996, p. 32). The graptolites are preserved parallel to bedding in all localities, and those within the '*persculptus* band' often show current alignment suggesting that these intervals represent allochthonous faunas.

Stratigraphic variation in graptolite morphotypes

The latest Ordovician strata of central Wales are characterised by assemblages of morphologically similar graptolites with doubly sigmoidal, curved thecae and well-developed geniculae. Previous workers have tentatively assigned such graptolite taxa to the genus *Normalograptus* Legrand (1987) emend. Melchin & Mitchell (1991). For example, Zalasiewicz and Tunnicliff (1994) recognised '*N? persculptus*' and '*N? parvulus*' in central Wales. These taxa are respectively larger and smaller forms that show a notable plasticity in degree of thecal curvature, genicular sharpness and waviness of the median septum. This variation is further accentuated by preservation and aspect differences. Both taxa have astogenetic pattern H (Mitchell 1987) and show differences from 'typical' normalograptid morphology (cf. Melchin and Mitchell 1991). With this in mind, Koren' & Rickards (1996) proposed the monotypic genus *Persculptograptus* for graptolites with doubly

sigmoidal thecae and an undulose median septum such as *P. persculptus*. In addition, Chen *et al.* (2005a, p. 252) noted that there is a distinctive species group in the latest Ordovician and earliest Silurian that shares these characters. Although *Persculptograptus* remains monotypic, it may be that this genus could include other taxa including some of those documented in this paper. However, as the focus of this paper is stratigraphic rather than taxonomic, we adopt the established generic names and refer the four morphotypes to *?N. parvulus*, *N? cf. parvulus*, *P. persculptus*, and *P. persculptus?*.

The following parameters have been measured: dorsoventral width at thecal apertures 1, 3, 5 and 10; two-theca repeat distances (*sensu* Howe 1983) at theca 1, 3, 5, 10 and 15; position of the median septum's insertion on the reverse side; total rhabdosome and sicula length; distance from proximal end to the apertures of theca 1¹ and theca 1² apertures (see Loydell 1991 for illustrations of these descriptive terms). Additionally, the lengths of the nema and virgella were recorded where possible (although these did not show any significant trends). The full dataset is deposited at the British Geological Survey, Keyworth, Nottingham, in 1:50000 sheet file Rhayader (Sheet 179). The mean and standard deviation were calculated for dorsoventral widths, two-theca repeat distances (hereafter 2TRDS) and the rhabdosome length for each horizon, with individual localities positioned in stratigraphic order where applicable. In total over 300 well-preserved specimens were measured from the material described above (Table 2). Analysis of the material showed considerable variation between specimens at different stratigraphic levels, with four clear morphologies identified.

First interval: P. persculptus

The lowermost graptolite-bearing part of the '*persculptus* Band' yields *P. persculptus*. This relatively broad graptolite with weakly geniculate thecae occurs at both Cerig Gwynion Quarry and Ystradffin (C1 and Y1 respectively, Figs 2 & 3). These specimens have similar dimensions to the lectotype (Fig 5S; Table 1) and other specimens that have been referred to *P. persculptus* from elsewhere (Figs 3, 5A-E, 6; Table 1). The sharpness of the geniculum

decreases distally. The insertion of the median septum on the reverse side is displayed in 58 specimens from C1 and in 15 specimens from Y1 and occurs as early as theca 1¹ (Fig. 5A-E). These specimens are from the lower part of the *persculptus* Biozone.

Second interval: N? cf. parvulus

Specimens of *N? cf. parvulus* occur some 30 cm above level C1 at Cerig Gwynion Quarry, and a similar distance above level Y1 at Ystradffin, being the upper of the two graptolite-bearing levels in the '*persculptus* band' (C2 and Y2 respectively, Figs 2 & 3). These are approximately parallel-sided, geniculate, narrow graptolites (Fig. 5F-M). These specimens closely resemble *N? parvulus* in outline and although they have widths comparable to specimens referred to this taxon, they have noticeably greater 2TRDs (Lapworth 1900; Zalasiewicz & Tunnicliff 1994; Loydell *et al.* 2002; Chen *et al.* 2005a; Loydell 2007; see also Fig. 5Q & Table 1). With this in mind we have referred it to *N? cf. parvulus* reflecting the relative uncertainties in both its genus and species. In the collection from Y2, there is a slight hint of bimodality in graptolite size (Fig. 6), with a small number of larger graptolites having sizes approaching those of *P. persculptus*. It is unclear whether this reflects a few rare, larger specimens of *N? cf. parvulus* or the presence of two species (i.e. *N? cf. parvulus* and *P. persculptus*). This uncertainty is in part due to the sample size. Regardless, 41 specimens from C2 and 39 specimens from Y2 specimens show the median septum being inserted on their reverse side at or just after theca 1² (Fig. 5F-M). At this horizon (particularly at Cerig Gwynion Quarry), large numbers of sicalae are evident on many of the bedding surfaces. These specimens are from the lower part of the *persculptus* Biozone, but this assemblage is from slightly higher strata than those of C1 and Y1.

Third interval: ?N. parvulus

Stratigraphically higher levels (C3-C6, Fig. 3) yield specimens assigned to *?N. parvulus*. These are sub-parallel sided, geniculate and narrow graptolites with

a similar outline to the specimens from C2, though they have generally smaller 2TRDs (Fig. 3; Table 1). Because of the sub-parallel sided nature of the rhabdosome and its slightly larger size compared to other specimens of *N? parvulus* (Lapworth 1900; Zalasiewicz & Tunnicliff 1994; Loydell *et al.* 2002; Chen *et al.* 2005a; Loydell 2007; see also Fig. 5Q & Table 1) we refer to these specimens as *?N. parvulus*. At horizons C3 to C6, 16 specimens show the median septum inserted on the reverse side at or inbetween thecal pairs 3 and 7 with notable variation occurring within any one assemblage (Figs 3, 5N). These specimens range from the middle *persculptus* to lower *acuminatus* biozones.

Fourth interval: P. persculptus?

The stratigraphically highest graptolites in this study are assigned to *P. cf. persculptus*. These specimens occur in the Prysg section (C7, Fig. 3) and comprise broad and strongly geniculate specimens (Figs 3, 5O-P). This horizon yields 11 specimens preserving their reverse aspect, but the median septum is not apparent in any of these graptolites representing a delay in insertion to greater than theca 15 (Figs 3, 5O-P). They are referred to as *P. persculptus?* because the size and shape of the rhabdosome differs slightly from the lectotype of *P. persculptus* and other specimens including those from horizons C1 and Y1 (cf. Fig 5A-E, R-S; Table 1). These specimens are from the middle *acuminatus* Biozone.

A tool for correlation

The graptolites we have examined from the *persculptus* to mid-*acuminatus* biozones interval in central Wales define at least four stratigraphic intervals. These occur within the post-glacial maximum late Ordovician and early Silurian sequence and these taxa can be used for regional correlation. The succession is summarised in Fig. 3 and comprises: (a) an early *persculptus* Biozone interval defined by broad forms with an early insertion point for the median septum on their reverse side (theca 1¹); (b) an adjacent but younger

level with narrower forms having a slightly later insertion point on their reverse side (theca 1²); (c) a third interval, encompassing the later part of the *persculptus* Biozone (i.e. above the level of horizons C2 and Y2) to the level of the early *acuminatus* Biozone with forms having the full median septum delayed to the level of theca 3-7; and (d) a younger interval, from the mid *acuminatus* Biozone with specimens that do not display the median septum on their reverse side. Though dorsoventral width and 2TRD may be diagnostic if several tens of specimens are measured, the principal stratigraphic tool we have used in defining these intervals is the delay in the insertion point of the median septum.

This subdivision of the *persculptus* and *acuminatus* biozones can be used to refine correlation of late Ordovician and early Silurian (Cwmere Formation) strata through central Wales (as suggested by K.A. Davies 1929). In the Wye Valley, Zalasiewicz and Tunnicliff (1994) identified '*N.?* *persculptus*' which lacked a median septum on its reverse side indicative of the *acuminatus* Biozone, and equivalent to the uppermost interval in the scheme we present above. Recent mapping by the British Geological Survey for the Llanidloes Sheet has identified a new section through the Mottled Mudstone Member (including the '*persculptus* Band') into the succeeding Cwmere Formation in the Hafren Forest (Grid Reference SN 8415 8990). Here, anoxic laminated hemipelagites present in the lower 2 m of the Mottled Mudstone Member yield "robust" *P. persculptus* with dorsoventral widths at theca 1¹ exceeding 1 mm, and 1.5 mm at theca 5, and with an early insertion of the median septum (from the level of theca 1). This represents a level equivalent to horizons C1 and Y1 at Cerig Gwynion Quarry and Ystradffin. Meanwhile, the uppermost part of this anoxic unit yields smaller parallel-sided specimens with a similar outline to *N?* cf. *parvulus*, which have a typical dorsoventral width of 1.1 mm distally, and an early insertion point for the median septum at theca 1². This level is equivalent to horizons C2 and Y2 (Fig. 3). Above the bioturbated facies of the Mottled Mudstone Member in Hafren Forest, the lower metre of the succeeding Cwmere Formation yields "robust" specimens (dorsoventral width up to 1.5 mm distally), which again show an early insertion point for the median septum. This level is almost certainly lower in the succession than horizons C3 and C4 at Cerig Gwynion

Quarry. These collections, made by the BGS independently of those at Cerig Gwynion Quarry and Ystradffin, confirm that these successive morphological changes can be used for refined correlation of this interval throughout central Wales. Extensive Hafren Forest exposures in the graptolitic Cwmere Formation overlying the Mottled Mudstone Member provide potential to investigate graptolites for strata equivalent to the interval between levels C2 and C3 at Cerig Gwynion Quarry.

Further subdivision of these biozones may possibly be achieved by comparing the above data with the occurrence of potentially diagnostic taxa from the Cerig Gwynion Quarry and Prysg succession (see Zalasiewicz & Tunncliff 1994, Text-figs 1 & 3). Zalasiewicz and Tunncliff (1994) recognised the graptolites *G? avitus*, *A. ascensus* and *P. acuminatus* in this succession (Fig. 3). These taxa have been employed in biostratigraphy elsewhere, with the first appearance of *A. ascensus* and *P. acuminatus* used to define the base of their eponymous biozones (e.g. Chen *et al.* 2000) and *G? avitus* occurring in middle *persculptus* to lower *acuminatus* biozone strata in Scotland (Williams 1983). In the Cerig Gwynion Quarry succession the first appearances of *G? avitus* and *?N. parvulus* occur at horizon C3 (middle *persculptus* Biozone), whilst the first appearance of *A. ascensus* is at horizon C5 (upper *persculptus* Biozone) where *?N. parvulus* also occurs. The last appearance of *?N. parvulus* and *A. ascensus* is at horizon C6 (lower *acuminatus* Biozone), which also sees the first appearance of *P. acuminatus*. Though it would be premature to divide the *persculptus* Biozone into separate *persculptus* and *ascensus* Biozones based on a single section, detailing the occurrence of these taxa at this locality may be of use for comparison with other successions in central Wales (e.g. the Hafren Forest section described above).

Whilst *N? parvulus* is known from both Ordovician and Silurian strata, *P. persculptus* is only definitely known from Ordovician strata (Loydell 2007). Thus the occurrence of *P. persculptus?* in the *acuminatus* Biozone in the Prysg section may be of interest.

Graptolite evolution and the median septum

Distinguishing between N? parvulus and P. persculptus

The graptolites *N.? parvulus* (Lapworth 1900, p. 132) and *P. persculptus* (Elles & Wood 1907, p. 257) bear a striking resemblance to each other, so much so that these species have at times been conflated (see synonymy in Chen *et al.* 2005a, p. 266, for example). This might in part reflect the poor preservation of their lectotypes and lack of illustrated topotype material for either taxon (Williams 1983; Zalasiewicz & Tunnicliff 1994) meaning that the morphological variation of the type population remains uncertain. Both *P. persculptus* and *N.? parvulus* are based on late Ordovician material from central Wales, and the two types are refigured here for comparison (Fig. 5Q, S). The type of *N.? parvulus* has an incomplete proximal end (Fig. 5Q) and does not extend beyond its fifth thecal pair. The type of *P. persculptus* is preserved as a distally incomplete compression (Fig. 5R), however lying adjacent to the type is a well-preserved topotype suitable for measurement (Fig. 5S). These taxa have been recognised worldwide with *N.? parvulus* displaying closer thecal spacing and narrower dorsoventral widths than *P. persculptus* (e.g. Williams 1983; Koren' & Rickards 1997; Loydell *et al.* 2002; Chen *et al.* 2005b; Loydell 2007; Table 1). However, these specimens occupy a morphological continuum based on the measurements of widths and 2TRDs for proximal thecae, and Zalasiewicz & Tunnicliff (1994, p. 705) suggested that *N.? parvulus* and *P. persculptus* may represent “end member[s] of a single, variable species.”

Recent work has led to a slightly revised concept of *N.? parvulus*, with several authors diagnosing it on its distal morphology (e.g. Loydell 2002, 2007; Chen *et al.* 2005a). Loydell (2007, Text-fig. 9) distinguished ‘*N. parvulus*’ from ‘*N. persculptus*’ on the basis of its 2TRD at theca 10¹, though even these specimens display a notable overlap in their dorsal ventral widths and more proximal morphology. Table 1 compares the range of variation in our material with type specimens of *N.? parvulus* (Lapworth 1900) from *P. persculptus* (Elles & Wood 1907) and the material assigned to ‘*N. parvulus*’ and ‘*N. persculptus*’ by Loydell (2007), the dimensions of which seem typical of other material assigned to these taxa (e.g. Hutt 1974; Williams 1993; Chen

et al. 2005a). Though our specimens are usually only complete to the sixth or seventh thecal pair, there are a few longer specimens amongst the collection enabling a more accurate comparison with occurrences of the taxa reported elsewhere (Table 1). Any ambiguity in differentiating these taxa may be further reduced if topotype populations were better known; however, the topotype material of *P. persculptus* is poorly preserved (Williams 1983) and only a single specimen is known from the type locality of *N? parvulus* (Zalasiewicz & Tunnicliff 1994).

?N. parvulus and P. persculptus: one or two lineages?

This study shows that there is considerable variation in the morphotype of these normalograptids with time, showing an alternation between broader and narrower forms. These may represent either one or two lineages. A single lineage united by the progressive delay in the median septum comprising *P. persculptus* - *?N. parvulus* - *N.? cf. parvulus* - *P. cf. persculptus* would require considerable morphological plasticity with regard to graptolite size. Conversely, our material could perhaps represent two lineages, a narrower *N? cf. parvulus* - *?N. parvulus* lineage and a broader *P. persculptus* - *P. persculptus?* lineage. This scenario would require both lineages to undergo parallel evolution with regard to the median septum and display a 'see-saw' pattern of abundance through time. Though the precise evolutionary relationship of these taxa is as yet uncertain, the progressive delay in insertion of the median septum in these taxa is unambiguous.

Delayed insertion of the median septum

Progressive delay in the insertion point of the median septum is also known to occur within other lineages of biserial graptolites and may provide a mechanism for the evolution of aseptate forms. In *Rhaphidograptus toernquisti* (see Rickards 1970, Hutt 1974, p. 53) the median septum occurs at thecal pair 9 in specimens from the early Aeronian (*triangulatus* and *magnus* Biozones) and at thecal pairs 9-11 in stratigraphically younger

specimens (*argenteus* Biozone). Similar delay in the median septum was recorded in the early Silurian Baltic taxa '*Climacograptus scalaris transgrediens* n. var. forma α - δ ' and '*C. medius*' (Waern 1948, pp. 449, 454). Waern noted a progressive delay in the insertion point of the median septum (on the reverse side) from between theca 2¹ and 3¹ to between theca 3¹ and 4¹, and subsequently to thecal pair 4-5. We are not aware of a graptolite lineage in which the insertion point of the median septum becomes more proximal at stratigraphically higher levels.

A complete median septum divides the rhabdosome into two portions, forming the dorsal wall of two separately growing stipes. The point of insertion of the full median septum marks the position of the dicalyc and the point at which one stipe with alternately growing thecae divides into two. However, certain cryptoseptate species exist in which these separately growing stipes were connected through a series of foramina that punctuated an otherwise complete median septum (e.g. Fortey 1971, Text-fig. 4). The median septum may have also served to strengthen the rhabdosome. It inserts in the obverse and reverse walls of the rhabdosome but does not protrude distally beyond the rhabdosome, consistent with it serving as a cross-brace and probably precluding a hydrodynamic function. The creeping tubes of modern pterobranchs consist of a series of fusellae-like increments that readily detach from each other given even the mildest perturbation (AAP unpublished observations). As noted above, the reverse section of the median septum is lost or proximally atrophied in several taxa, and is not secondarily regained. If it served to strengthen the rhabdosome, its loss could perhaps be compensated for by the secretion of cortical bandages, which tend to have a criss-cross habit oblique to fusellae (Crowther 1981), and may provide an alternative means of strengthening the partially septate portion of the rhabdosome.

Conclusions

Morphometric analysis of graptolites from the latest Ordovician through earliest Silurian of central Wales identifies four successive *persculptus/parvulus*-like morphologies, revealed particularly by changes in

the insertion point of the median septum. The progressive delay in the insertion of the median septum suggests these taxa underwent directional microevolution; however, it is as yet unclear whether they represent either one or two lineages. These taxa can be used for refined stratigraphic correlation with a sub-graptolite biozone resolution. Presently, such patterns have not been recorded when these taxa occur in other Avalonian sequences (e.g. Hutt 1974) or elsewhere, perhaps reflecting the scarcity of numerous and well-preserved specimens in these collections.

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Fig. 1. Geographical location of the graptolite collections from central Wales: A, distribution of Llandovery strata in Wales; B, D, Cerig Gwynion Quarry and Prysog; C, Ystradffin.

Fig. 2. Rock exposures of the “*persculptus* band”: A, Cerig Gwynion Quarry; B, Ystradffin (photograph taken from near waterfall looking east). For position of sampled horizons see Fig. 1.

Fig. 3. Stratigraphic position of horizons C1 to C7 within the Cwmere Formation at the Cerig Gwynion Quarry and Prysog sections. Summary morphological and morphometric information for graptolites recovered from these horizons provided as means plus or minus one standard deviation for measurements of 2TRD (*sensu* Howe 1983) and dorsoventral width (DVW). The precise rock interval between horizon C6 (the uppermost horizon in Cerig Gwynion Quarry) and C7 (Prysog) cannot be determined. Biostratigraphy, lithostratigraphy and first appearance datums (FADs) of biostratigraphically important graptolites as Zalasiewicz & Tunncliffe (1994)

Fig. 4. Preservation of graptolites from central Wales. A-B, E-F are backscattered electron micrographs, C, G are secondary electron micrographs, and D, H are light micrographs of specimens whitened by coating with ammonium chloride. A-B, graptolites from horizon C5, oblique and orthogonal profiles at x33 and x36. The ‘white phase’ is a pyrite or sphalerite steinkern and the ‘light’ and ‘mid grey’-phases are phyllosilicate “strain fringes”. C-D, pyritised graptolites from Cerig Gwynion Quarry, showing preservation of fusellar increments in both kerogenised periderm, charcoal grey, and pyrite steinkern, light grey (C) and in pyrite (D), magnifications x23 and x14. E-F, graptolites from horizon Y1, orthogonal profiles through undistorted and tectonically deformed specimens at x26 and x38, phases are as A & B, except the darkest grey phase is a silica strain fringe. G, pyritised graptolite with preservation of fusellae in kerogenised periderm, and fibrous phyllosilicate “strain fringes”, magnification, x41. H, pyritised and diagenetically flattened graptolites, x10.

Fig. 5. Graptolites from the latest Ordovician and earliest Silurian of central Wales. A-E, R-S, *Persculptograptus persculptus* (Elles & Wood), including topotype (R) and lectotype as designated by Williams (1983) (S); F-M, *Normalograptus? cf. parvulus* (Lapworth); N, ?*Normalograptus parvulus* (H. Lapworth); O-P, *Persculptograptus persculptus* (Elles & Wood); Q, *Normalograptus? parvulus* (Lapworth) lectotype as designated by Zalasiewicz & Tunnicliff (1994). A, EJB412, horizon C1. B, EJB408, horizon C1. C, EJB953, horizon Y1. D, EJB958, horizon Y1. E, EJB963, horizon Y1. F, JZ4681, horizon C2. G, JZ4890, horizon C2. H, JZ4877, horizon C2. I, JZ4858, horizon C2. J, EJB412, horizon C2. K, EJB129, horizon Y2. L, M, EJB97, horizon Y2. N, JZ4761, horizon C5. O, DJ8812, horizon C7. P, JZ417, horizon C7. Q, BU 1293, Gwastaden, Rhayader, *persculptus* or *acuminatus* Biozone (see Zalasiewicz & Tunnicliff 1994). R-S, GSM11782, Ogofau, Pumpsaint, *persculptus* or *acuminatus* Biozone (see Williams 1983). A-B, H-J, N-P, Cerig Gwynion Quarry and Prysg stream section. C-E, K-M, Ystradffin. Specimens prefixed EJB, JZ, DJ and GSM are in the collections of the British Geological Survey, Keyworth. BU is Birmingham University, Lapworth Museum. A-Q x10, R-S x5.

Fig. 6. Dorsoventral width (left column) and 2TRD (*sensu* Howe 1983) for specimens from Cerig Gwynion Quarry (horizons C1, C2) and Ystradffin (horizon Y2). Using these criteria, the range of variation between *parvulus*-like and *persculptus*-like specimens in our collections is continuous. However, the insertion point of the median septum and overall shape of the rhabdosome, in conjunction with dorsoventral width, can be used to define four stratigraphically discrete morphotypes as noted in the text.

Table 1. Total range of variation in our specimens compared to the types of *N? parvulus* (Lapworth 1900) and *P. persculptus* (Elles & Wood 1907) and specimens assigned to '*N. persculptus*' and '*N. parvulus*' in Loydell (2007, pp. 41-44, Text-fig 9) . Abbreviations as Fig. 3.

Table 2. Measured specimens from Cerig Gwynion, Prysg and Ystradffin sections.

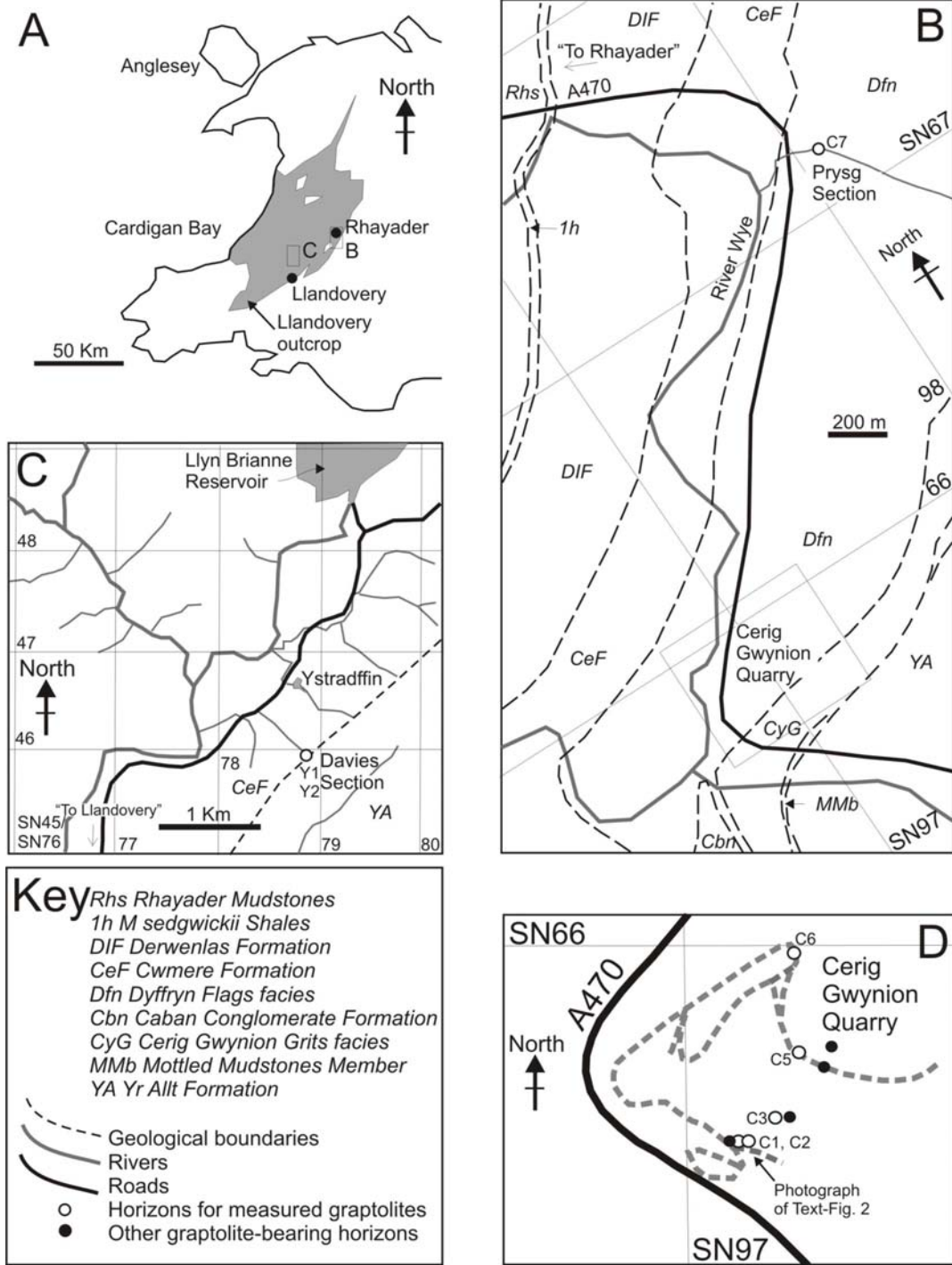


Fig. 1

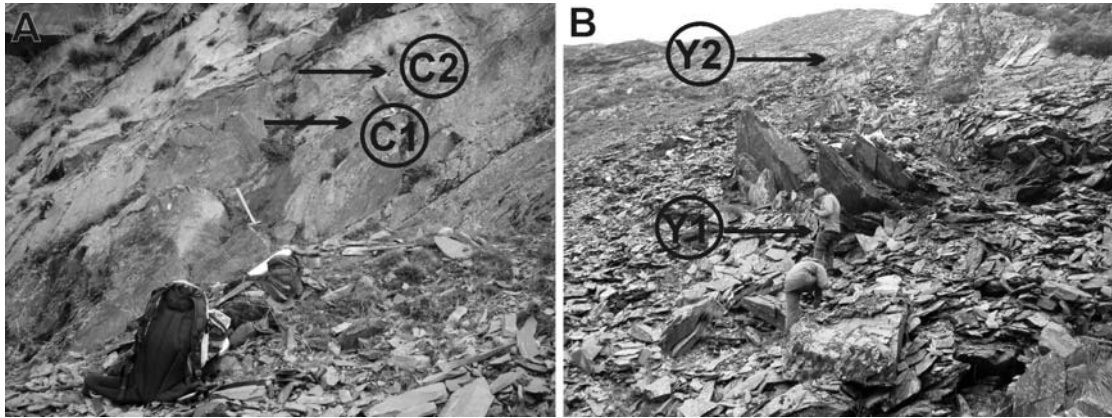


Fig. 2

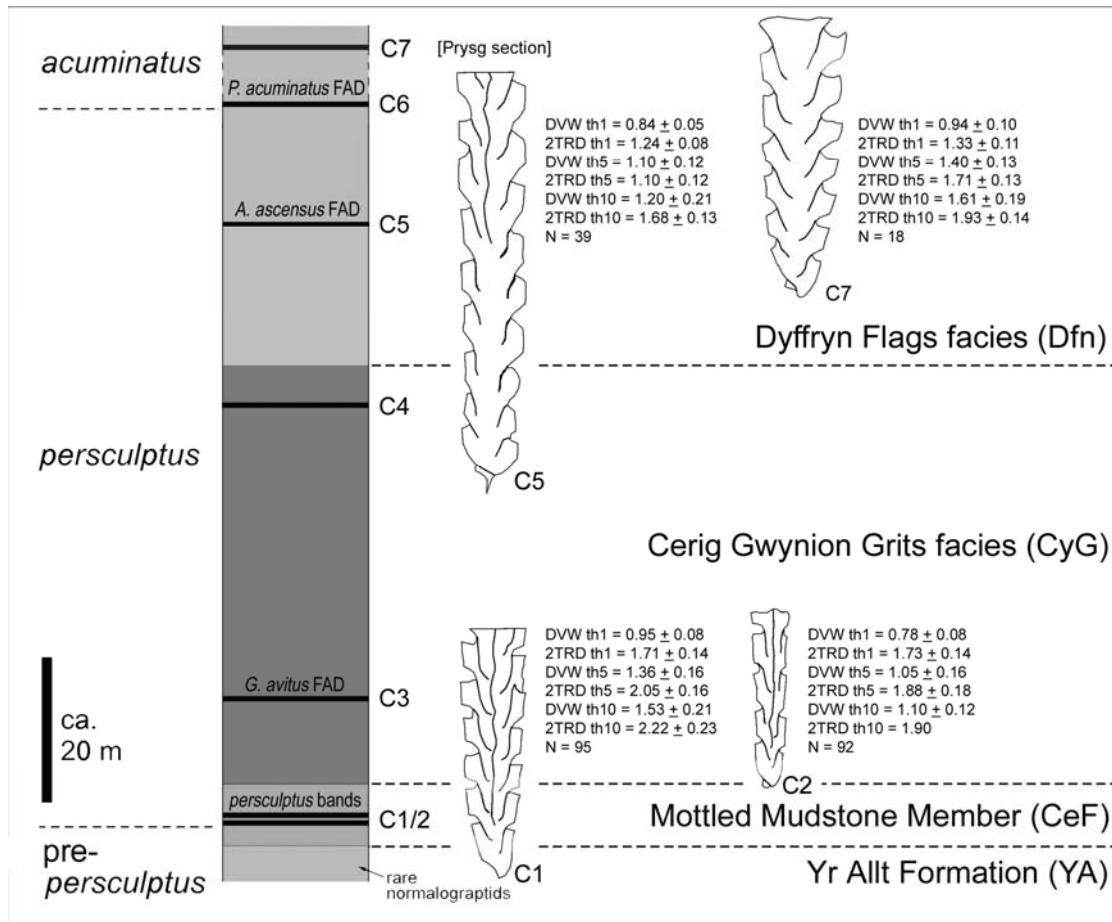


Fig. 3

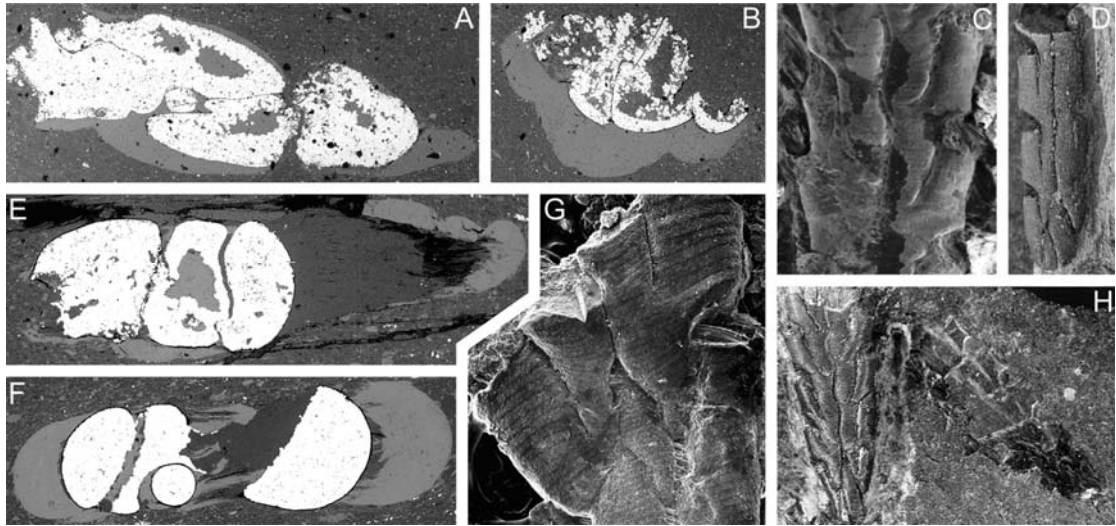


Fig. 4

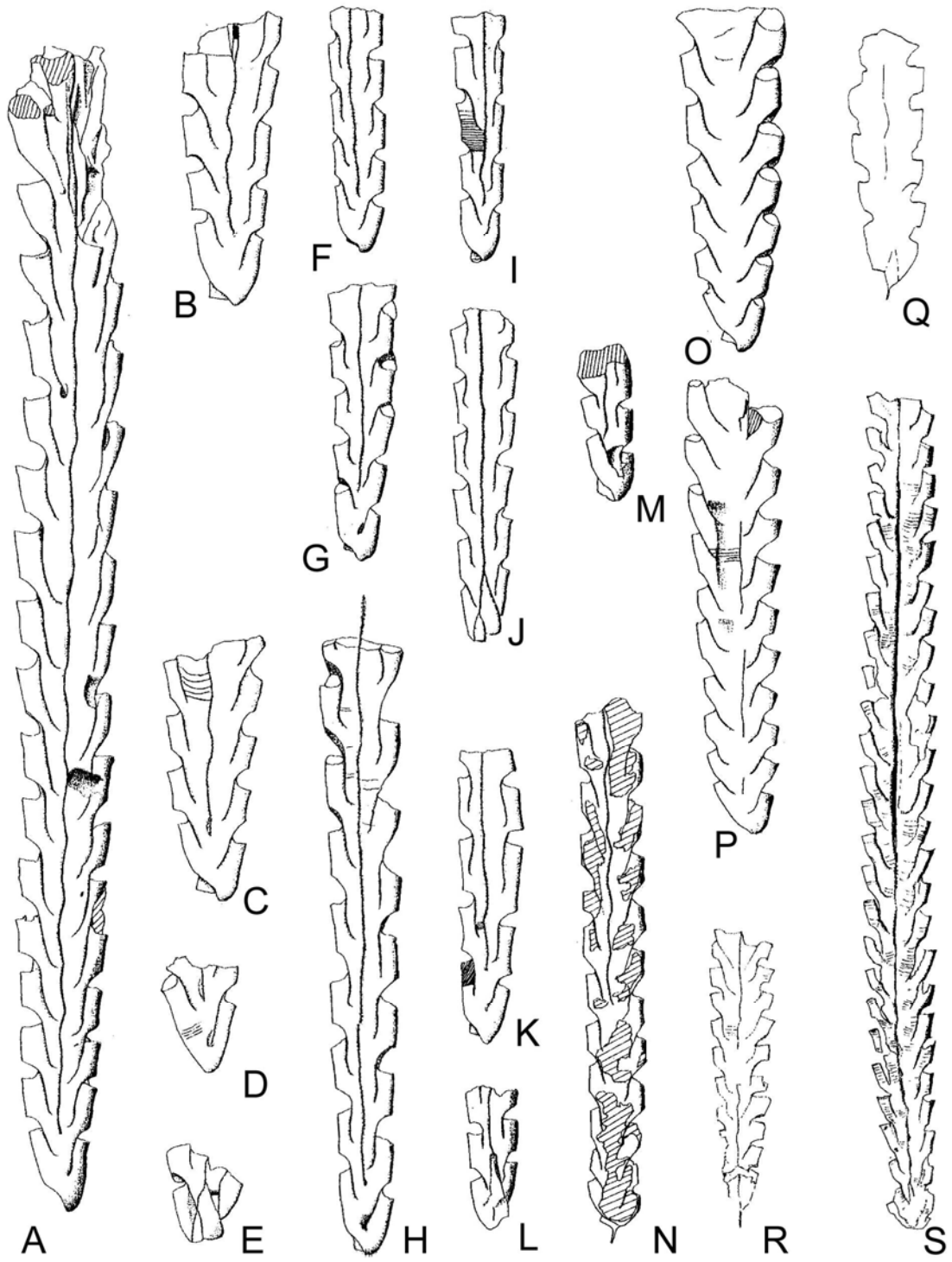


Fig. 5

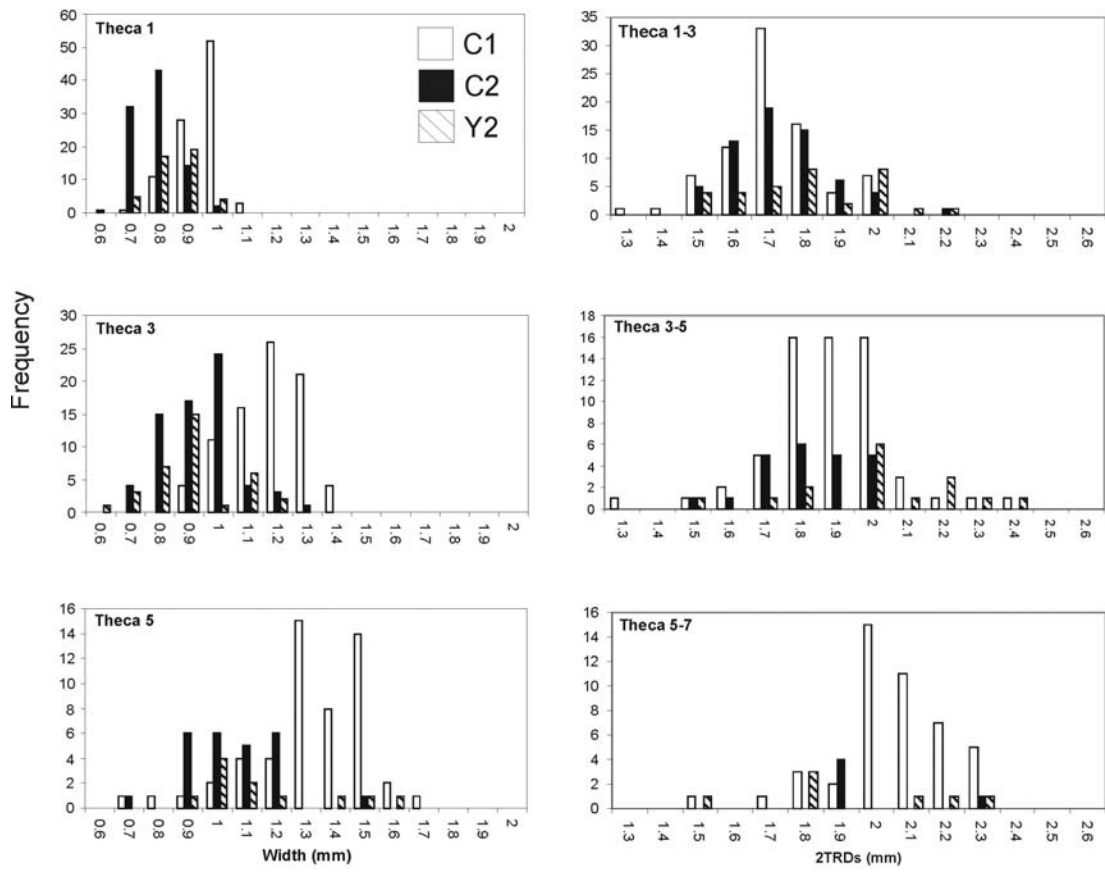


Fig. 6

Table 1

* th2-4 † th4

Taxon	Material	Locality	Biozone	DVW th1	2TRD th1-3	DVW th5	2TRD th5-7	DVW th10	2TRD th10-12
<i>P. persculptus</i>	C1, Y1 (Table 2)	Cerig Gwynion Quarry, Rhayader, and Ystradffin, Wales.	earliest <i>persculptus</i> Biozone	0.70 – 1.10 mm	1.30 – 2.00 mm	1.00 – 1.70 mm	1.50 – 2.30 mm	1.10 – 2.00 mm	1.70 – 2.60 mm
<i>N? cf. parvulus</i>	C2, Y2 (Table 2)	Cerig Gwynion Quarry, Rhayader, and Ystradffin, Wales.	early <i>persculptus</i> Biozone	0.60 – 1.00 mm	1.50 – 2.20 mm	0.90 – 1.50 mm	1.70 – 2.40 mm	0.90 – 1.20 mm	1.90 mm
? <i>N. parvulus</i>	C3-6 (Table 2)	Cerig Gwynion Quarry, Rhayader, Wales.	mid <i>persculptus</i> Biozone - early <i>acuminatus</i> Biozone	0.70 – 1.00 mm	1.10 – 1.60 mm	0.90 – 1.40 mm	1.40 – 1.80 mm	0.90 – 1.80 mm	1.50 – 1.90 mm
<i>P. persculptus?</i>	C7 (Table 2)	Prysg Stream section, Rhayader, Wales.	mid <i>acuminatus</i> Biozone	0.80 – 1.20 mm	1.20 – 1.50 mm	1.20 – 1.60 mm	1.50 – 1.90 mm	1.40 – 1.90 mm	1.70 – 2.10 mm
<i>N? parvulus</i>	lectotype	Gwastaden, Rhayader, Wales.	<i>persculptus</i> or <i>acuminatus</i> Biozone	0.90 mm	1.50 mm	†1.25 mm	-	-	-
<i>P. persculptus</i>	topotype	Ogofau, Pumpsaint, Wales.	<i>persculptus</i> or <i>acuminatus</i> Biozone	1.40 mm	1.70 mm	1.90 mm	1.90 mm	2.0 mm	-
' <i>N. parvulus</i> '	<i>sensu</i> Loydell (2007)	United States (Loydell <i>et al.</i> 2002), Jordan (Loydell 2007), Scotland (Williams 1983).	<i>persculptus</i> Biozone - <i>acuminatus</i> Biozone	0.70 – 1.00 mm	*1.05 – 1.65 mm	1.05 – 1.60 mm	1.20 – 1.80 mm	1.25 – 1.70 mm	1.15 – 1.75 mm
' <i>N. persculptus</i> '	<i>sensu</i> Loydell (2007)	Kazakhstan (Koren' <i>et al.</i> 1980), Wales & Bohemia (Štorch & Loydell 1996).	<i>persculptus</i> Biozone	0.85 – 1.15 mm	1.25 – 1.70 mm	1.05 – 1.60 mm	1.25 – 2.10 mm	1.40 – 2.25 mm	1.80 – 2.30 mm

Table 2

C1- Cerig Gwynion	EJB 194, EJB 198, EJB 198a, EJB 199, EJB 199b, EJB 199d, EJB 201, EJB 203, EJB 205, EJB 208, EJB 213, EJB 215, EJB 217f, EJB 223, EJB 230, EJB 233, EJB 233a, EJB 237, EJB 238, EJB 240f, EJB 242, EJB 246, EJB 247, EJB 252, EJB 255, EJB 270, EJB 273, EJB 274, EJB 275, EJB 275a, EJB 275c, EJB 279, EJB 280, EJB 284, EJB 288, EJB 289, EJB 290, EJB 293, EJB 299, EJB 310, EJB 311, EJB 321, EJB 322, EJB 329, 333, EJB 349, EJB 350, EJB 351, EJB 356, EJB 362, EJB 362a, EJB 364, EJB 368, EJB 373, EJB 373a, EJB 375, EJB 376, EJB 378, EJB 379, EJB 383, EJB 383a, EJB 383b, EJB 384, EJB 389, EJB 392, EJB 393, EJB 394, EJB 394a, EJB 398, EJB 400, EJB 408a, EJB 412, EJB 420, EJB 421, EJB 421a, EJB 431, EJB 432, EJB 437, EJB 438, EJB 439, EJB 440, EJB 444, EJB 450, EJB 450a, EJB 451, EJB 452, EJB 462, EJB 463, EJB 468b.		
C2- Cerig Gwynion	EJB 488, EJB 490, EJB 475, EJB 477, EJB 476a, EJB 476b, EJB 478, EJB 480, EJB 480a, EJB 481, EJB 484, EJB 491, EJB 494, EJB 496, EJB 494, EJB 497, EJB 505, EJB 504, EJB 503, EJB 502, EJB 506, EJB 507, EJB 510, EJB 514, EJB 514a, EJB 515, EJB 515b, EJB 518, EJB 518a, EJB 519, EJB 520, EJB 521, EJB 522, EJB 522a, EJB 522b, EJB 523, EJB 524, EJB 524a, EJB 529, EJB 534, EJB 533, EJB 536, EJB 543, EJB 552, EJB 548, EJB 554, EJB 556, EJB 556a, EJB 559, EJB 562a, EJB 556, EJB 64, EJB 567, EJB 569, EJB 573, EJB 578, EJB 581, EJB 582, EJB 582a, EJB 585, EJB 586, EJB 586a, EJB 589, EJB 589a, EJB 589b, EJB 602, EJB 607, EJB 616, EJB 619, EJB 625, EJB 626, EJB 628, EJB 630, EJB 633. JZ 4851, JZ 4851a, JZ 4852, JZ 4855, JZ 4857, JZ 4858, JZ 4859, JZ 4861, JZ 4867, JZ 4867b, JZ 4872a, JZ 4872b, JZ 4874, JZ 4875a, JZ 4877, JZ 4878, JZ 4888, JZ 4888b, JZ 4890, JZ 4891, JZ 4887.		
C3- Cerig Gwynion	C5- Cerig Gwynion	C6- Cerig Gwynion	C7- Prysg
JZ 4909, JZ 4916.	EJB 641, EJB 642, EJB 642a, EJB 643, EJB 643a, EJB 644, EJB 645, EJB 646, EJB 646a, EJB 646b, EJB 647, EJB 649, EJB 650, EJB 657, EJB 658, EJB 659, EJB 659a, EJB 662, EJB 664, EJB 665, EJB 671, EJB 671a. JZ 4761, JZ 4762, JZ 4765, JZ 4766, JZ 4766a, JZ 4767, JZ 4768, JZ 4769, JZ 4772, JZ 4779, JZ 4781, JZ 4782, JZ 4784, JZ 4802, JZ 4803, JZ 4817c, JZ 4828.	JZ 4833, JZ 4834, JZ 4837, JZ 4838, JZ 4838b, JZ 4838c, JZ 4847.	DJ 8799a, DJ 8799b, DJ 8799c, DJ 8821/22, DJ 8807, DJ 8812, DJ 8815, DJ 8818, DJ 8826, DJ 8829b, DJ 8829c. EJB 415, EJB 416, EJB 417a, EJB 417b, EJB 417c, EJB 417d, EJB 417e.
C4- Cerig Gwynion			
EJB 676, EJB 677, EJB 680			
Y1- Ystradffin	EJB 921a, EJB 921b, EJB 923, EJB 926, EJB 932a, EJB 932b, EJB 934, EJB 935, EJB 936, EJB 938a, EJB 940, EJB 941, EJB 942, EJB 943, EJB 944, EJB 946, EJB 948, EJB 949a, EJB 949b, EJB 949c, EJB 950, EJB 951, EJB 953a, EJB 953b, EJB 953c, EJB 953d, EJB 955, EJB 956, EJB 956a, EJB 956b, EJB 958, EJB 961, EJB 962, EJB 963, EJB 963a, EJB 964, EJB 968.		
Y2- Ystradffin	EJB 1, EJB 6, EJB 13, EJB 18, EJB 19, EJB 24, EJB 28b, EJB 29, EJB 30, EJB 42, EJB 45, EJB 58, EJB 65, EJB 68, EJB 74, EJB 97, EJB 101, EJB 107, EJB 110, EJB 116, EJB 123, EJB 124, EJB 125, EJB 129a, EJB 129c, EJB 139, EJB 142a, EJB 142, EJB 147, EJB 148, EJB 148A, EJB 149, EJB 175, EJB 180.		

