Gauging the impact of glacioeustasy on a mid-latitude early Silurian basin margin, mid Wales, UK

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Abstract

The early Silurian (Llandovery) Gondwanan South Polar ice sheet experienced episodes of ice retreat and readvance. Marine base level curves constructed for the interval are widely assumed to provide a record of the associated glacioeustasy. In revealing a series of progradational sequences (progrades) bounded by flooding surfaces, recent work on the Type Llandovery succession in mid Wales (UK) has provided an opportunity to test this hypothesis. The grouping of these progrades into three composite sequences underpins the construction of both low order (small amplitude, high frequency) and high order (large amplitude, low frequency) base level movement curves. Revised biostratigraphical datasets for the type succession permit the accurate dating of base level events. The composite sequences record progradational acmes in the *acinaces*, lower *convolutus* and upper *sedgwickii-halli* graptolite biozones. A series of transgressions that postdate the Hirnantian glacial maximum culminated in an upper *persculptus* Biozone high-stand. Maximum flooding events also occurred during the *revolutus* and lower *sedgwickii* biozones, and the base of the early Telychian *guerichi* Biozone also marked the onset of a pronounced deepening. A review of 62 published datasets, including global and other regional base level curves, records of glacial activity, isotope data, patterns of facies and faunal flux and putative climate models, permits an evaluation of the origins of these local base level events. The concept of a Eustasy Index is introduced and shows that the impacts of global sea level movements can only be demonstrated within narrow 'eustatic windows' coincident with times of ice sheet collapse. At other times, the geometry of Llandovery area progrades reflects their accumulation across a faulted basin margin where, during periods of slow ice sheet advance, epeirogenic processes outstripped sea level movements as the dominant forcing factors. Increased levels of Telychian subsidence at first enhanced and then overwhelmed the influence of glacioeustasy as part of the region's response to the north European Scandian deformation.

Keywords: Llandovery, Silurian, Glacioeustasy, Eustasy Index, Sequence stratigraphy, Biostratigraphy, Epeirogenesis

1. Introduction

Recent studies have shown that, following its maximum in the Late Ordovician (Hirnantian), the early Silurian retreat of the Gondwana-based South Polar ice sheet was punctuated by separate episodes of ice re-advance (e.g. Grahn and Caputo, 1992; Caputo, 1998; Dias-Martinez and Grahn, 2007). Glacioeustasy has been widely cited as significant in shaping Llandovery age successions around the world, including the Type Llandovery succession in mid Wales, UK (e.g. McKerrow, 1979; Johnson et al., 1991b), and in influencing the form of Silurian sea level curves (e.g. Haq and Schutter, 2008; Johnson, 2010; Munnecke et al., 2010). Remapping and extensive biostratigraphical resampling in the Llandovery area have allowed a new sedimentary architecture to be erected and the positions of key biozonal boundaries to be revised (Figs. 2–5) (Davies et al., 2013). Graptolite discoveries coupled to new microfossil analyses underpin major changes to the biozonal cross-correlations put forward by Cocks et al. (1984) that have informed global Llandovery analysis for over a generation. In allowing more precise comparisons with other regional datasets, these revisions have permitted a critical evaluation of the influence of glacioeustasy on the type succession.

Deposition of the Type Llandovery succession took place in a ramp-like setting located along the SE margin of the ensialic Lower Palaeozoic Welsh Basin, in mid-southern palaeolatitudes (Cherns et al., 2006; Woodcock and Strachan, 2012). Though traditionally recognised as forming part of the Eastern Avalonia microcraton, Waldron et al. (2011) suggested that the Welsh Basin has more complex crustal foundations. However, the term ‘Avalonian’ remains relevant in the biopalaeogeographical sense of Cocks and Fortey (1990) and as a label for a group of loosely associated crustal terranes, the ‘Anglo-Acadian belt’ of Cocks and Fortey (1982), that lay to the south of the contemporary Iapetus Ocean (Fig. 1). Docking of these ‘Avalonian’ terranes with the more easterly craton of Baltica took place along the northern European Tornquist Zone, and is recorded in Wales by the late Katian (mid Ashgill) ‘Shelvian’ deformation (Toghill, 1992). By Llandovery times, these once separate crustal elements formed part of a unified tectonic plate and faunal province (e.g. Cocks and Fortey, 1990). Early Llandovery closure of the northern sector of the Iapetus Ocean initiated the Scandian Orogeny in Baltica (e.g. Ladenberger et al., 2012) at the same time as the late stages of the Taconic and Salinic tectonic episodes were being felt in North America (e.g. Ettensohn and Brett, 1998). Hence, tectonism was ongoing during the Llandovery throughout the circum-Iapetus realm where, within migrating foreland basins and faulted-bounded depocentres, evolving patterns of subsidence competed with eustasy in the shaping of sedimentary successions (e.g. Baarli et al., 2003).

Nowhere is this more evident than in the Type Llandovery area, where active basin-bounding faults accommodated the subsidence of the basin to the west and uplift of source areas to the east (Davies et al., 2013). Notwithstanding this tectonic backdrop, early Hirnantian facies at Llandovery and throughout theWelsh Basin, as elsewhere, record the impact of Late Ordovician glacioeustasy (e.g. Brenchley and Cullen, 1984; Davies et al., 2009). Preserved in distal settings are strata that were deposited during the maximum drawdown in sea level, whereas an unconformity records the coincident emergence and deep erosion of proximal regions. Late Hirnantian units record the pulsed transgression that post-dated the glacial maximum, and the resulting re-ventilation and faunal re-stocking of theWelsh Basin and its marginal shelf. The current study seeks to evaluate the role that eustasy, specifically glacioeustasy, went on to play in the shaping of the succeeding Type Llandovery succession.

Telychian and lower Wenlock rocks at Llandovery provide a record of deep and distal shelfal sedimentation and of increased subsidence and disruption by synsedimentary slides. Coincidental increases in the volume and grade of sediment supplied to the Welsh Basin, sourced from new quadrants and accommodated by active faulting, confirm that the late Llandovery to early Wenlock was a time when regional tectonism was resurgent throughout Wales (e.g. Woodcock et al., 1996; Davies et al., 1997). However, preceding Rhuddanian and Aeronian rocks comprise a cyclical succession of variably bioturbated and fossiliferous sandstones, sandy mudstones and mudstones that has proved better suited for eustatic analysis. It is these strata, viewed in the context of a clinoform facies model (see Davies et al., 2013), on which this study principally focuses (Figs. 3, 6).

The parameters used to establish the base level history of the Llandovery area (Sections 3 and 4) allow comparison with global syntheses of Silurian sea level change and other regional base level datasets (Fig. 1) that sample tectonic settings ranging from cratonic interiors and passive margins to deep oceans and orogenic belts (Sections 5 and 6). They also enable comparison with datasets that, by charting the distribution of glacial facies, changing isotope ratios and faunal flux, purport to chronicle sea level-linked climatic events (Section 7). A novel method of assessing the levels of correspondence between these varied datasets and the record of base level movements in the Type Llandovery area is developed (Section 8).

2. Implications of revised biostratigraphical correlations

The revised cross-correlation of the various macro- and microfossil biozonal schemes applicable to the Type Llandovery area is presented in Fig. 5. This forms the basis for the nomenclature and calibration applied throughout the paper. The graptolite biozonal scheme is that developed by Zalasiewicz et al. (2009) for the UK Silurian, with wider comparisons based on Loydell's (2011) review of other regional schemes. Further information on relevant aspects of Welsh and global Llandovery biostratigraphy, and on the sources used to compile Fig. 5, are provided as Supplementary data.

Davies et al.'s (2013) re-examination of the type succession, and of the Aeronian and Telychian stage GSSPs that it hosts, has important implications for international correlation. Rhuddanian rocks in the type succession range into the *triangulatus* graptolite Biozone, and earliest Telychian rocks pre-date the local FAD of *guerichi* Biozone graptolites. However, to avoid confusion and facilitate global comparisons, the bases of the Aeronian and Telychian stages herein follow the graptolitic definitions of current international usage (i.e. base *triangulatus* Biozone = base Aeronian; base *guerichi* Biozone = base Telychian). The consequences of applying this to the type succession are shown in Fig. 5. Moreover, where stage recognition is based on the appearances of key brachiopod taxa, which is true of many non-graptolitic successions in Europe and North America, it is now likely that the regional stage boundaries correlate with neither the Type Llandovery GSSPs nor the graptolite zonal boundaries on which they are based (see Davies et al., 2013).

Similarly, correlations based on the A1-4, B1-3 and C1-6 quasi-chronozonal scheme erected in the Llandovery area by Jones (1925), which have been widely adopted as the standard means for subdividing Llandovery strata both in the UK (e.g. Williams, 1951; Ziegler, 1966; Ziegler et al., 1968b; Cocks et al., 1970; Cocks et al., 1984) and internationally (e.g. Berry and Boucot, 1970; Johnson et al., 1985; Brett et al., 1998), should no longer be relied upon without reference to the primary dating criteria.

3. A sequence stratigraphy for the Type Llandovery area

The event stratigraphy of uppermost Hirnantian strata in the Llandovery area has been assessed by Davies et al. (2009). The overlying Rhuddanian to Aeronian facies comprise a series of progradational sequences (progrades) bounded by flooding surfaces and correlative unconformities. Such sequences represent transgressive–regressive (T–R) cycles in the sense of Embry and Johannessen (1992; also Catuneanu et al., 2011) and ‘depositional sequences’ as defined by Embry et al. (2007; Embry, 2009). Lateral and vertical changes in lithology and biota, including trace fossil assemblages, record the repeated basinward migration of shallower, intensely bioturbated, sandy foreset facies across their deeper, more distal and muddy bottomset counterparts (Davies et al., 2013) (Fig. 3). The reduced levels of bioturbation displayed by bottomset facies and a trace fossil assemblage dominated by *Chondrites* are consistent with deposition at depths that lay beyond the colonising reach of contemporary shelly benthos. In contrast, foreset facies belts were home to a diverse and abundant assemblage of soft-bodied, burrowing organisms that lived alongside *Stricklandia* and deeper *Clorinda* community shelly benthic assemblages (e.g. Ziegler et al., 1968a). Topset facies were anchored to an active and erosion-prone fault footwall region, but their characteristic *Pentamerus* Community assemblages (Plate 1) extended into upper foreset settings where they serve to identify periods of maximum shallowing (Fig. 6). It is of note that, whereas appearances of *Stricklandia* and *Pentamerus* community assemblages in cratonic interior successions are normally viewed as evidence of off-shore deposition and deepening (e.g. Witzke, 1992), in the basin margin setting at Llandovery they are associated with peak shoaling episodes. Truncation surfaces are present locally at the top of each prograde. Shoreline ravinement (e.g. Embry, 2009) may have contributed to the development of these surfaces, but where they merge to form the compound unconformities that characterise condensed proximal successions (Figs. 3, 4) subaerial denudation was likely to have been the dominant erosive process.

Ten flooding surfaces define nine (low order) prograde sequences that span the late Hirnantian to Aeronian interval, the tenth and youngest of these flooding surfaces marking the redefined local base of the *guerichi* Biozone and Telychian Stage (Figs. 4, 6). Davies et al. (2013) labelled these progrades according to their dominant sandstone unit (e.g. Ceg^{0}, Ceg^{I}, Ceg^{II}, etc.) (Fig. 4). Differences in the scale, duration (as measured by graptolite biozones) and basinward reach of the progrades, as well as the lateral extent and vertical impact of erosion, allow these to be grouped into three compound (or high order) sequences according to the criteria established by Embry (1995) and Schlager (2004) (also Catuneanu et al., 2011; Embry, 2009) (Figs. 4, 6). In addition, many of the progrades comprise a succession of smaller scale parasequences. Local FADs and/or LADs of key taxa permit these newly recognised sequences to be dated using a range of biozonal criteria, with many FADs linked to flooding events (Davies et al., 2013). Radiometric dates available for the Llandovery Series suggest that the study interval spanned c. 6 myr (Cooper and Sadler, 2012; Melchin et al., 2012) and, hence, that the average duration of the prograde sequences recognised in the Llandovery area was well under 1 myr.

4. Relative marine base level movements

Facies and faunal variations within each sequence and compound sequence allow the construction of both low and high order relative marine base level movement curves (e.g. Embry, 2009; see also Section 6b) for the upper Hirnantian to lower Telychian succession (Fig. 6). These differ significantly from those compiled by McKerrow (1979) and Cocks et al. (2003). In the first instance, such curves plot the relative changes in depositional depth that occurred at any given location through time. However, each Llandovery area prograde appears to have been accompanied by the progressive erosion of its proximal portions, with the depth of erosion increasing in a landward direction. This suggests that these progrades do not simply record the cyclical infilling of accommodation space created by subsidence beneath a static or slowly rising base level, but periods when base level fell. It implies they were the product, at least in part, of forced regressions (e.g. Posamentier et al., 1992; Hunt and Gawthorpe, 2000). The deeper, more distal facies that closely overlie flooding surfaces provide a record of deposition during periods of rising and elevated relative base level within transgressive and high-stand system tracts. In contrast, each transition into shallower, more proximal facies signalled the onset of deposition within regressive/falling stage followed by low-stand system tracts (e.g. Catuneanu et al., 2011).

Compiled from data beyond the limits of erosion, Fig. 6 identifies the main Llandovery area base level events. The numbers used on this figure to identify sequence-defining flooding surfaces and the letters for periods of maximum flooding and shallowing are those cited throughout the remainder of the text. The first post-glacial maximum flooding surface (1), present in rocks barren of graptolites, underlies the first appearance in Wales of *taugourdeaui* Biozone chitinozoans (see Fig. 5 [12, 20]). A second flooding level (2) coincides with the FAD of *persculptus* Biozone graptolites in Wales, but which is now thought to be later than elsewhere (see Vandenbroucke et al., 2008; Davies et al., 2013; Challands et al., 2014; and Supplementary data). A third intra- Hirnantian event (3) is succeeded by Llandovery flooding surfaces that coincide with the local FADs of *revolutus* (4), *magnus* (6), middle and upper *convolutus* (7, 8) and lower *sedgwickii* (9) graptolite biozone assemblages. A further intra-*revolutus* Biozone event (5) is also recognised. The higher order base level curve points to maximum deepening events during the deposition of the upper *persculptus*, *revolutus* and lower *sedgwickii* Biozones (A–C). A marked flooding event that coincides with the local FAD of *guerichi* Biozone graptolites (10) is seen on both the high and low order datasets.

To facilitate the wider correlation of these events, it is important also to place them in the context of the revised ranges for the key brachiopod lineages and microfossil assemblages used in Llandovery correlation (Fig. 5). Thus, flooding events 1 and 2 lie within the range of the Hirnantia Fauna (Davies et al., 2009) and event 3 is closely related to the first appearance of primitive forms of *Stricklandia lens*. Event 4 coincides with the FAD of the more evolved *S. lens intermedia* alongside *eoplanktonica* Biozone acritarchs. Flooding events 5 and 6 also fall within the range of *S. lens intermedia*, event 5 marking the appearance of *maennili* Biozone chitinozoans, and event 6 of a precursor of the chitinozoan *Eisenackitina dolioliformis* within the range of *tenuis* Biozone conodonts. The intra-*convolutus* Biozone transition between *S. lens intermedia* and *S. lens progressa*, well documented in theWelsh Borderland (Cocks and Rickards, 1969; Ziegler et al., 1968b), appears related to event 7, which also marks the entry of *microcladum* Biozone acritarchs. Fully evolved forms of *S. lens progressa* are first recorded above flooding level 8, coincident with the local FADs of *estillis* Biozone acritarchs and *dolioliformis* Biozone chitinozoans. The earliest records of *Eocoelia hemispherica* at Llandovery are also from above this flooding surface, though the species is believed to first appear in the *leptotheca* graptolite Biozone (e.g. Cocks et al., 1984; Bassett, 1989). Event 9 marks the entry of the more highly evolved *E. intermedia* alongside *S. laevis*, yet specimens from above this level identified as *E. hemispherica* and *S. lens progressa* (Williams, 1951; Cocks et al., 1984) confirm an interval of overlapping ranges within the lower parts of the *sedgwickii* graptolite Biozone and the *staurognathoides* conodont Biozone. The records of *E. curtisi* at Llandovery are from a slump deposit (Davies et al., 2010, 2011), but this more evolved taxon has elsewhere also been shown to have its FAD in rocks of *sedgwickii* Biozone age (Doyle et al., 1991). No in situ shelly assemblages have been recognised closely overlying event 10 at Llandovery. However, data from elsewhere appear to confirm that only *S. laevis* and *E. curtisi* survive into and above the *guerichi* Biozone (Bassett, 1989), within which *encantador* Biozone acritarchs first appear (Davies et al., 2013).

The fault-generated uplift and deep erosion of proximal parts of the succession preclude the construction of an onlap curve (e.g. Haq and Schutter, 2008). However, the lateral extent of each of the main progrades provides an arbitrary measure of the basinward shift of facies belts associated with each relative lowering of base level (Fig. 6). The three composite sequences reached their progradational acmes (D, E and F) during the *acinaces*, lower *convolutus* and upper *sedgwickii-halli* graptolite biozones. Significant lower order progradations occurred during the *revolutus*, *triangulatus* and in the middle and upper *convolutus* biozones.

Was the forcing mechanism for these Llandovery area progrades regional isostasy, tectonism, or global eustasy and, if the latter, was this glacioeustasy, and did these factors operate in concert or separately at different times? Regional base level movement curves differ conceptually from true sea level movement curves (e.g. Grabau, 1940; Artyushkov and Chekhovich, 2001; Miall, 2004). The latter seek to provide a record of changes in sea level elevation through geological time relative to a fixed global datum, nominally taken to be modern sea level (e.g. Vail et al., 1977; Haq and Schutter, 2008). Such changes, if properly identified, must be eustatic (i.e. of global reach), even though their impacts might be rendered unrecognisable by local isostatic and/ or tectonic effects. In reality, local and regional variations in rates of subsidence, source area uplift and sediment supply, all of which are linked to ambient epeirogenesis, must play a role in fashioning the detailed shape of such curves (e.g. Artyushkov and Chekhovich, 2001, 2003; Zhang et al., 2006) and can be the dominant factors, as during the Telychian in Wales (e.g. Schofield et al., 2009). These same factors make it unlikely that the base level history and hierarchy recognised in one area will be fully replicated in another.

When seeking to discern whether regional base level movements record a global (eustatic) signal, it is therefore gross trends, major flooding surfaces and peak events that offer the best potential for testing. For this reason, the Llandovery area base level history depicted on Figs. 7 to 14 is divided into broad intervals of deepening and elevated base level (coloured blue) and of shallowing and lowered base level (coloured red) rather than simply into transgressive and regressive components. Parasequence-scale movements (Fig. 6) have been ignored. Where the boundaries between these sectors coincide with flooding surfaces, their location is precise, but where they are located on the regressive portions of the curves their placement is more arbitrary. Nevertheless, in providing a single template for comparison, this approach emerges as a practical means of gauging the broad similarities and differences displayed by a range of datasets (see Section 8).

5. Regional and UK comparisons (Fig. 7)

Comparisons with other successions appear to confirm that many of the late Hirnantian–early Telychian base level events recognised in the type area occur widely throughout the UK (Fig. 7). To the east of Llandovery, in a palaeo-landward direction, the coeval rocks of the Welsh Borderland, notably in the Church Stretton area, testify to the pulsed transgression of a dissected topography (Johnson et al., 1998). Rhuddanian rocks were either largely excluded or subsequently eroded from much of this region. The work of Ziegler et al. (1968b; also Cocks and Rickards, 1969), reinterpreted in the light of the Type Llandovery findings, point to an initial inundation of more deeply incised settings around the Rhuddanian–Aeronian boundary (B),with evidence for subsequent pre- and intra-*convolutus* Biozone flooding episodes (6 and 7). Transgressive *Pentamerus*-bearing sandstones of *sedgwickii* Biozone age bear testimony to a more extensive inundation (9 and C), and the subsequent deepening that widely introduced *Clorinda* Community benthic assemblages can be matched to the *guerichi* Biozone flooding event at Llandovery (10).

Further west, in the contiguous, graptolitic, deep water Welsh Basin succession, many of the events documented in the type area are mirrored by the alternation of oxic and anoxic mudstones facies and by evolving patterns of coarse clastic deposition (e.g. Woodcock et al., 1996; Davies et al., 1997; Schofield et al., 2009) (Fig. 7). Periods of falling base level are argued to have promoted the better mixing of surface and deep water layers. The introduction of oxygenated waters then allowed a burrowing fauna to colonise the basin floor (e.g. Page et al., 2007; Challands et al., 2008). The resulting mudstone facies are, accordingly, strongly burrow-mottled. The coincident rejuvenation of sediment source areas and increased clastic input is recorded by the expansion and migration of sand-dominated turbidite lobes locally present on the basin floor (e.g. Cave and Hains, 1986; Davies and Waters, 1995; Davies et al., 2006 a, b;Wilson et al., 2016). In contrast, episodes of rising base level have been linked to the establishment of a strongly stratified basin water column, the imposition of anoxic (anaerobic) bottom waters and, due to the exclusion of burrowing organisms, the accumulation of laminated, organic-rich mudstones (e.g. Leggett, 1978). The coeval drowning of source areas and the decline in sediment supply is reflected in the synchronous contraction of the basin's deepwater sandy systems (e.g. Schofield et al., 2009).

This level of linkage between the successions of the Welsh Basin and its contiguous margin is to be expected. Closely comparable oxic/anoxic alternations are recognised in Llandovery successions that also formed along the southern seaboard of Iapetus at Llanystumdwy and Conway (North Wales) and in the English Lake District (e.g. Baker, 1981; Rickards, 1970; Rickards and Woodcock, 2005) (Fig. 2). Their presence in the Llandovery succession at Dob's Linn in the Scottish Southern Uplands is more telling. There, in Aeronian strata, units that are barren of graptolites, with quasi-oxic mudstone beds, alternate with richly graptolitic, anoxic intervals (Toghill, 1968) in a pattern that can be matched to that in the Welsh Basin (Baker, 1981; Loydell, 1998; Page et al., 2007) and, by extrapolation, to many Type Llandovery events. This is significant since the succession in Scotland has been interpreted as an accretionary prism of Iapetus ocean floor sediments accreted during subduction along the southern edge of Laurentia (e.g. Leggett et al., 1979;Woodcock and Strachan, 2012; but see Stone et al., 1987). Hence, it offers evidence that many of the base level events recognised in the Llandovery area can be linked to changes in seawater chemistry that affected both intra-cratonic and oceanic settings alike. Only in the mid Rhuddanian do these successions fail to provide clear evidence of correlatable changes in facies and base level.

6. Llandovery eustasy

Whether it is feasible to discern a eustatic signal in ancient sedimentary successions is widely questioned by those who argue that the 'noise' of regional factors is always likely to 'drown out' the impacts of all but the largest and most rapid global sea level movements (e.g. Miall, 2010) (see Section 8). Those who have published on Silurian eustasy take care to acknowledge and to counter such concerns (e.g. Witzke, 1992; Johnson, 2010). They point to facies, faunal and, increasingly, isotopic shifts that can be linked to changes in bathymetry, and appear to be widely correlatable, as evidence of global movements in marine base level. Johnson et al. (1991b) labelled this empirical approach the pursuit of 'practical eustasy' and, utilising regional datasets, many have since attempted to construct curves that purport to chart changing Silurian sea levels (Fig. 8).

The varied methods used in the construction of Silurian sea level curves and the concepts that underpin them have been reviewed by Johnson (2006, 2010). In shallow shelfal settings, systematic changes in benthic brachiopod (e.g. Johnson, 1987, 1996; Johnson et al., 1991a) and conodont (e.g. Zhang and Barnes, 2002b) assemblages have proved effective in identifying gross trends and peak events, despite the misgivings of some (e.g. Aldridge et al., 1993; Loydell, 1998). Johnson et al. (1985) (also Rong et al., 1984) suggest that variations in graptolite diversity may similarly reveal the impact of sea level changes in otherwise uniform deep water mudstones. Linked changes in lithofacies and biofacies have been used in both shallow water carbonate (e.g. Witzke, 1992; Copper and Long, 1998) and siliciclastic successions (e.g. Brett et al., 1998; Melchin and Holmden, 2006), and, in a variant of this approach, Baarli (1988, 1998; also Baarli et al., 1992) and Long (2007) chart changes in the frequency and thickness of storm beds (tempestites). Johnson et al. (1998) gauged the onlap of palaeotopography. Many of these studies deliberately target the successions of cratonic interiors on the assumption that tectonically stable regions are those most likely to preserve the imprint of eustatic events (e.g. Johnson et al., 1991b). Evidence of regional epeirogenesis within and along the margins of intra-cratonic basins in which many of the most extensively studied Llandovery successions accumulated tells a different story (e.g. Artyushkov and Chekhovich, 2001, 2003; Baarli et al., 2003; Davies et al., 1997).

The 'graptolitic approach' of Loydell (1998) benefits from the precise dating achievable for graptolite-bearing intervals, which, when shown to be widely correlatable, are argued to record global flooding events and, as a consequence, widespread anoxia (e.g. Leggett, 1980; Davies et al., 1997; see Section 5). Other explanations for anoxic events, however, such as basin restriction and/or locally elevated levels of organic productivity, suggest that the link between widespread anoxia and eustasy may be more complex (e.g. Challands et al., 2008). This is illustrated in recent studies documenting redox control on faunal (Vandenbroucke et al., 2015) and facies variations (McLaughlin et al., 2012) that have previously been used to infer changes in Silurian sea level. Regional sequence analysis, used in tandem with these other methods, is widely seen as a prerequisite to curve construction (e.g. Harris et al., 1998; Brett et al., 1998, 2009; Haq and Schutter, 2008) and is the approach adopted here.

6.1. Methodology

This study replicates the approach applied to North American datasets by Johnson (1987) and first attempted on a global scale by McKerrow (1979), prior to the influential studies of Johnson et al. (1991b), Johnson and McKerrow (1991) and Johnson (1996). Figs. 8 to 12 present a range of published curves that purport to chart either regional or global movements in late Hirnantian to early Telychian marine base level. Many of their authors label them 'sea level curves'. These are compared with the base level trends and events recognised at Llandovery in an effort to gauge the levels of similarity. The implicit assumption is that trends and events that can be shown to be widely correlatable are those most likely to be eustatic (see Section 8). For many regions, more than one curve is included. This reflects the availability of datasets compiled using different methods to gauge bathymetry. Some of these reveal a coincidence of trends and events, as for example on Anticosti Island (e.g. Zhang and Barnes, 2002b; Long, 2007). However, intra-regional curves that display marked differences and may reveal the impacts of local tectonism and/or isostasy, notably in Siberia and on the Yangtze Platform of China (e.g. Johnson et al., 1985; Yolkin et al., 2003), are also utilised for purposes of objectivity. Other Llandovery datasets (Figs. 13, 14) argued to provide a proxy record of sea level change, based on physical evidence of glacial advance and retreat and the flux of stable isotope ratios, faunas and ocean states are assessed in Section 8.

6.2. Curve construction and alignment

Given the current paucity of radiometric dates and stable isotope profiles, the correlation of many Llandovery successions necessarily remains reliant on biostratigraphical methods. To facilitate this, all the curves presented in Figs. 8 to 13 have been recalibrated to align with the UK Llandovery graptolite biozonation (Fig. 5), and this has required the vertical warping of many. In recalibrating each curve, the dating criteria provided by their authors have largely been relied upon. The justification for any amendments is provided via the numbered references [in square brackets] to Supplementary data. The use of FADs and LADs has been a common theme in such re-evaluations and brings the virtue of consistency to the datasets. Nevertheless, the roles of facies control, provincialism, diachronous and divergent patterns of dispersal and cryptic omission, as well as collecting bias, all introduce uncertainty (e.g. Zalasiewicz et al., 2009; Miall, 2004). Sadler (2004; also Sadler et al., 2009) shows that FAD and LAD-based biozonal boundaries when correlated on a global scale can rarely be viewed as truly isochronous and Cramer et al. (2015) suggest that, by using multiple high resolution datasets, it may soon be possible evaluate these levels of uncertainty. As it is, Silurian chronostratigraphy remains predicated on the assumption that such uncertainties fall within geologically acceptable limits (e.g. Cramer et al., 2011a; Melchin et al., 2012) and, as Witzke (1992) argues, that in the pursuit of 'practical eustasy', "parallel changes in relative sea level coincident with biozonal boundaries are most reasonably interpreted as synchronous."

The horizontal axes of the curves are as used by their authors and reflect the different criteria they employed for calibration. Very few claim to chart changes in absolute bathymetric value, those of Ross and Ross (1996), Johnson et al. (1998), Artyushkov and Chekhovich (2001) and Haq and Schutter (2008) being notable exceptions. This use of varied criteria emphasises the need, when seeking to identify correlatable events, to focus on abrupt changes and gross trends rather than to compare precise profiles.

Before drawing conclusions from curve comparisons it is also important to consider the relative orders of movement and the relationships between the events that such curves portray. That different orders of sea level movement, superimposed upon one another, can be discerned in the stratigraphical record and that these record not just differences in vertical scale and duration, but ultimately in causative mechanism is a concept that has evolved (e.g. Vail et al., 1977; Duval et al., 1992; Embry, 1995; Schlager, 2004; Miller et al., 2005). Catuneanu et al. (2011) point to inconsistencies in this approach and highlight the misuse of numerical (1st, 2nd, 3rd, etc.) and comparative (high, low) hierarchies. In this account, high order refers to sea level curves that purport to record vertical movements of many 10s or 100s of metres that took place over time periods that can range up to several millions of years. Lower order curves depict more frequent, lower amplitude events. The concept is valuable in enabling different levels of comparison between published datasets and offering a potentially broader insight into the origins of the base level movements recorded, but the distinction is not always straightforward (e.g. Embry, 1995; Schlager, 2004) and can result in the arbitrary inclusion of lower order events on high order curves.

Periods of high order global deepening may be interrupted at the local level by prograde events that record the impact of either low order eustatic regressions and/or local influences on sediment supply and accommodation space. In the same way, low order flooding events can be expected to punctuate episodes of high order global shallowing. The offset between high order, global maxima and regional, lower order oscillations accounts, arguably, for many of the marked discrepancies in the shapes of published curves and the problems encountered when attempting to match events. It follows that modest perturbations on high order curves may reflect the impact of lower order events that, at the local level and in the field, can appear every bit as significant as those associated with high order peaks. Conversely, detailed dating can show that what appears to be a minor event in the field – a mudstone on mudstone contact for example – conceals a more significant base level history, as with the contact between the Lower and Upper Sodus Shale in New York State (Brett et al., 1998) (see Supplementary data). It is against these difficulties that the correlations presented on Figs. 8 to 12 should be viewed.

6.3. Analysis: global sea level curves (Fig. 8)

In Fig. 8, a selection of some of the most widely cited global sea level curves for the late Hirnantian to early Telychian interval are compared with the inferred base level movements recognised in the Llandovery area. Informed by the plots of McKerrow (1979), the curve of Johnson et al. (1991b) established what many came to view as the 'standard' for Silurian sea level movements, and the ages it established for key high-stand events remain essentially unmodified in all Johnson's subsequent reviews (1996, 2006, 2010). Yet, from a comparison of some of the most recent and authoritative examples of global sea level curves by Haq and

Schutter (2008) and Johnson (2010), it is clear that a consensus is some way off. The suspicion also emerges (see below) that some of the most commonly used curves are over-reliant on the data from a single region (e.g. Ross and Ross, 1996) and/or are a conflation of higher and lower order base level events, but are fully representative of neither.

In the first instance it is worth comparing the late Rhuddanian to early Telychian portion of the high order Type Llandovery curve with the same part of many of the other curves. The broad alignment of independently constructed peaks appears to offer support for a global signal within the Type Llandovery data. Several recognise a high order Rhuddanian transgression that peaked in the *revolutus* Biozone (B) (e.g. Ross and Ross, 1996; Page et al., 2007) or close to the *revolutus–triangulatus* biozonal boundary (e.g. Johnson, 1996, 2010). Loydell (1998) and Haq and Schutter (2008) delay the culmination of this event until the *magnus* Biozone and it is not inconsistent to suggest that flooding levels 4, 5 and 6 seen at Llandovery were lower order increments that contributed to this global high-stand.

The lower *sedgwickii* Biozone is also widely seen as a period of elevated sea levels (C). Some see this as the peak of a prolonged deepening episode that spanned much of the preceding *convolutus* Biozone (e.g. Johnson, 2010), and to which lower order events (7, 8, and 9) may again have contributed. Others, by showing it as a pronounced, but short-lived deepening event (e.g. Ross and Ross, 1996), imply a wider significance for the basal *sedgwickii* Biozone flooding surface (9). The late *sedgwickii-halli* biozonal interval is widely recognised as a period of falling sea levels, shown by Johnson (1996), Ross and Ross (1996) and Page et al. (2007) to have reached its acme close to the base of the *guerichi* Biozone (F). Loydell's (1998) curve is notably at odds with the majority in its depiction of late Aeronian sea level movements.

Many curves acknowledge the presence of a pre-*sedgwickii* Biozone Aeronian low-stand, but opinions differ as to its scale and timing. Ross and Ross (1996; also Page et al., 2007) restrict it to the *convolutus* Biozone. Others, by recognising its peak in the mid Aeronian *leptotheca* Biozone (e.g. Loydell, 1998, 2007; Johnson, 1996, 2010), imply a link with at least part of shoaling episode E. The depiction of a discrete early Aeronian lowering of sea level by Ross and Ross (1996) is replicated in the subsequent curves of Page et al. (2007) and Haq and Schutter (2008). It compares with a lower order progradation (Ceg^0) seen at Llandovery, but the biostratigraphical dating of this global event is suspect (see Fig. 9 and Supplementary data). Evidence of other lower order events, including both mid (7) and upper (8) *convolutus* Biozone flooding levels is provided by the curves of Loydell (1998, 2007). In marked contrast to the Type Llandovery data, most global curves show the early-mid Rhuddanian as a period of steadily rising sea levels. There is no indication of a discrete *persculptus* Biozone deepening maximum (A), or of a subsequent shallowing event on the scale seen at Llandovery (D). Ross and Ross (1996) and Page et al. (2007) depict what appears to be a low order pre-*revolutus* Biozone regression, but the dating and global credentials of this event are again questionable (see below and Supplementary data). The marked *guerichi* Biozone deepening at Llandovery (10) appears to show the abrupt termination of the preceding progradation (F) and the rapid onset of deep and distal sedimentation. This is consistent with the onset of regional subsidence (Davies et al., 2013) and of a period when contemporary orogenesis became the dominant influence on sedimentation within the Welsh Basin (e.g. Woodcock et al., 1996; Davies et al., 1997). A broadly coeval event widely recognised in the global datasets suggests that there was a coincidence of local and global forcing mechanisms, although the curves of Haq and Schutter (2008) and Johnson (2010) are inconsistent with this.

6.4. Analysis: regional curves from circum-Iapetus provinces (Figs. 9, 10)

Following the studies of Johnson (e.g. 1979, 1987; Johnson et al., 1985; Johnson et al., 1991b) and Witzke (1992; Witzke and Bunker, 1996), Johnson (1996) recognised Laurentian-based eastern Iowa as the ‘type district’ for his four Llandovery high-stand events. The adjacent, closely comparable succession in Illinois appears to have influenced Ross and Ross (1996, Fig. 2) in the construction of their sea level curve published in the same volume. Thus, the dating and interpretation of these mid USA successions has been critical in the evolution and application of the eustatic concept to the early Silurian in North America and globally. This is significant as the dating of many of the key events recognised in Iowa and Illinois is open to question (see Supplementary data) and has implications for their wider correlation. Despite this, recalibrated regional curves mainly from Laurentian North America and from Baltica (e.g. Baarli et al., 2003) offer insights into the number and scale of lower order base level events in these areas (Figs. 9, 10).

The *revolutus* Biozone deepening maximum (B) and the *sedgwickii* Biozone transgression (9), deepening maximum (C) and subsequent progradation (F) appear to be widely recorded in many of the recalibrated Laurentian datasets (e.g. Harris and Sheehan, 1997, 1998). A deepening during the *guerichi* Biozone (10) is also acknowledged where rocks of this age have escaped intra-Telychian erosion (Kluessendorf and Mikulic, 1996), as on Anticosti Island and in Arctic Canada (e.g. Zhang and Barnes, 2002b; Melchin and Holmden, 2006). In contrast to the global datasets, several North American curves (Figs. 9, 10) suggest the presence of both early and mid Aeronian shallowing events, though, with the exception of the curve for Iowa (Fig. 9, curve 1), few endorse the scale and duration of prograde E seen at Llandovery. In addition to the base *magnus* Biozone transgression (6), multiple flooding events in strata believed to span the *leptotheca* and *convolutus* biozones (e.g. Harris et al., 1998; Long, 2007) raise the possibility that flooding surfaces matching those that define parasequences at Llandovery may be present, as well as those that define Llandovery area sequences (7 and 8). On the other hand, it is clear that significant non-sequences interrupt many of these successions and, whilst offering evidence of shallowing and subaerial erosion, these may also account for the non-preservation of key flooding levels (see Section 8). Zhang and Barnes (2002b) recorded a marked lowstand on Anticosti Island that matches closely the upper *convolutus* Biozone prograde at Llandovery. It succeeds a pre-*sedgwickii* Biozone deepening episode (8) and underlies a flooding surface that marks the local FAD of *sedgwickii* Biozone graptolites (9). The recalibrated curves for Iowa and Illinois offer evidence for a comparable shoaling between the regional FADs of *S. lens progressa* and *S. laevis* (Johnson, 1975;Witzke, 1992). The data from Baltica (Norway, Sweden, Estonia and

Russia) are more varied (Fig. 10), consistent with deposition in tectonically active basins (e.g. Baarli et al., 2003; Dahlqvist and Bergström, 2005). In northern Estonia, Nestor and Einasto (1997) recognised flooding levels consistent with events 4, 5 and 6 at Llandovery. This level of detail is not replicated by other Baltic datasets, although most show a *revolutus* Biozone deepening episode (B) (e.g. Johnson et al., 1991a; Baarli et al., 2003). Many of the recalibrated Baltic curves also indicate a period of sustained Aeronian shallowing. In the Russian Timan–Petchora Basin, this peaked during the *leptotheca* Biozone, but it is shown elsewhere to have extended into the *convolutus* Biozone (E). The impact of a deepening that spanned the late *convolutus* to early *sedgwickii* biozonal interval, consistent with the conflation of flooding events 7, 8 and 9 and high-stand C, is seen throughout the Baltic region. Also widely acknowledged are a late Aeronian shallowing (F) and a subsequent *guerichi* Biozone deepening (10), the latter marked in Estonia by the transgressive base of the Rumba Formation (e.g. Nestor and Nestor, 2002; but see Supplementary data).

Strata of *persculptus* Biozone age are absent from many circum-Iapetus sections (see Section 7a), but where preserved in Iowa and Illinois, on Anticosti Island and in Arctic Canada, there is evidence of a deepening maximum (A) (e.g. Witzke and Bunker, 1996; Dewing, 1999; Zhang and Barnes, 2002b; Melchin and Holmden, 2006; Long, 2007). Other curves show a deepening episode extending from the Hirnantian that peaked at different times during the early Rhuddanian (e.g. Johnson et al., 1991a; Nestor and Einasto, 1997; Copper and Long, 1998). Nonetheless, several regional base level curves, notably from North America, record a subsequent high-order regression that, in common with the Llandovery area (D), peaked prior to the *revolutus* Biozone and was followed by a deepening episode (4).

The Cornwallis Island (Arctic Canada) curve of Melchin and Holmden (2006) differs significantly from other Laurentian, 'Avalonian' and Baltic datasets (Fig. 10). It shows the early–mid Aeronian as a period of slowly rising base level that culminated in an early *convolutus* Biozone high-stand, and the early *sedgwickii* Biozone as a time of falling base level that peaked well below the base of the *guerichi* Biozone. From a comparison of depth-controlled conodont assemblages, Zhang et al. (2006) concluded that Anticosti Island and Cornwallis Island experienced very different tectonic and base level movement histories.

6.5. Analysis: curves from other palaeoplates (Figs. 11, 12)

Interpreting base level curves compiled for Llandovery successions that accumulated on other early Silurian palaeoplates is more challenging. Many of these curves appear to focus on high order events and very few extend down into the Hirnantian. An exception is the well-dated, high southern palaeolatitude Gondwanan succession examined by Underwood et al. (1998). This (Fig. 12, curve 21) provides evidence of a late Hirnantian flooding episode (2) that, in common with the Llandovery area, culminated in an upper *persculptus* Biozone highstand (A). A subsequent shoaling into the *atavus* to *acinaces* biozonal interval (commonly also referred to as the *vesiculosus* graptolite Biozone) is also recognised in the Murzuq Basin of Saharan North Africa (Legrand, 2003) (Fig. 12, curve 22), where Loydell et al. (2009; 2013) view it as evidence for a glacioeustatic sea-level fall. However, the likely impact of glacioisostasy in this region persuaded Johnson (2010) that the local record of base level movements may not accurately reflect global events (see also Berry and Boucot, 1973). Certainly, curves for more northerly Gondwanan successions, which typically show the Rhuddanian as a time of generally rising and elevated base levels, more closely resemble many global datasets (Fig. 8). The Gondwanan curves for Australia (Jell and Talent, 1989; Talent et al., 2003) and the Himalayas (Talent and Bhargava, 2003) (Fig. 12, curves 23, 24), and for parts of Cathaysia (South China) (Johnson et al., 1985; also Rong et al., 2003) and Siberia (Artyushkov and Chekhovich, 2001; Yolkin et al., 2003) (Fig. 11) offer some support for a high order, *revolutus* Biozone flooding maximum (B).

Many curves, including that for the Peri-Gondwanan Prague Basin (Fig. 12, curve 18), mirror the Llandovery data in their depiction of the early-mid Aeronian as a time of falling or lowered base levels. There is evidence locally of a shoaling peak close to the base of the *convolutus* Biozone (E) followed by a high-stand event that could be viewed as a conflation of flooding episodes 7, 8 and 9. However, a majority of the curves presented by Koren et al. (2003) for Kazakhstan (Fig. 11) show only a base *sedgwickii* Biozone transgression (9). Siberian datasets, including Tesakov et al. (1998), though they record Aeronian base level movements on a range of scales, are significant for the lateral variability in base level histories that they imply. Artyushkov and Chekhovich (2001) viewed this as evidence that regional isostasy was more influential than eustasy. Many curves associate the *sedgwickii-halli* biozonal interval with a period of shoal deposition (F) and, though the form of the subsequent deepening episode differs markedly on curves for Cathaysia, Siberia, Peri-Gondwana and Gondwanan North Africa and Australia, the *guerichi* Biozone is shown overlapping a period of elevated base levels in all these areas (e.g. Kříž et al., 2003; Jell and Talent, 1989; Talent et al., 2003). In contrast, the records of base level change during this latter interval in other parts of Gondwana, in India and in Kazakhstan for example, show this as a period of base level lowering.

7. Glacioeustatic credentials

Davies et al. (2009) assessed the latest Hirnantian facies present in the Type Llandovery area that encompass events 1–3 of Fig. 6. These record the pulsed early progress in Wales of the global transgression that immediately followed the period of maximum Gondwanan ice sheet expansion (e.g. Hambrey, 1985; Ghienne, 2003; Ghienne et al., 2014). They suggested that, following the deep erosion associated with the Hirnantian glacial maximum, it was only in basin margin settings, or where there was deeply incised palaeotopography, that the earliest phases of the late Hirnantian transgression were likely to be felt and its deposits preserved. Such palaeotopography was locally effective in excluding much of the late Hirnantian (*persculptus* Biozone) to Rhuddanian succession from the Laurentian interior (e.g. Witzke, 1992; Ross and Ross, 1996; Johnson and Baarli, 2007), Baltica (e.g. Nestor, 1997) and Africa (e.g. Underwood et al., 1998). Such exclusion may account for the poor and inconsistent record of events within this interval (see Section 8). However, it is now acknowledged that this global transgressive event marked only the partial collapse of the ice sheet (e.g. Le Heron and Craig, 2008). The discovery of Llandovery glacigenic deposits in South America (e.g. Caputo, 1998) suggested to Dias-Martinez and Grahn (2007) that the locus of the

Gondwanan-based glaciation shifted over time, although facies of comparable age recently reported from Libya (e.g. Le Heron et al., 2013) confirm that a diminished ice mass continued to occupy parts of Africa. These findings support the widely held assumption that many Llandovery base level events, both high and low order, provide a record of sea level change linked to dynamic changes in the shape and extent of an extant South Polar Ice Sheet (e.g. Ross and Ross, 1996; Loydell, 1998, 2007; Nestor et al., 2003; Zhang and Barnes, 2002b; Page et al., 2007; Haq and Schutter, 2008; Johnson, 2010; Munnecke et al., 2010). It is argued that the changes in global climate and ocean state associated with these glacial events are reflected in plots of stable isotope ratios and faunal flux, fostering the belief that these too provide a proxy record of Llandovery glacioeustasy (e.g. Melchin and Holmden, 2006; Cramer et al., 2011a). The scale and duration of many Silurian base level events are also seen as consistent with glacioeustatic forcing (e.g. Johnson and McKerrow, 1991), vertical movements of 10s of metres over time periods of less than a million years generally being seen as too great for epeirogenic effects to achieve on their own (e.g. Miller et al., 2005; Csato and Catuneanu, 2012). However, this is not to say that glacioeustasy alone was instrumental, or was always dominant, particularly in tectonic settings such as the faulted margin of the Welsh Basin, where high rates of subsidence were likely to have been a significant factor (cf. Gawthorpe et al., 1994).

7.1. Analysis: known glacial events (Fig. 13)

The limited dating available for the South American glaciogenic successions, reviewed by Kaljo et al. (2003), is based principally on chitinozoans recovered from interbedded marine deposits. These data suggest that an extensive South Polar ice mass continued to occupy that part of Gondwana during the early Rhuddanian. The late Rhuddanian deepening seen in most global and some regional curves appears to reflect the first major period of melting of the South American ice mass (e.g. Dias-Martinez and Grahn, 2007). Subsequently, according to Caputo's (1998) log of glacigenic deposits (Fig. 13), a re-advance during the *triangulatus* Biozone established an extensive, slowly down-wasting ice mass that was sustained throughout much of the Aeronian, prior to an abrupt and marked retreat at or close to the base of the *sedgwickii* Biozone. This preceded a late Aeronian to early Telychian re-advance and there is evidence also for a discrete late Telychian glaciation. Periods of ice retreat (interglacials), it can be assumed, were also periods of sea level rise.

Given the paucity and nature of the fossil evidence, the suspicion persists that the dating of these glacial events is based partly on their ‘best fit’ to the ‘standard’ Llandovery sea level curve and lacks both independent corroboration and precision. At face value, the findings from South America can be seen broadly to endorse glacioeustatic credentials of the late Rhuddanian (*revolutus* Biozone) base level events seen at Llandovery (4, 5, B). Waxing and waning of the Aeronian ice sheet may account for the base level movements noted at the base of the *magnus* Biozone (6) and within the *leptotheca-convolutus* biozonal interval (7, 8), though the limited data from South America offer nothing to confirm this and these are the events that many other datasets fail to depict (see Section 8). Evidence of a discrete mid Aeronian ice advance on the scale and duration implied by the prograde seen at Llandovery

(E) is also lacking. However, episodes of interglacial deepening are seen to offer a ready explanation for the *sedgwickii* Biozone (9, C) and *guerichi* Biozone (10) deepening events.

7.2. Analysis: proxy records of climate change (Figs. 13, 14)

Key datasets include those compiled for a range of stable isotopes and for faunal events. Here, any alignment of trends and peaks with those shown by base level curves does not offer direct proof of glacially linked sea level movements, but does imply that there may have been a causative link (e.g. Munnecke et al., 2010).

7.2.1. Isotopic trends and excursions

Curves showing temporal variations in $\delta^{18}O$ and $\delta^{13}C$ are thought to reflect changes in global temperature and ice volume, and organic productivity and carbon burial respectively (e.g. Azmy et al., 1998, 1999; Cooper and Sadler, 2004; Page et al., 2007; Munnecke et al., 2010; Cramer et al., 2011a; McLaughlin et al., 2012; Melchin et al., 2013; Vandenbroucke et al., 2013). A review of the causal relationships between environmental and isotopic flux is outside the scope of this paper (see Griffiths, 1998; Gradstein et al., 2012 and references therein). The mechanisms by which isotopic fractionation is achieved are hotly debated (e.g. Attendorn and Bowen, 1997; Melchin and Holmden, 2006; Stanley, 2010; Gouldley et al., 2010) and the patterns of flux in oxygen and carbon isotope values do not always match one another (e.g. Long, 1993). Nevertheless, as many of the positive excursions seen in these isotope datasets appear to be widely correlatable, such curves have been seen to offer a proxy record of Late Ordovician and Silurian climatic events and, by extension, associated glacioeustasy.

The abundant $\delta^{13}C$ isotope data now available for the Hirnantian Series generally support linked climatic and sea level changes that facies and faunal variations appear to record, including a *persculptus* Biozone deepening maximum (A) (e.g. Underwood et al., 1997; Kaljo et al., 2008; Desrochers et al., 2010; Finnegan et al., 2011). Published curves for the Rhuddanian to early Telychian interval, including Cramer et al.'s (2011a) synthesis of published $\delta^{13}C$ carb data, depict negative excursions consistent with the late Rhuddanian high-stand and its component events (4, 5 and B) (e.g. Melchin and Holmden, 2006; Gouldley et al., 2010). Support for the pronounced flooding surface (7) that terminated the *convolutus* Biozone Ceg^1 prograde, for an early *sedgwickii* Biozone deepening episode (9), and for a deepening event that spanned the Aeronian–Telychian boundary (10), is also provided. Positive $\delta^{13}C$ excursions in the early and late Aeronian have been linked to periods of global cooling, glacial advance and sea level fall (Fig. 13). Cramer et al. (2011a) recognised their early Aeronian positive excursion as peaking during the *triangulatus* Biozone. This would endorse the glacioeustatic credentials of the Ceg^0 progradation and its defining flooding event (6), but it is unclear whether this level of precision is justified (e.g. Melchin and Holmden, 2006). The isotopic evidence for a *sedgwickii-halli* biozone shoaling event (F) is also ambiguous, both in terms of its timing and impact. The regional curves of Melchin and Holmden (2006) and Gouldley et al. (2010; based on Kaljo and Martma, 2000) differ from global sea level curves (Fig. 8) in providing support for a mid Rhuddanian shallowing as seen at Llandovery (D). Isotope excursions on the brachiopod-derived $\delta^{18}O$ curve of Azmy et al. (1998) broadly align with the main $\delta^{13}C$ excursions and offer support for Llandovery highstands during the late Rhuddanian (B) and mid Aeronian and for early and late Aeronian glacially induced regressions (Fig. 13). In common with other datasets, support for a *leptotheca*-lower *convolutus* Biozone low-stand event (E) is lacking and the impacts of a base *sedgwickii* Biozone deepening are not seen. However, the processes that led to these excursions, particularly the role played by biodiagenesis, are debated, and many authors question the unambiguous relationship between sea levels and $\delta^{18}O$ values (see Munnecke et al., 2010).

7.2.2. Graptolite faunal flux

Many of the flooding surfaces that define the Llandovery area prograde sequences are associated with the local FADs of biozonal graptolite assemblages. This implies an empirical relationship between base level events and changes in contemporary graptolite assemblages. Melchin et al. (1998) (also Storch, 1995) discussed the complex interplay of climatic, oceanic and ecological factors that likely contributed to the flux in Silurian graptolite populations. Cooper et al. (2014) pointed to an empirical relationship between Llandovery population dynamics and the global $\delta^{13}C$ curve, from which they too inferred climatic influence. It follows that the plots produced by these studies provide a further proxy means of assessing the impacts of glacioeustasy at Llandovery (Fig. 14).

In general, these plots fail to endorse biozonal scale, low order base level events, but trends that match the high order, Type Llandovery curve are clearly apparent. Cooper et al. (2014) recorded patterns of reduced extinction and elevated origination for highstands that span the *persculptus–ascensus-acuminatus* (A) interval and the *revolutus–magnus* biozones (B). The flux in populations also mirror the mid Rhuddanian (D) and mid Aeronian (E) shoaling episodes and the rising base levels associated with the *convolutus-sedgwickii* biozonal boundary (C), though in these cases the relationships between diversity, extinction and putative sea level movements appear contrary to that proposed by Melchin et al. (1998). The impacts of a late *sedgwickii-halli* Biozone shoaling event (F) and subsequent *guerichi* Biozone transgression (10) are also evident in the graptolite plots.

7.2.3. Oceanic and climate models

It is pertinent briefly to discuss the influential, if controversial oceanic model of Jeppsson (1990, 1998). Based on empirical associations of sedimentary facies and faunas, particularly patterns of conodont extinction, Jeppsson (1990, 1998) contended that the Silurian global ocean passed repeatedly between two distinct states: 'primo episodes' linked to periods of glacial advance; and 'secundo episodes' associated with times of ice retreat (see Johnson, 2006). It follows that glacially driven movements in sea level should closely mirror the pattern of primo and secundo states. Page et al. (2007), in their extension to this model, argued for a cyclical, self-regulating mechanism. They contended that the sequestration of carbon in deep water black shales and shallow water carbonates during periods of elevated global temperature led to cooling, glacial re-advance, and sea level fall. This, in turn, triggered the shutdown of mass sequestration, rising atmospheric CO_2 levels then promoting the next warming phase. Whether glacioeustasy was the cause or the effect is a moot point, but it is clear that there should be a close alignment of chemostratigraphical and sea level events.

Many dispute the universal applicability of the Jeppsson model and point to inconsistencies between its key events and those based on other sedimentary and fossil criteria (e.g. Johnson, 2006). Nevertheless, Jeppsson's (1998) schematic model of changing sea level elevations offers support for curves that show the Rhuddanian and early Aeronian as a period of elevated sea levels (e.g. Loydell, 1998) (Fig. 14). There is no evidence for a putative early Aeronian glacial advance, but there is evidence for mid-Aeronian shallowing linked to the *convolutus* Biozone (E). Jeppsson's (1998) Sandvika Event records a primo-secundo transition that is consistent with an early *sedgwickii* Biozone deepening (9 and C), but his model is at odds with many other datasets in suggesting that the resulting high-stand persisted throughout the remainder of the biozone and much of the early Telychian.

8. An index of Llandovery eustasy

In the pursuit of 'practical eustasy', there is always a temptation to invoke the periodic prevalence of local forces to explain discrepancies between regional and global trends, both in timing and scale. Subsidence is always on hand to account for regional deepening events that fall outside eustatic templates, just as tectonic uplift can be used to account for unexpected shoaling episodes. The assumption by critics of deep-time eustatic research is that it is for the exponents of eustasy to demonstrate the widespread correlatability of events (Miall, 2004). Yet, the absence of objective proof for one forcing factor does not of itself confirm the importance of others. For the relative roles played by tectonism and isostasy in fashioning local stratigraphies to be properly quantified, the relative impact of contemporary eustasy in creating and destroying accommodation space must also be evaluated (e.g. Ettensohn and Brett, 1998; Artyushkov and Chekhovich, 2001, 2003; Dahlqvist and Bergström, 2005). The need to calibrate the ambient eustatic signal is essential to both camps, particularly during 'icehouse' periods when ongoing glacioeustasy can be anticipated (e.g. Zecchin 2007; Csato and Catuneanu, 2012). The Eustasy Index methodology presented herein is intended as a possible first step towards untangling these conflicting factors at the regional level.

8.1. Eustasy index methodology

The range of techniques used to compile the 62 datasets examined as part of this study, allied to their wide palaeogeographical distribution (Fig. 1; Table 1), supports their use in an attempt to quantify the role played by eustasy in shaping the Type Llandovery succession. Each of the twelve UK graptolite biozones that have been the focus for this study (upper *persculptus* to *guerichi* biozones) have been arbitrarily subdivided into three to create a matrix with 36 rows for scoring the levels of similarity (see Supplementary data). For each of the studied datasets (Figs. 7–14), every subdivision that displays a trend comparable to (or, for proxy datasets, inferred to be consistent with) the low order curve at Llandovery – and is coloured blue or red for 50% or more of its duration – has been given a score of 1.0 (see Eustasy Index scores in Supplementary data). Segments displaying trends that compare more closely with the high order base level curve at Llandovery rather than the low order curve, indicated by the diagonal ornament on Figs. 7 to 14, are given a score of 0.5.

Account is also taken of the incomplete nature of many datasets. Where this reflects limitations of outcrop or exposure, or, as for some proxy curves, the restricted range of the sampled interval (e.g. Underwood et al., 1997), the 'missing' subdivisions are omitted from the scoring process. More difficult to account for are gaps that record the local impacts of emergence and erosion. Those of short duration – a subdivision or less – are included since it is reasonable to infer that they record the impacts of a single, short-lived episode of local base level lowering. However, where non-sequences span several subdivisions and record prolonged and/or multiple phases of emergence, it is likely that evidence of local base level movements has been lost. Therefore, with the exception of the final subdivision prior to the resumption of deposition, these too are omitted from the scoring mechanism. Analysis of the levels of representation (Fig. 15) confirms that late Hirnantian and early Rhuddanian deposits, which might otherwise record the early progress of the post-glacial maximum transgression, have been widely excluded from many of the areas for which Llandovery base level and proxy curves have been compiled. The score for each subdivision across the complete range of datasets, expressed as a percentage of its level of representation, provides the Eustasy Index (EI) for that section of the Type Llandovery base level curve (Fig. 15 and Supplementary data):

$$EI = (EIr/tR)\% \qquad (1)$$

where EIr is the sum of the Eustasy Index raw scores for a subdivision and tR is the total number of datasets in which that subdivision is represented.

The scores obtained for each subdivision of the Llandovery curve should be viewed as providing an indication only of the likelihood that eustasy was a significant factor rather than a measure of the relative importance of sea level movements in any absolute sense. Since Llandovery area events that obtain the highest EI scores are those recognised on a majority of the other datasets, it follows that eustasy was likely a factor in shaping these events wherever they have been identified. Conversely, intervals with low EI values, for which matching events in other successions are least apparent, are more likely to have been periods when regional influences on the Llandovery succession were dominant. Importantly, this need not imply that eustasy was insignificant during low scoring events (see below), or was not the dominant factor in shaping other datasets.

8.2. Eustasy Index results (Fig. 15)

At first sight, the results of this analysis appear paradoxical. Their high eustasy indices show that the Type Llandovery highstands that peaked during the *persculptus* (A), *revolutus* (B) and early *sedgwickii* biozone (C) align with episodes of global deepening, as does the basal *guerichi* Biozone flooding event (10). Many of the lower order flooding events that contributed to these deepening episodes, in the early *revolutus* Biozone and linked to the appearance of *magnus* and mid and late *convolutus* biozonal assemblages, are also inferred to have had a strong eustatic component. However, the intervening lowstands are characterised by low Eustasy Index values, notably in the early–mid Rhuddanian and mid Aeronian intervals.

The low eustasy indices for the principal Llandovery area progrades perhaps testifies to their accumulation along the margins of a tectonically active basin, a setting where regional epeirogenesis operated alongside eustasy to rejuvenate source areas and create accommodation space. Widespread source area uplift coincident with the early stages of the Scandian Orogeny and reactivation of the Tornquist Zone in Europe (e.g. Johnson et al., 1991a; Baarli et al., 2003), and with late stages of the Taconic Orogeny in North America (e.g. Ettensohn and Brett, 1998; also Brett et al., 1998), can be invoked as an alternative or enhancing mechanism for the marked early–mid Rhuddanian shallowing not widely seen outside the circum-Iapetus realm (but see below). It is principally the datasets from this same region that offer evidence of a *leptotheca* to lower *convolutus* Biozone shoaling episode on the scale observed at Llandovery. However, such analysis illustrates the difficulties of ‘practical eustasy’ as a thesis that requires us to focus on the similarities in the datasets. An alternative interpretation, consistent with its tectonic setting, is to see the influence of regional epeirogenesis on Type Llandovery base levels as normally dominant (cf. Gawthorpe et al., 1994). Periods with a high Eustasy Index can then be seen as episodes either of tectonic quiescence, during which global sea level movements were able preferentially to influence sedimentation, or when such movements were of sufficient magnitude and rate to overwhelm the regional signal. It may not be a coincidence that it is base level movements linked to interglacial high-stand events that are most clearly identified as eustatic at Llandovery (Fig. 13). The rapid and substantial rises in sea level associated with the disintegration and collapse of maritime ice sheets are those most likely to overwhelm regional epeirogenic processes, whereas the slowly falling sea levels that accompany periods of gradual ice sheet expansion are less able to outstrip regional effects as the most active forcing factors (e.g. Berry and Boucot, 1973; Morton and Suter, 1996). Yet, it remains curious that at least two of the major lowstand episodes seen at Llandovery overlap with known periods of ice sheet expansion seen in South America (Fig. 13) when glacioeustatic drawdown would be anticipated to have had an impact.

8.3. Significance of glacioeustatic, epeirogenic and orogenic interactions (Fig. 16)

EI scores, as obtained for the Type Llandovery succession, are a function of global and regional forcing factors, the detailed form of any regional base level curve reflecting the interplay between eustasy and near-field orogenesis, epeirogenesis and sediment supply. High levels of subsidence can serve locally to exaggerate the impacts of marine transgressions, in terms of both rate and reach, and to offset and mask the effects of falling sea levels (cf. Artyushkov and Chekhovich, 2003). Changes in sea level on at first drained and then flooded shelves are also accompanied by the removal and then the imposition of hydrostatic and sediment load (e.g. Long, 2007). Such changes in load will be accommodated either by isostasy or, in tectonically active settings, by the differential movement of faulted blocks (e.g. McGuire, 2012; Stammer et al., 2013; Steffen et al., 2014). Similar adjustments must have affected early Silurian source areas and depocentres, notably during periods of falling sea level when, it can be inferred, the deep erosion of a landscape supporting little vegetation (e.g. Wellman et al., 2013) resulted in the rapid transfer of sediment to marine shelves and basins (e.g. Davies and Gibling, 2010). Hence, glacioeustatic regressions and transgressions would themselves have been forcing factors in regional Silurian epeirogenesis.

Accordingly, low Eustasy Index scores should not be taken as evidence that changes in sea level were insignificant during the development of Llandovery area lowstands (Fig. 16). Coeval glacioeustasy likely contributed to these base level events, but, as sediment source areas were exposed, the rapid transfer of sediment to the subsidence prone basin margin triggered a self-sustaining epeirogenic response that quickly outstripped eustasy as the dominant forcing factor. Local base level movements then diverged from global trends. Viewed in this way, Eustasy Index results can be seen not simply as offering a measure of when eustatic forcing was dominant, but also of changing rates of eustasy (or eustatic flux). Intervals with high eustasy indices appear to equate with periods of rapid and/or frequent sea level movement. Periods with lower scores may record times when sea levels changed more slowly and epeirogenic forcing was able to dominate. These may have been periods of slowly rising or static sea level, but can also be seen as consistent with the slow, but possibly substantial falls in sea level that accompanied episodes of sustained glacial advance. Such analysis negates the need to invoke episodic tectonic events. It implies a self-regulating mechanism to account for why global and regional influences alternated in their impacts on local sedimentation, and it explains why the eustasy indices for parts of the Type Llandovery succession fail to track precisely the pronounced falls in sea level that must have accompanied known periods of ice sheet growth in South America (Caputo, 1998; Dias-Martinez and Grahn, 2007; Fig. 13). This model can be applied more widely. It is likely to have been interglacial flooding events that were most successful in drowning cratonic interiors and therefore these that are recorded preferentially by base level curves for cratonic successions. It is clear too that ‘practical eustasy’ as a methodology has tended to focus on the timing of flooding events rather than lowstands (e.g. Johnson et al., 1991b) and therefore unsurprising that Johnson's (1996, 2006, 2010) ‘standard’ sea level curve for the early Silurian, based on a ‘type district’ in Laurentian Iowa, is also biased towards such events.

Subsequently, in Wales, the Telychian onset of a more dynamic phase of regional tectonism, though it seems initially coincident with glacioeustatic deepening, signalled a long-term departure from the far field influence of glacial activity on sedimentation. The erosion of upper Aeronian and lower Telychian strata across much of Laurentia and eastern Baltica suggests that broadly coeval effects were again widely felt throughout circum-Iapetus regions where, in Europe, they record an encroaching Scandian orogenic front (e.g. Kirkland et al., 2006).

8.4. Wider implications

The Eustasy Index calculations for the Llandovery succession have implications for global sea level models. Contrary to Haq and Schutter (2008), these calculations strongly endorse the separate early and late Aeronian highstand events that the majority of global curves depict (Fig. 8). Johnson (2010) departed from previous models (e.g. Johnson, 1996) in showing the early Telychian as a lowstand, but the Llandovery area data offer support for curves that recognise this as a time of rising or elevated sea levels (e.g. Johnson et al., 1991b; Loydell, 2007; Page et al., 2007). Of particular interest is the high Eustasy Index obtained for a discrete late *persculptus* Biozone highstand seen at Llandovery (Fig. 15).

The Type Llandovery base level curves fail to offer support for the precise timing, duration and scale of glacial lowstands. Nevertheless, glaciogenic deposits in South America show that separate episodes of Gondwanan ice re-advance during the Aeronian (Fig. 13; see Section 7) overlap two of the main Llandovery area lowstands characterised by reduced rates of eustatic flux (see above). The Llandovery area findings challenge researchers to look for evidence of such activity during the comparable Rhuddanian interval also. The findings of Dias-Martinez and Grahn (2007) imply that an extensive ice mass was in place in South America at this time. The work in Africa of Underwood et al. (1998), Legrand (2003) and Loydell et al. (2009; 2013) suggests this may, in part, have been the product of a discrete intra-Rhuddanian re-advance (Fig. 12) for which some proxy datasets offer support (Figs. 13, 14). Confirmation of such an event has implications for the interpretation of shallow and deep water Rhuddanian facies in Wales previously seen as unrelated to eustatic events (e.g. Davies and Waters, 1995; Schofield et al., 2009; Davies et al., 2013). It would also imply that all the most widely cited global curves (Fig. 8) may be in error in depicting the late Hirnantian to late Rhuddanian as a period of almost uninterrupted rising sea levels.

It follows that the Eustasy Index methodology should now be applied more widely and that many of the datasets examined herein could be the focus of similar analysis. The results of such studies will serve to distinguish the impacts of local epeirogenesis and, when viewed collectively, allow the ‘standard sea level curve’ for the Llandovery to be refined. Moreover, this methodology has the potential to be used in assessing the base level credentials of correlatable marine successions of any age.

9. Conclusions

For the first time, a detailed and biostratigraphically well-constrained sequence stratigraphy is available for the Type Llandovery Series succession in mid Wales. The recognition of a series of prograde sequences with bounding flooding surfaces has enabled the construction of both high and low order relative base level movement curves for those parts of the succession that preceded the onset of Telychian tectonism in Wales. Qualified comparisons with widely cited sea level curves, isotope data, examples of facies and faunal flux and nascent climatic models allow the relative importance of global (eustatic) and regional (tectonic/isostatic) forcing to be evaluated, and the far field impacts of glacioeustasy to be tested.

The concept of a Eustasy Index emerges as a useful tool to evaluate the potentially complex interplay of local, regional and global forcing factors that shaped base level curves. Its application to the Llandovery succession suggests the presence of ‘eustatic windows’ linked to interglacial global highstands. In contrast, the glacioeustasy that accompanied the slow re-growth of contemporary ice sheets is suggested to have triggered regional epeirogenic responses that saw base level patterns during the main Llandovery area lowstands diverge from global trends, negating the need to invoke episodic tectonic events. Such an analysis invites speculation that a significant ice advance unrecognised by current global Silurian sea level models occurred during the mid Rhuddanian. Subsequently, the Telychian response to the Scandian Orogeny, though initially coincident with glacioeustatic deepening, signalled a long-term departure from the far field influence of glacial activity on sedimentation in Wales.

It is anticipated that future application of the Eustasy Index methodology to other marine successions will similarly highlight the impacts of local epeirogenesis and, in so doing, allow a more precise history of global sea level activity to be elucidated, both during the Llandovery and for other time intervals.

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Figure Captions

Fig. 1. Global Llandovery palaeogeography (after Torsvik, 2012, 440Ma) showing the distribution of tectonic plates and the locations of sections used in this study (numbers are those used on Fig. 7, Fig. 8, Fig. 9, Fig. 10, Fig. 11 and Fig. 12). Abbreviation: Su, Southern Uplands. Note, according to Ladenberger et al. (2012), the collision between Laurentia and Baltica that initiated the northern Europe Scandian Orogeny was already in progress during earliest Llandovery times (but see Kirkland et al., 2006). Cathaysia is commonly referred to as South China.

Fig. 2. a) Key areas of Llandovery aged rocks in the UK; b) Llandovery Series rocks in Wales; c) Type Llandovery area showing location of traverse lines used in the construction of Fig. 4 (after Davies et al., 2013). Abbreviations: BF, Bala Fault; CSFZ, Church Stretton Fault Zone; ELD, English Lake District; LL, Llandovery town; LPWB, Lower Palaeozoic Welsh Basin; PL, Pontesford Lineament; SSU, Scottish Southern Uplands; TL, Tywi Lineament; WBFS, Welsh Borderland Fault System.

Fig. 3. Facies model for Rhuddanian and Aeronian strata at Llandovery showing the sedimentary and faunal characteristics of the principal facies (after Davies et al., 2013). Benthic Communities are those of Ziegler et al. (1968a); BA refers to the broadly equivalent Benthic Associations of Boucot (1975); BI refers to the Bioturbation Index of Taylor and Goldring (1993). For other abbreviations see Fig. 4.

Fig. 4. Architectural models for the Type Llandovery succession (after Davies et al., 2013): a) lithostratigraphy and thickness; b) chronostratigraphy model calibrated using UK graptolite biozonation of Zalasiewicz et al. (2009); c) as b, but recast to show distribution of facies belts and progradational sequences (numbers refer to facies belts of Fig. 3). See Fig. 2 for location of lines of traverse. Abbreviations for stratigraphical nomenclature: BrF, Bronydd Formation; CcF; Crychan Formation; Ceg, Cefngarreg Sandstone Formation; Cer, Cerig Formation; ChF, Chwefri Formation; db, slump-disturbed units; DD, Derwyddon Formation; GHF, Garth House Formation; Gol, Goleugoed Formation; Rdg, Rhydings Formation; TfF, Trefawr Formation; Wow, Wormwood Formation; Ydw, Ydw Member; Yst, Ystradwalter Member. Note in b use of symbols such as Ceg0, Ceg1, etc. to distinguish separate prograde units within individual formations; and in b and c alternative base positions for the Aeronian and Telychian stages based either on current GSSPs (*) or internationally applied biozonal criteria (see Fig. 5 and Davies et al., 2013).

Fig. 5. Compilation of selected biostratigraphical ranges and biozonal schemes in use for the late Hirnantian and Llandovery series. Principal sources for columns: A, Zalasiewicz et al. (2009); B, Cocks et al. (1984), Baarli (1986; also Baarli and Johnson, 1988), Temple (1987) and Davies et al. (2013); C, Aldridge and Schonlaub (1989), Dahlqvist and Bergström (2005), Mannik (2007) and Cramer et al., 2011a and Cramer et al., 2011b; D, Verniers et al. (1995), Loydell et al. (2010), Nestor (2012) and Davies et al. (2013); E, Davies et al. (2013); F, Burgess (1991); G, Brett et al. (1998); H, Loydell (2011); I, Bergström et al. (2009) and Cramer et al. (2011a) with selected GTS 2012 (Spline) Ages of Melchin et al. (2012). Notes:

1, historic base of the Silurian System in Wales (see Davies et al., 2009; note that recent syntheses suggest that the FADs of both *taugourdeaui* Biozone chitinozoans (t) and *persculptus* Biozone graptolites (p) are significantly younger in Wales than in other parts of the world; see Supplementary data); 2, base of former Idwian Stage; 3, base Aeronian according to internationally applied criteria (Melchin et al., 2012); 4, approximate base of former Fronian Stage; 5, former base Telychian of Cocks et al. (1970); 6, base Telychian based on internationally applied criteria (Cocks, 1989 and Melchin et al., 2012); 7, historic base Wenlock Series, but see discussion in Melchin et al. (2012); T = onset of post-glacial maximum transgression in Wales (see Supplementary data for discussion re revised age of this event); GSSP = positions of current stage stratotypes (see Davies et al., 2013). In Column B solid lines show known ranges of brachiopod taxa in the Type Llandovery area; dashed lines show known ranges in Wales and the Welsh Borderlands; and dotted lines show known ranges in other areas. In other columns horizontal dashed lines denote uncertainty. Note the *persculptus* and *convolutus* biozones are expanded to allow FADs and LADs to be better illustrated; post-*guerichi* biozones are foreshortened; subdivisions 1–4 of the upper *persculptus* Biozone refer to the successive morphotypes of *Normalograptus*? *parvulus* recognised in Wales by Blackett et al. (2009). For additional sources and discussion see the notes and numbered links [in square brackets] to information submitted as Supplementary data.

Fig. 6. Generalised log of the late Hirnantian to early Telychian succession in the Type Llandovery area showing sequence stratigraphy and derived base level movement curves. UK graptolite biozone bases are taken at the first appearances (FADs) of diagnostic biozonal assemblages using the criteria of Zalasiewicz et al. (2009) (see also Fig. 5). GSSPI — relative position of Aeronian Stage GSSP; GSSPII — relative position of Telychian Stage GSSP (see text and Supplementary data). See Fig. 2 and Fig. 3 for lithostratigraphical abbreviations and explanation of facies belts. N.B. sequence stratigraphy has not been applied to Telychian strata and parasequence-scale base level movements within the *convolutus* Biozone have been omitted for clarity. *See Supplementary data for usage of upper *persculptus* Biozone; numbers 1, 2 and 3, 4 show inferred ranges of Blackett et al.'s (2009) divisions (see Fig. 5).

Fig. 7. Comparison of the Type Llandovery relative base level curves with other UK Llandovery datasets (see Fig. 1 and Fig. 2 for locations). Coloured blocks identify trends in these datasets inferred to be consistent with the base level changes recognised at Llandovery (see text) without necessarily implying a causal relationship; diagonal ruling is used for segments of datasets consistent only with inferred high order base level movements at Llandovery. All datasets have been recalibrated to fit the standard UK graptolite biozonal scheme of Zalasiewicz et al. (2009); the biozones are not drawn to scale, and are divided into three or, in the case of the *atavus-acinaces* and *sedgwickii-halli* biozonal intervals, six arbitrary subdivisions to facilitate comparisons between the datasets (see Section 8). Numbers [in square brackets] refer to notes provided as Supplementary data; dashed vertical lines on subsequent figures indicate the presence of putative non-sequences (see Section 8a).

Fig. 8. Comparison of the Type Llandovery relative base level curves with a selection of published late Hirnantian to early Telychian global sea level curves showing levels of correspondence (see Fig. 7 for explanation).

Fig. 9. Comparison of the Type Llandovery relative base level curves with a selection of published late Hirnantian to early Telychian regional base level curves for Laurentia showing levels of correspondence (see Fig. 7 for explanation). The curve of Zhang and Barnes (2002b) is simplified; that of Dewing (1999) shows the late Hirnantian–Rhuddanian portion only.

Fig. 10. Comparison of the Type Llandovery relative base level curves with a selection of published late Hirnantian to early Telychian regional base level curves for Laurentia and Baltica showing levels of correspondence (see Fig. 7 for explanation).

Fig. 11. Comparison of the Type Llandovery relative base level curves with a selection of published late Hirnantian to early Telychian regional base level curves for Siberia, Kazakhstan and Cathaysia (South China) showing levels of correspondence (see Fig. 7 for explanation).

Fig. 12. Comparison of the Type Llandovery relative base level curves with a selection of published late Hirnantian to early Telychian regional base level curves for Peri-Gondwana and Gondwana showing levels of correspondence (see Fig. 7 for explanation). Note, the curve for the Murzuq Basin is a conflation of two overlapping curves from different parts of the basin.

Fig. 13. Comparison of the Type Llandovery relative base level curves with a selection of published proxy datasets (including distribution of South American glacial facies and isotope curves) for the late Hirnantian to early Telychian showing levels of correspondence (see Fig. 7 for explanation).

Fig. 14. Comparison of the Type Llandovery relative base level curves with a selection of published datasets of trends in late Hirnantian to early Telychian graptolite populations and the oceanic events of Jeppsson (1998), showing levels of correspondence (see Fig. 7 for explanation).

Fig. 15. Eustasy Index for late Hirnantian to early Telychian base level movements in the Type Llandovery area based on a comparison of the Type Llandovery relative base level curve with the 62* regional and global datasets presented in Fig. 7, Fig. 8, Fig. 9, Fig. 10, Fig. 11, Fig. 12, Fig. 13 and Fig. 14 (see Supplementary data for detailed breakdown of scores). Shaded areas indicate base level events that score incrementally higher than the mean EI value (see Supplementary data) considered those most likely to include a dominant eustatic component. *The 62 datasets exclude the Type Llandovery relative base level curves, but include the part curve of Dewing (1999) used on Fig. 9; the Welsh Basin turbidite sandbodies shown on Fig. 7 are considered as a single dataset.

Fig. 16. Matrix of global and regional forcing factors that interact to influence Eustasy Index scores (see text).

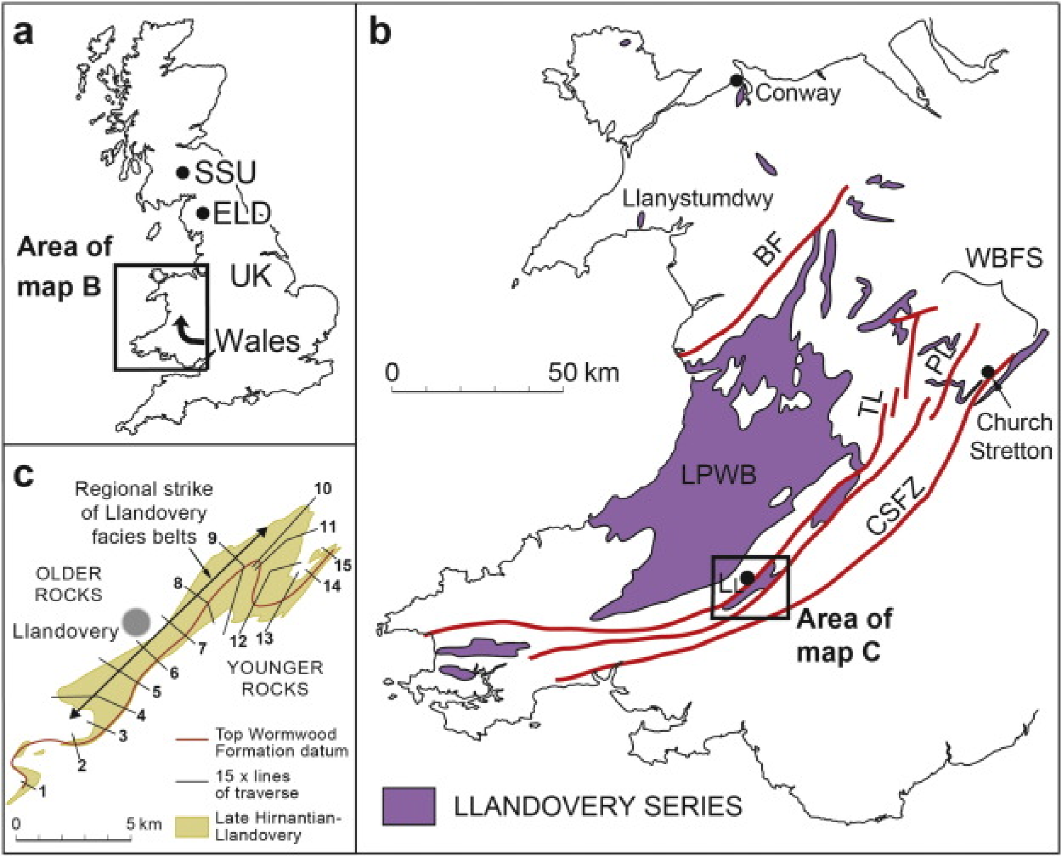
Plate caption

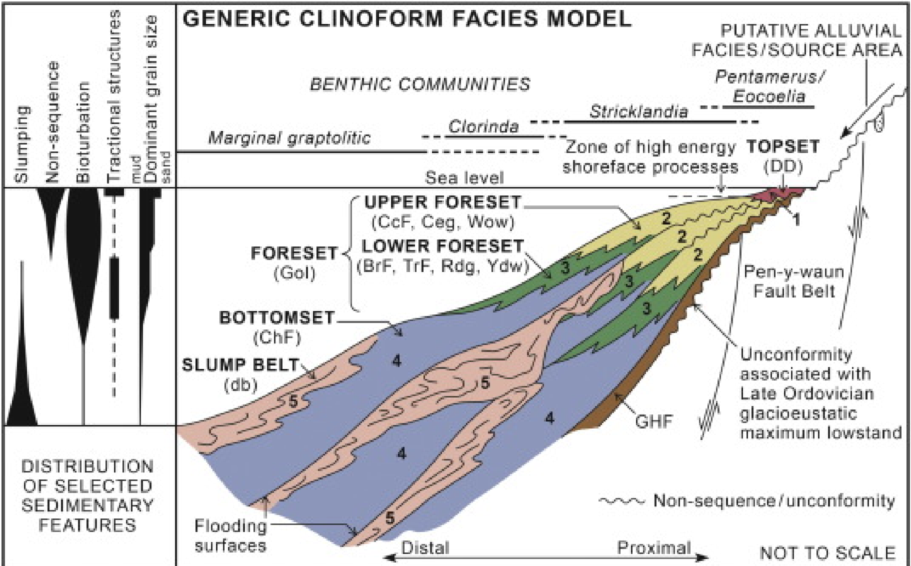
Plate 1. Coquina of adult and juvenile *Pentamerus oblongus* valves, solitary rugose corals and bivalves in topset sandstone facies, Derwyddon Formation, Crychan Forest track section, UK National Grid Reference [SN 853 385] (Torsvik, 2012).

Table caption

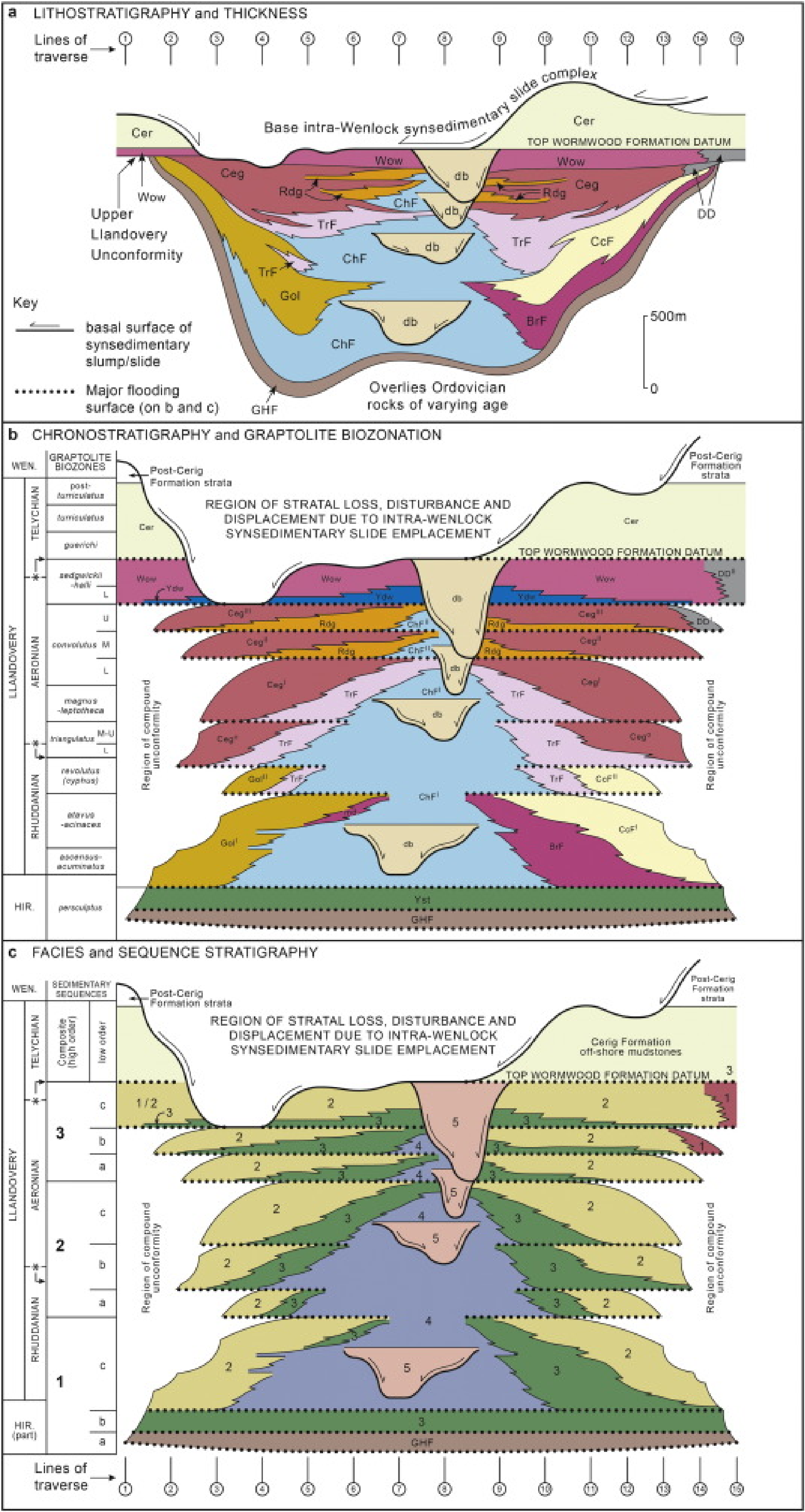
Table 1. Range of palaeogeographical (see Fig. 1) and proxy datasets used in the calculation of the Eustasy Index for Type Llandovery base level movements as shown on Fig. 15 (see text and Supplementary data).

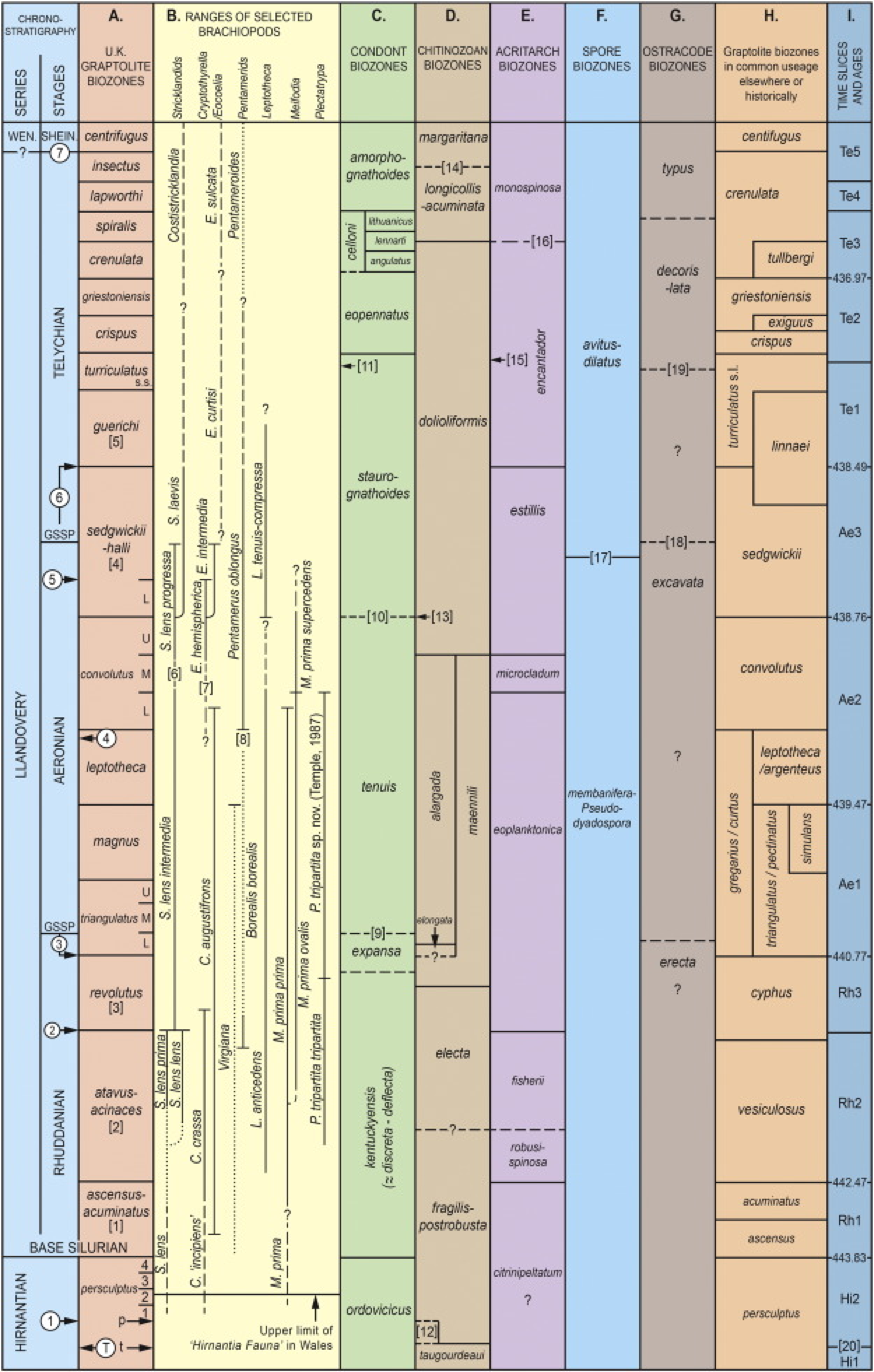
SIBERIA
14
15
Fig 11
CATHAYSIA
16
17
KAZAKHSTAN
24
Australia
Equator
Fig 10
8
7
LAURENTIA
North
America
Scotland
13
BALTICA
6
1
Fig 9
3
2
5
4
Su
9
11
12
Fig 7
10
Appalachian
Foreland Basin
IAPETUS Oc.
Avalonian
terranes
Wales &
England
RHEIC
OCEAN
18
PERI-GONDWANA
19
20
21
22
India
23
Fig 12
GONDWANA
Africa
South America

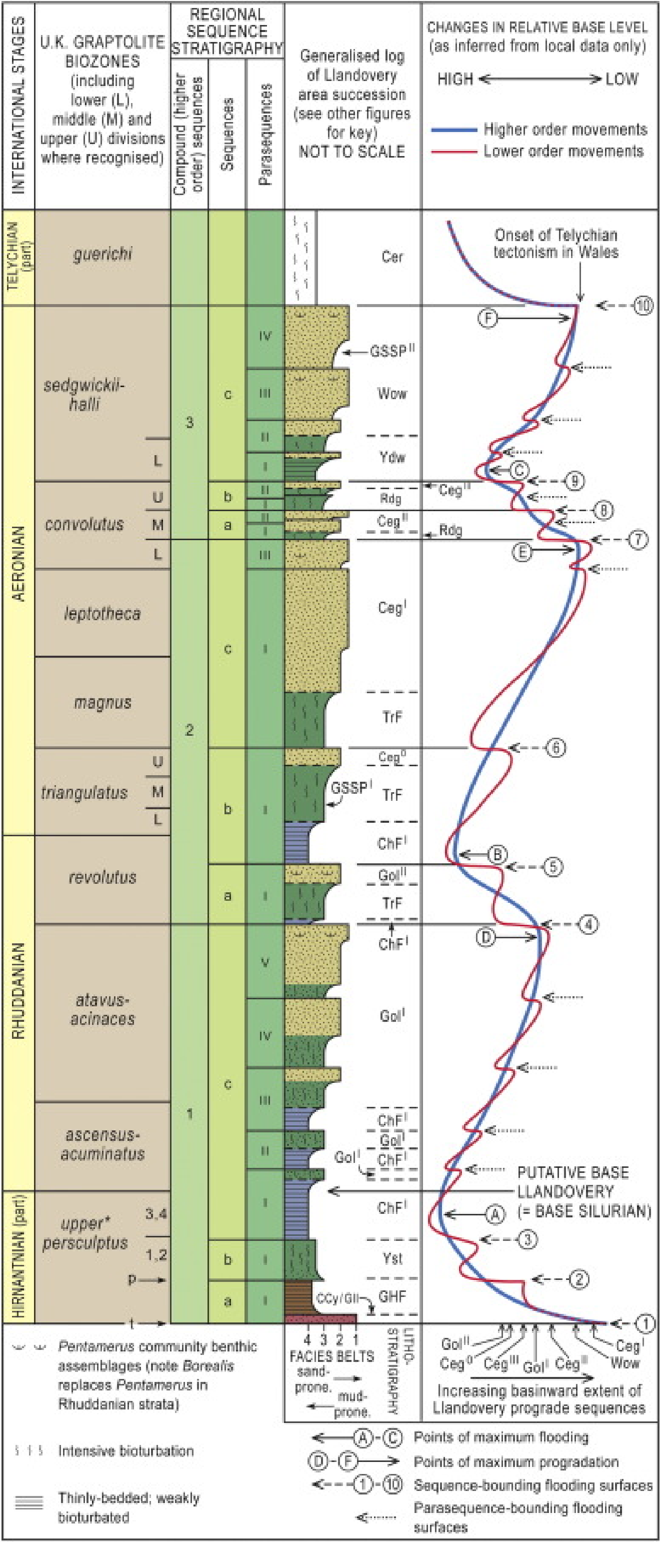

a
SSU
ELD
Area of map B
UK
Wales
b
Conway
Llanystumdwy
BF
WBFS
0
50 km
TL
PL
Church Stretton
LPWB
CSFZ
LL
Area of map C
LLANDOVERY SERIES
c
Regional strike of Llandovery facies belts
OLDER ROCKS
Llandovery
YOUNGER ROCKS
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Top Wormwood Formation datum
15 x lines of traverse
Late Hirnantian-Llandovery
0
5 km



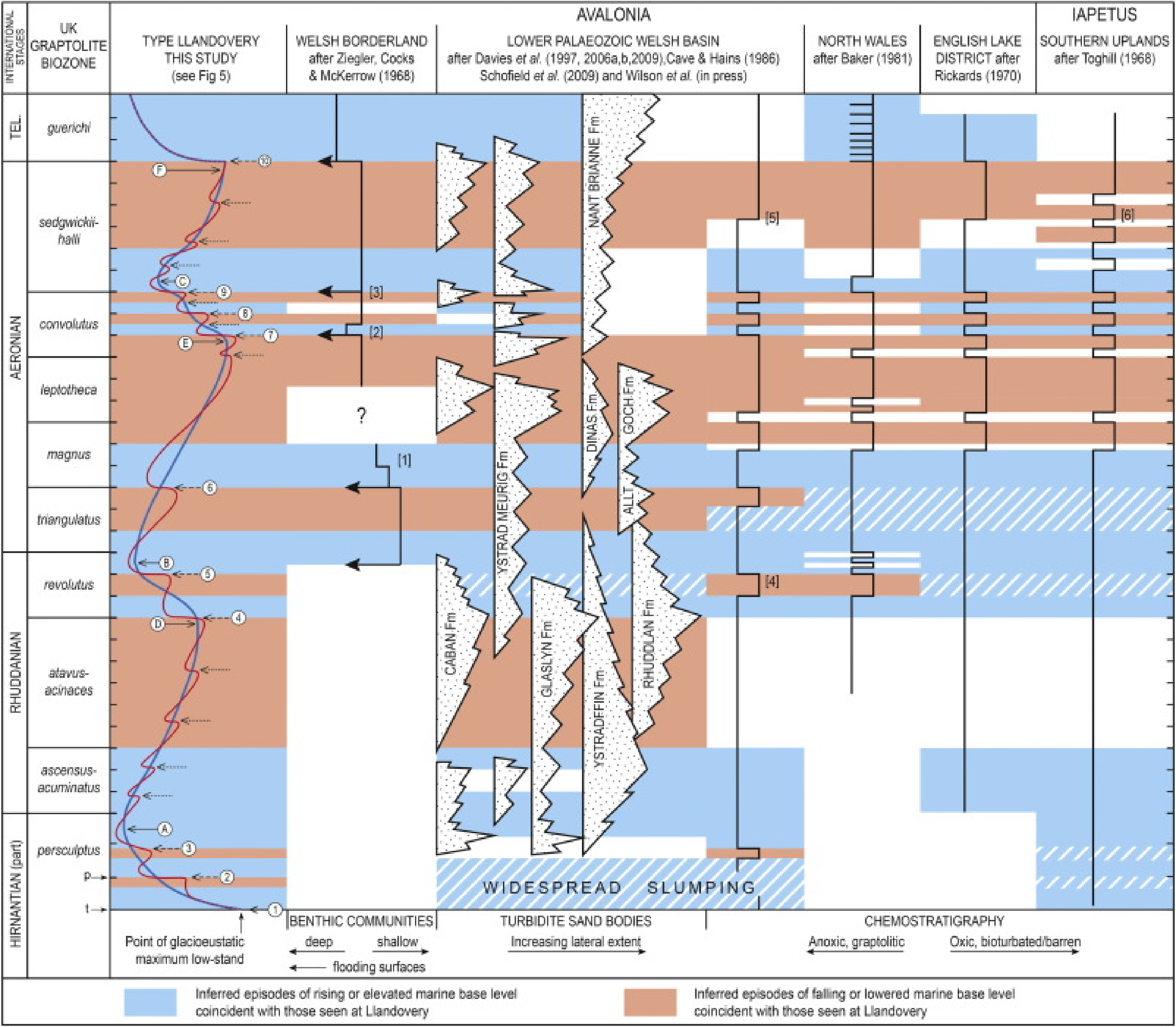
Clinoform facies belts	Principal component lithologies (inc. typical relative percentages)	Formation/ member	Principal sedimentary structures	BA	BI	Selected trace fossils
1 TOPSET	Sandstone, medium-bedded, medium- to coarse-grained (95)	**DD, Wow**	Cross-stratification; pentamerid brachiopod coquinas; common burrow-mottling	2/3	2-4	*Skolithos*, *Diplocraterion*
	Pebble and granule conglomerate (2-5)					
2 UPPER FORESET	Sandstone, intensely bioturbated, thick-bedded, fine- to medium-grained, with dispersed granules and pebbles (20)	**CcF, Ceg, Wow, Gol**	Pervasive burrow-mottling; parallel- and cross-lamination only common in thin sandstone beds; pebble and granule lags	3/4	4-5	*Teichichnus*, *Palaeophycus*, *Planolites*, *Zoophycus*, *Chondrites*
	Muddy sandstone, intensely bioturbated, thick-bedded, fine- to medium-grained, with dispersed granules and pebbles (70)					
	Sandstone as thin, sharp-based beds and laminae with bioturbated tops (2-10)					
3 LOWER FORESET	Sandy mudstone, strongly bioturbated, medium bedded, with dispersed coarse sand grains and granules (85)	**BrF, TrF, Rdg, Gol, Yst, Ydw**	Pervasive burrow-mottling (sparse in Ydw); parallel- and cross-lamination only common in thin sandstone and siltstone beds	5	3-4	*Thalassinoides*, *Planolites*, *Zoophycus*, *Chondrites*
	Sandstone as thin, sharp-based beds and laminae with bioturbated tops (2-10)					
	Silty mudstone with thin, weakly bioturbated sandstone and siltstone beds and laminae (5)	**Ydw**			2-3	*Zoophycus*, *Chondrites*
4 BOTTOMSET	Mudstone, silty, thin-bedded with diffuse colour banding (90)	**ChF**	Poorly preserved hemipelagic lamination; sparse burrow-mottling; minor slump-related convolutions	6	1-2	*Chondrites* (small diameter)
	Thin, unbioturbated beds and laminae of sandstone and siltstone (2-10)					
5 SLUMP BELT	Disturbed bottomset mudstone (75-95)	**db (locally affects most formations)**	Slump folds and convolute bedding; listric surfaces; basal and internal slide planes	Not applicable		
	Mélange/debrite – mudstone with ill-sorted angular and rounded clasts (5-20)					
	Large displaced rafts of other facies belt lithologies (dominant in some slump complexes)					


a LITHOSTRATIGRAPHY and THICKNESS
Lines of traverse
Base intra-Wenlock synsedimentary slide complex
TOP WORMWOOD FORMATION DATUM
Cer
Wow
Ceg
Rdg
ChF
db
TrF
CcF
DD
Gol
BrF
Upper Llandovery Unconformity
Key
basal surface of synsedimentary slump/slide
Major flooding surface (on b and c)
500m
0
GHF
Overlies Ordovician rocks of varying age
b CHRONOSTRATIGRAPHY and GRAPTOLITE BIOZONATION
WEN.
GRAPTOLITE BIOZONES
LLANDOVERY
TELYCHIAN
AERONIAN
RHUDDANIAN
HIR.
post-turriculatus
turriculatus
guerichi
sedgwickii-halli
convolutus
magnus-leptotheca
triangulatus
revolutus (cyphus)
atavus-acinaces
ascensus-acuminatus
persculptus
Post-Cerig Formation strata
REGION OF STRATAL LOSS, DISTURBANCE AND DISPLACEMENT DUE TO INTRA-WENLOCK SYNSEDIMENTARY SLIDE EMPLACEMENT
Region of compound unconformity
Yst
c FACIES and SEQUENCE STRATIGRAPHY
SEDIMENTARY SEQUENCES
Composite (high order)
low order
HIR. (part)
Cerig Formation off-shore mudstones
Lines of traverse

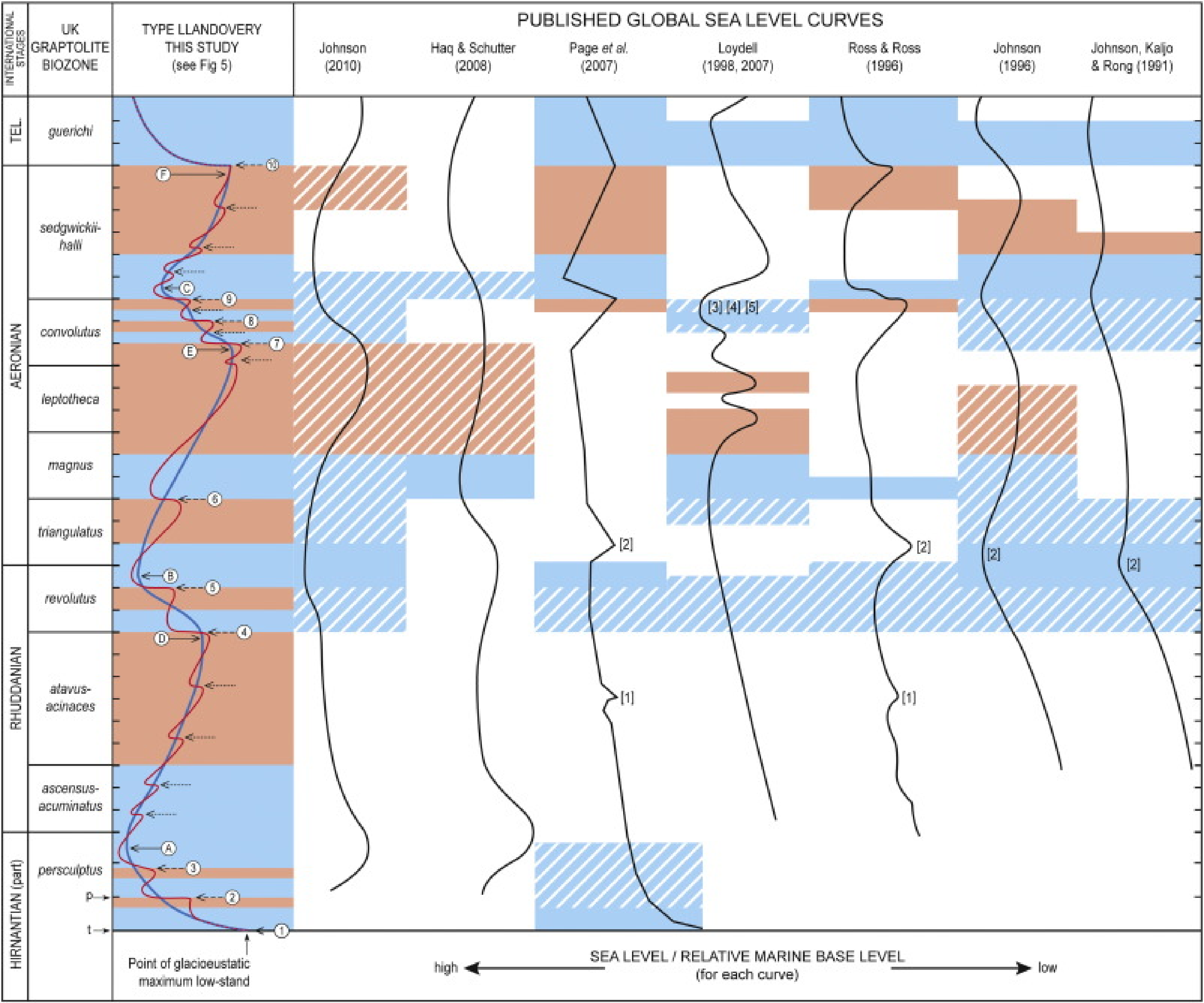

CHRONO-STRATIGRAPHY
SERIES
STAGES
A. U.K. GRAPTOLITE BIOZONES
B. RANGES OF SELECTED BRACHIOPODS
Stricklandiids
Cryptothyrella /Eocoelia
Pentamerids
Leptotheca
Meifodia
Plectatrypa
C. CONDONT BIOZONES
D. CHITINOZOAN BIOZONES
E. ACRITARCH BIOZONES
F. SPORE BIOZONES
G. OSTRACODE BIOZONES
H. Graptolite biozones in common useage elsewhere or historically
I. TIME SLICES AND AGES
WEN.
SHEIN.
TELYCHIAN
AERONIAN
RHUDDANIAN
LLANDOVERY
HIRNANTIAN
GSSP
BASE SILURIAN
centrifugus
insectus
lapworthi
spiralis
crenulata
griestoniensis
crispus
turriculatus s.s.
guerichi [5]
sedgwickii -halli [4]
convolutus
leptotheca
magnus
triangulatus
revolutus [3]
atavus-acinaces [2]
ascensus-acuminatus [1]
persculptus
U
M
L
p
t
Costistricklandia
S. laevis
S. lens progressa
S. lens intermedia
S. lens prima
S. lens lens
S. lens
E. sulcata
E. curtisi
E. intermedia
E. hemispherica
C. augustifrons
C. crassa
C. 'incipiens'
Virginiana
Pentameroides
Pentamerus oblongus
Borealis borealis
L. tenuis-compressa
L. antiquedens
M. prima supercedens
M. prima ovalis
M. prima prima
M. prima
P. tripartita sp. nov. (Temple, 1987)
P. tripartita tripartita
[6]
[7]
[8]
Upper limit of 'Hirnantia Fauna' in Wales
amorpho-gnathoides
celloni
lithuanicus
lennarti
angulatus
eopennatus
[11]
stauro-gnathoides
[10]
tenuis
[9]
expansa
kentuckyensis (≈ discreta - deflecta)
ordovicicus
margaritana
[14]
longicollis -acuminata
dolioliformis
[13]
alargada
maennili
elongata
electa
fragilis-postrobusta
[12]
taugourdeaui
monospinosa
[16]
encantador
[15]
estillis
microcladum
eoplanktonica
fisherii
robusi-spinosa
citrinipeltatum
avitus-dilatus
[17]
membranifera-Pseudo-dyadospora
typus
decoris -lata
[19]
[18]
excavata
erecta
centifugus
crenulata
tullbergi
griestoniensis
exiguus
crispus
turriculatus s.l.
linnaei
sedgwickii
convolutus
gregarius / curtus
leptotheca /argenteus
triangulatus / pectinatus
simulans
cyphus
vesiculosus
acuminatus
ascensus
persculptus
Te5
Te4
Te3
436.97
Te2
Te1
438.49
Ae3
438.76
Ae2
439.47
Ae1
440.77
Rh3
Rh2
442.47
Rh1
443.83
Hi2
[20]
Hi1



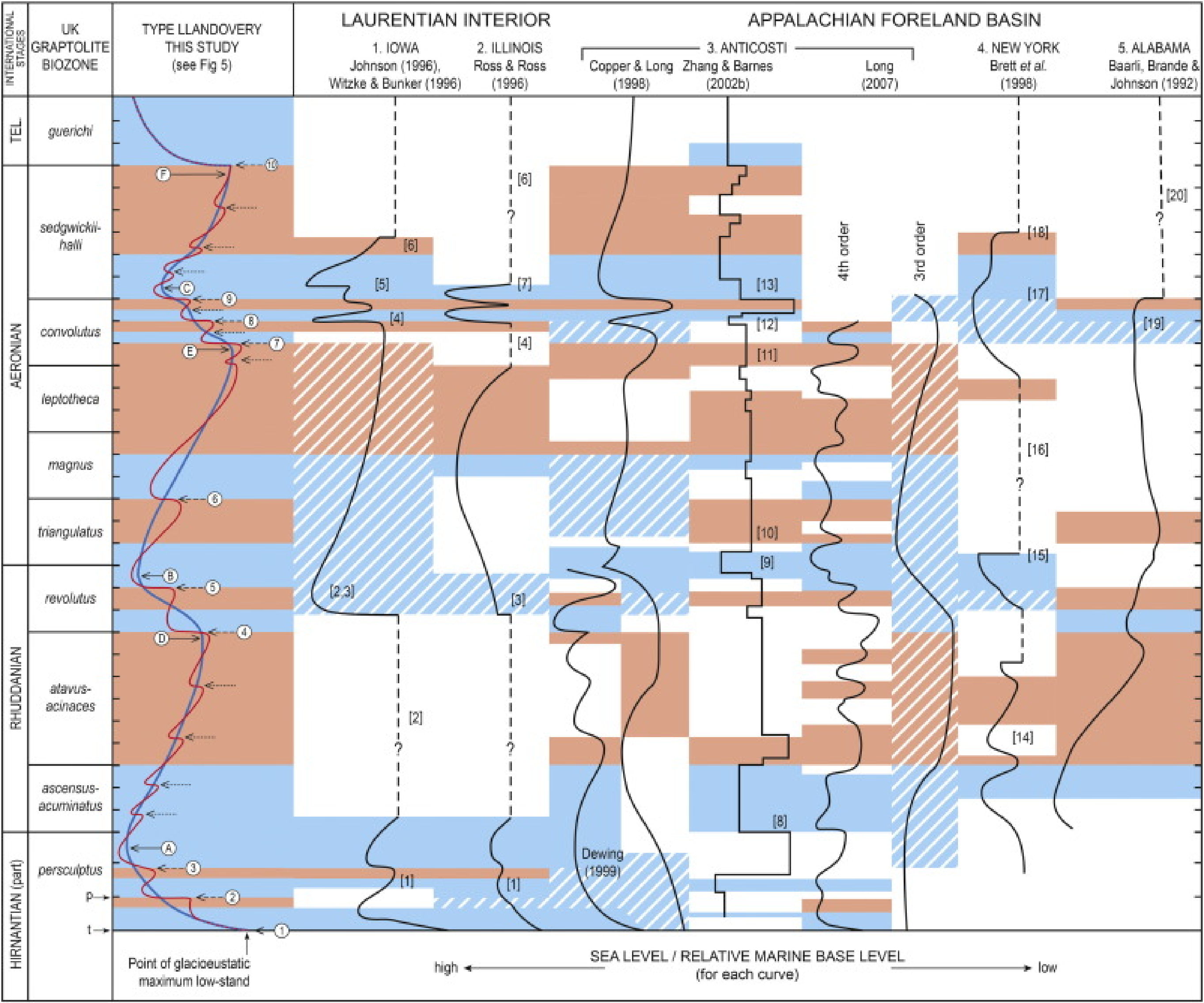
INTERNATIONAL STAGES
U.K. GRAPTOLITE BIOZONES (including lower (L), middle (M) and upper (U) divisions where recognised)
REGIONAL SEQUENCE STRATIGRAPHY
Compound (higher order) sequences
Sequences
Parasequences
Generalised log of Llandovery area succession (see other figures for key) NOT TO SCALE
CHANGES IN RELATIVE BASE LEVEL (as inferred from local data only)
HIGH
LOW
Higher order movements
Lower order movements
TELYCHIAN (part)
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
upper* persculptus
3,4
1,2
p
t
Onset of Telychian tectonism in Wales
PUTATIVE BASE LLANDOVERY (= BASE SILURIAN)
Cer
Wow
Ydw
Rdg
Ceg
TrF
ChF
Gol
Yst
GHF
CCy/Gll
GSSP II
GSSP I
FACIES BELTS
sand-prone.
mud-prone.
LITHO-STRATIGRAPHY
Increasing basinward extent of Llandovery prograde sequences
Pentamerus community benthic assemblages (note Borealis replaces Pentamerus in Rhuddanian strata)
Intensive bioturbation
Thinly-bedded; weakly bioturbated
A - C Points of maximum flooding
D - F Points of maximum progradation
1 - 10 Sequence-bounding flooding surfaces
Parasequence-bounding flooding surfaces

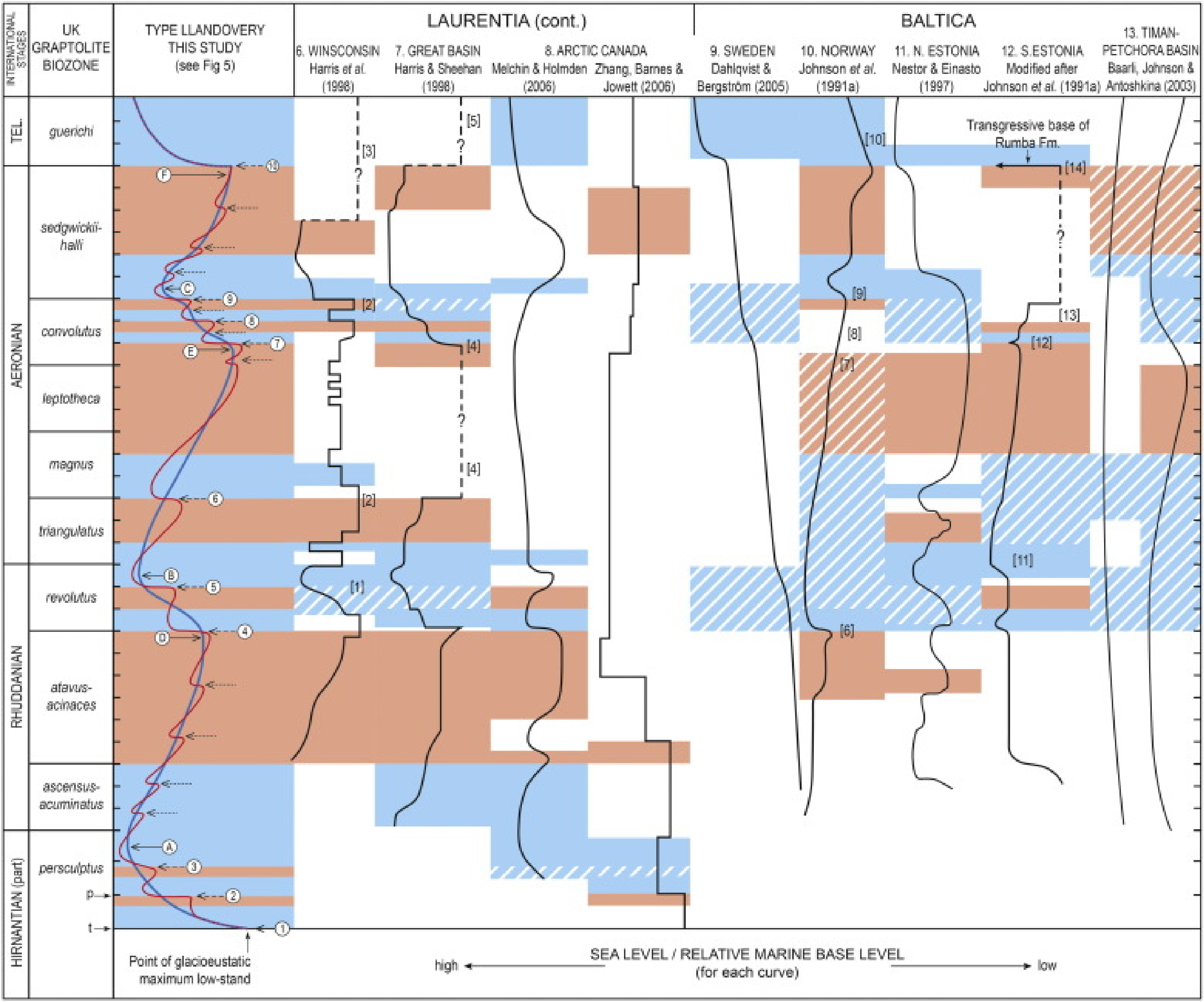


INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
AVALONIA
IAPETUS
TYPE LLANDOVERY THIS STUDY (see Fig 5)
WELSH BORDERLAND after Ziegler, Cocks & McKerrow (1968)
LOWER PALAEOZOIC WELSH BASIN after Davies et al. (1997, 2006a,b,2009),Cave & Hains (1986) Schofield et al. (2009) and Wilson et al. (in press)
NORTH WALES after Baker (1981)
ENGLISH LAKE DISTRICT after Rickards (1970)
SOUTHERN UPLANDS after Toghill (1968)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
A
B
C
D
E
F
1
2
3
4
5
6
7
8
9
10
[1]
[2]
[3]
[4]
[5]
[6]
?
NANT BRIANNE Fm
YSTRAD MEURIG Fm
DINAS Fm
GOCH Fm
ALLT
CABAN Fm
GLASLYN Fm
YSTRADFFIN Fm
RHUDDLAN Fm
WIDESPREAD SLUMPING
Point of glacioeustatic maximum low-stand
BENTHIC COMMUNITIES
deep
shallow
flooding surfaces
TURBIDITE SAND BODIES
Increasing lateral extent
CHEMOSTRATIGRAPHY
Anoxic, graptolitic
Oxic, bioturbated/barren
Inferred episodes of rising or elevated marine base level coincident with those seen at Llandovery
Inferred episodes of falling or lowered marine base level coincident with those seen at Llandovery

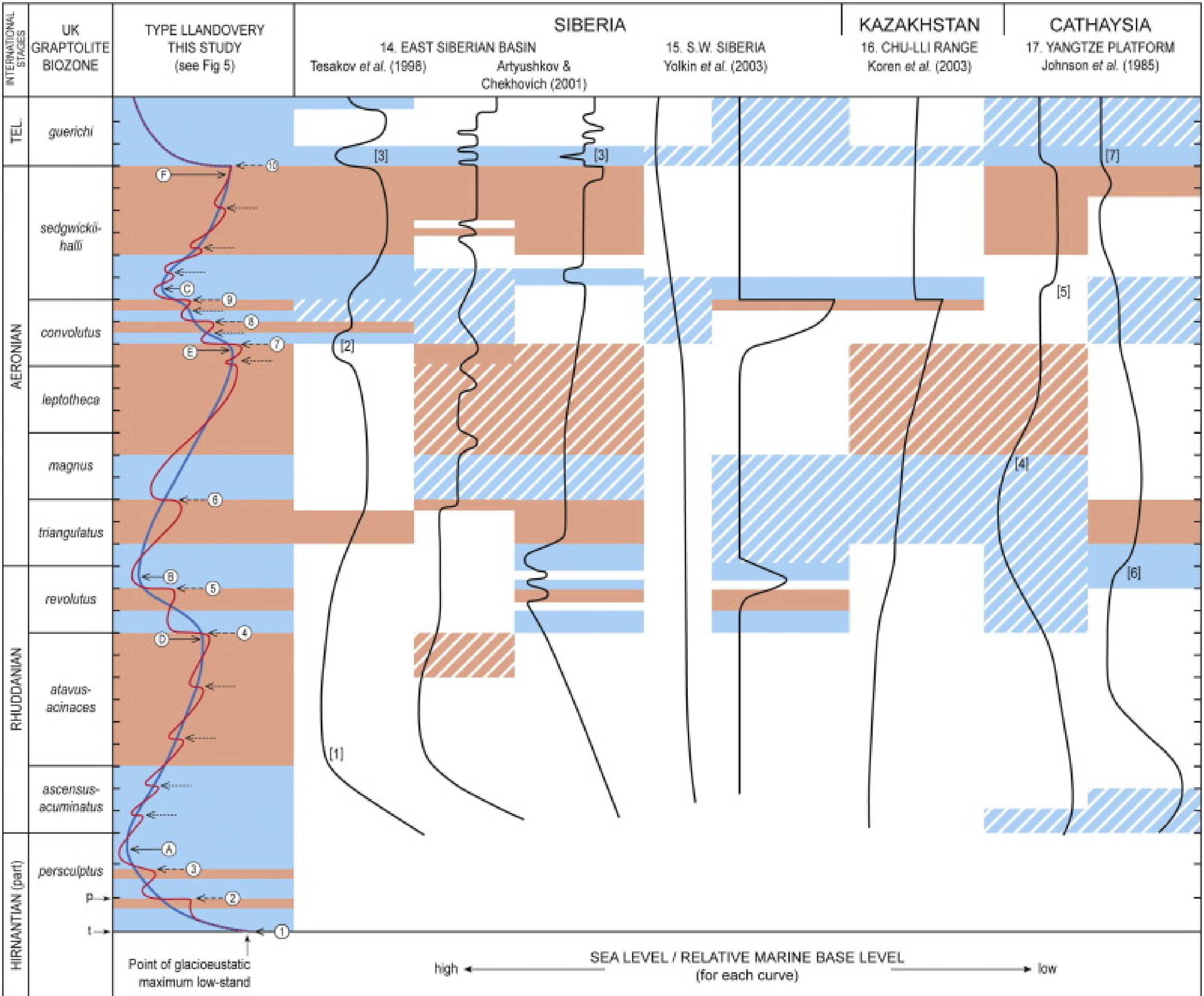


INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
PUBLISHED GLOBAL SEA LEVEL CURVES
Johnson (2010)
Haq & Schutter (2008)
Page et al. (2007)
Loydell (1998, 2007)
Ross & Ross (1996)
Johnson (1996)
Johnson, Kaljo & Rong (1991)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
A
B
C
D
E
F
1
2
3
4
5
6
7
8
9
10
[1]
[2]
[3] [4] [5]
Point of glacioeustatic maximum low-stand
high
SEA LEVEL / RELATIVE MARINE BASE LEVEL (for each curve)
low

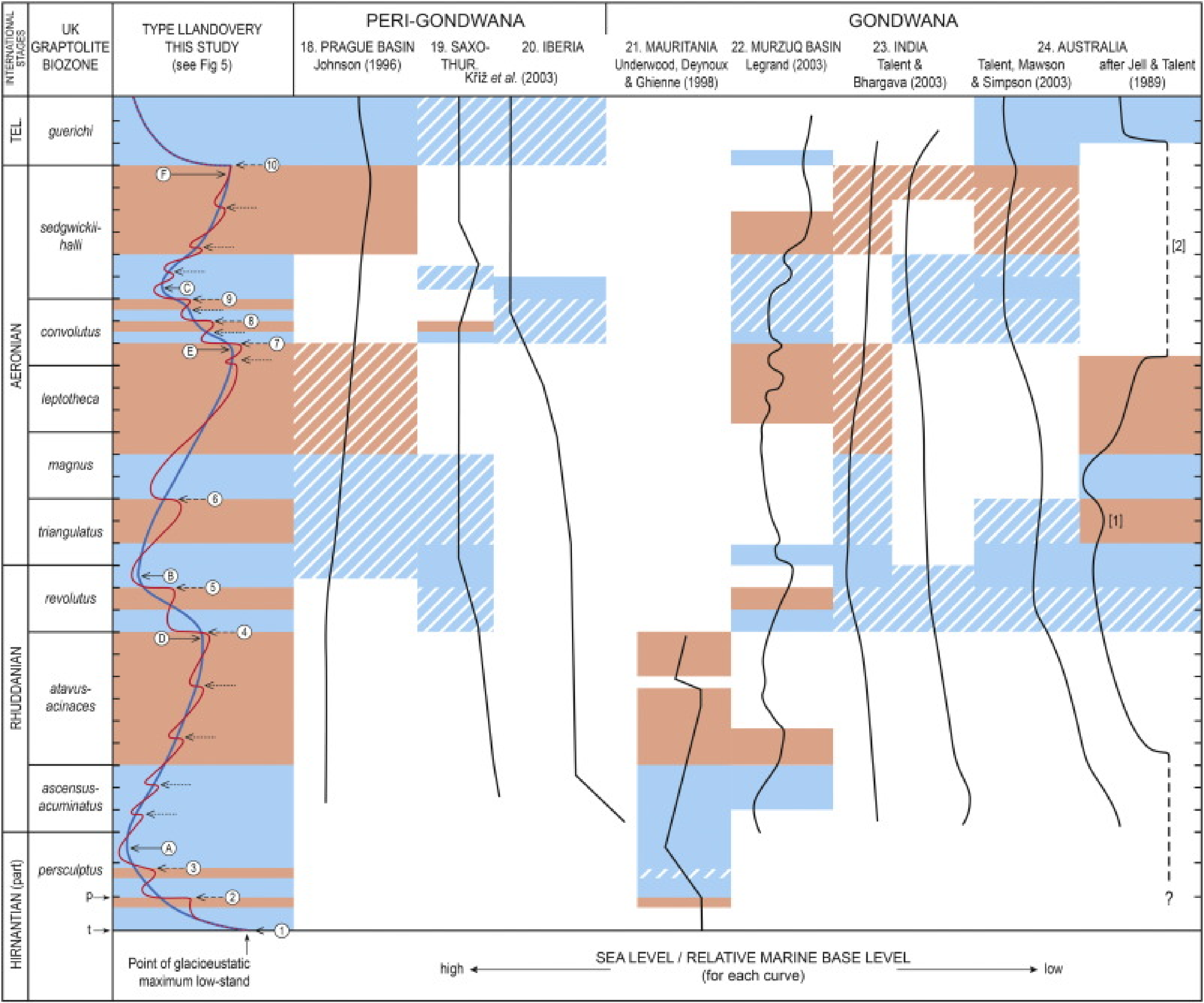

INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
LAURENTIAN INTERIOR
APPALACHIAN FORELAND BASIN
1. IOWA Johnson (1996), Witzke & Bunker (1996)
2. ILLINOIS Ross & Ross (1996)
3. ANTICOSTI
Copper & Long (1998)
Zhang & Barnes (2002b)
Long (2007)
4. NEW YORK Brett et al. (1998)
5. ALABAMA Baarli, Brande & Johnson (1992)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
4th order
3rd order
Dewing (1999)
Point of glacioeustatic maximum low-stand
SEA LEVEL / RELATIVE MARINE BASE LEVEL (for each curve)
high
low



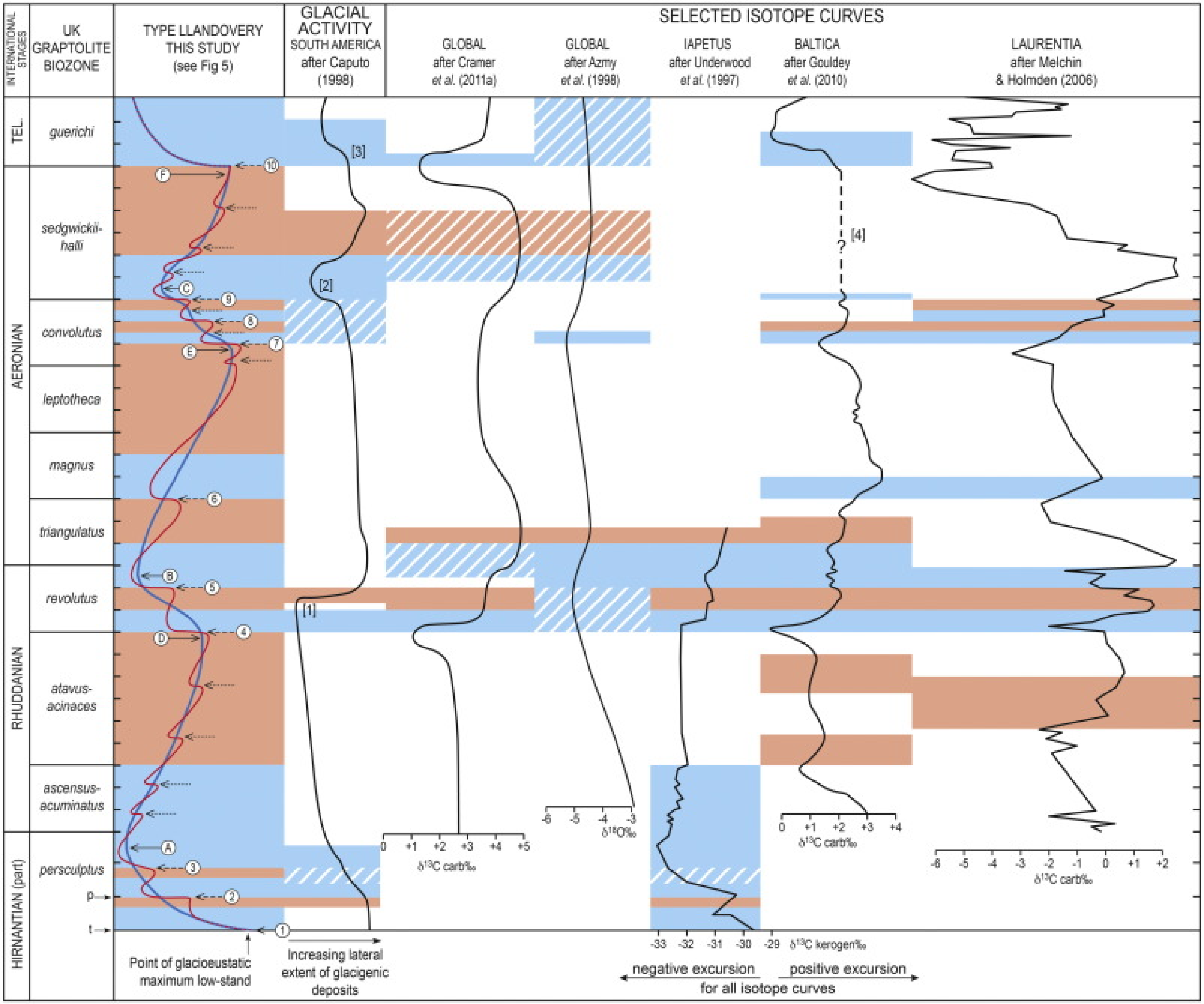
INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
LAURENTIA (cont.)
6. WINSCONSIN Harris et al. (1998)
7. GREAT BASIN Harris & Sheehan (1998)
8. ARCTIC CANADA Melchin & Holmden (2006) Zhang, Barnes & Jowett (2006)
BALTICA
9. SWEDEN Dahlqvist & Bergström (2005)
10. NORWAY Johnson et al. (1991a)
11. N. ESTONIA Nestor & Einasto (1997)
12. S.ESTONIA Modified after Johnson et al. (1991a)
13. TIMAN-PETCHORA BASIN Baarli, Johnson & Antoshkina (2003)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
Transgressive base of Rumba Fm.
Point of glacioeustatic maximum low-stand
SEA LEVEL / RELATIVE MARINE BASE LEVEL (for each curve)
high
low



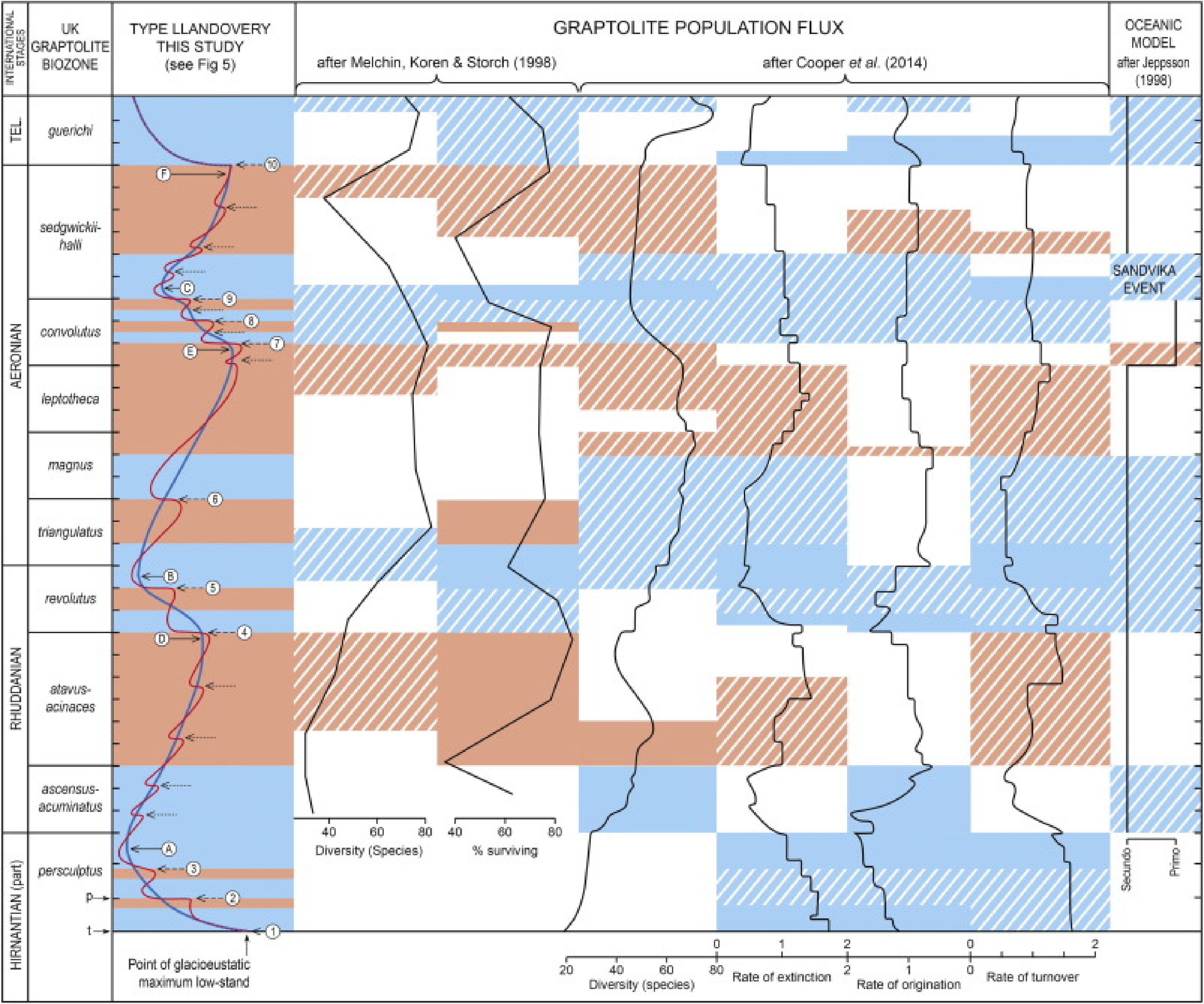
INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
SIBERIA
14. EAST SIBERIAN BASIN
Tesakov et al. (1998)
Artyushkov & Chekhovich (2001)
15. S.W. SIBERIA
Yolkin et al. (2003)
KAZAKHSTAN
16. CHU-LLI RANGE
Koren et al. (2003)
CATHAYSIA
17. YANGTZE PLATFORM
Johnson et al. (1985)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
[1]
[2]
[3]
[4]
[5]
[6]
[7]
Point of glacioeustatic maximum low-stand
SEA LEVEL / RELATIVE MARINE BASE LEVEL (for each curve)
high
low



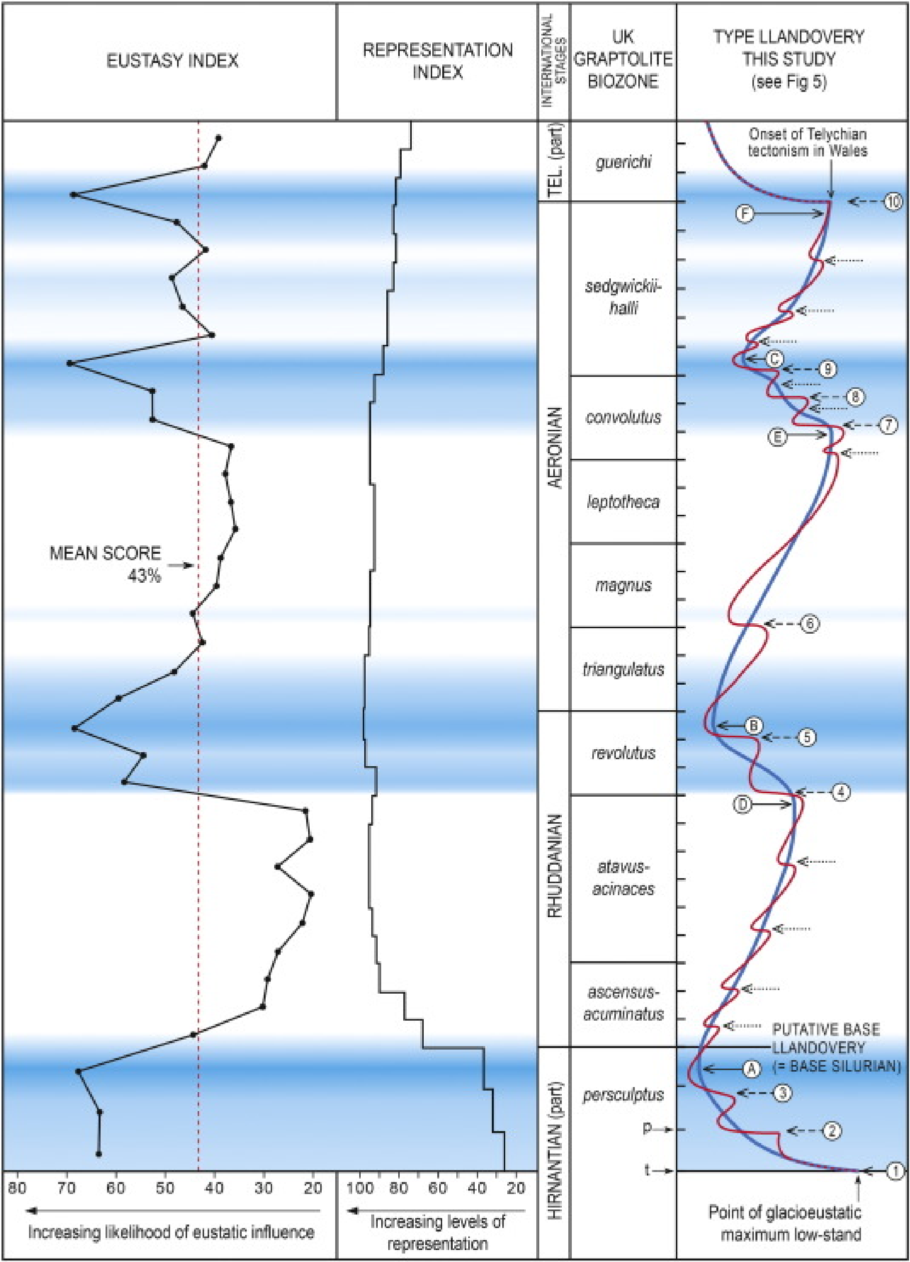
INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
PERI-GONDWANA
18. PRAGUE BASIN Johnson (1996)
19. SAXO-THUR.
20. IBERIA
Kříž et al. (2003)
GONDWANA
21. MAURITANIA Underwood, Deynoux & Ghienne (1998)
22. MURZUQ BASIN Legrand (2003)
23. INDIA Talent & Bhargava (2003)
24. AUSTRALIA
Talent, Mawson & Simpson (2003)
after Jell & Talent (1989)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
[1]
[2]
?
Point of glacioeustatic maximum low-stand
SEA LEVEL / RELATIVE MARINE BASE LEVEL (for each curve)
high
low



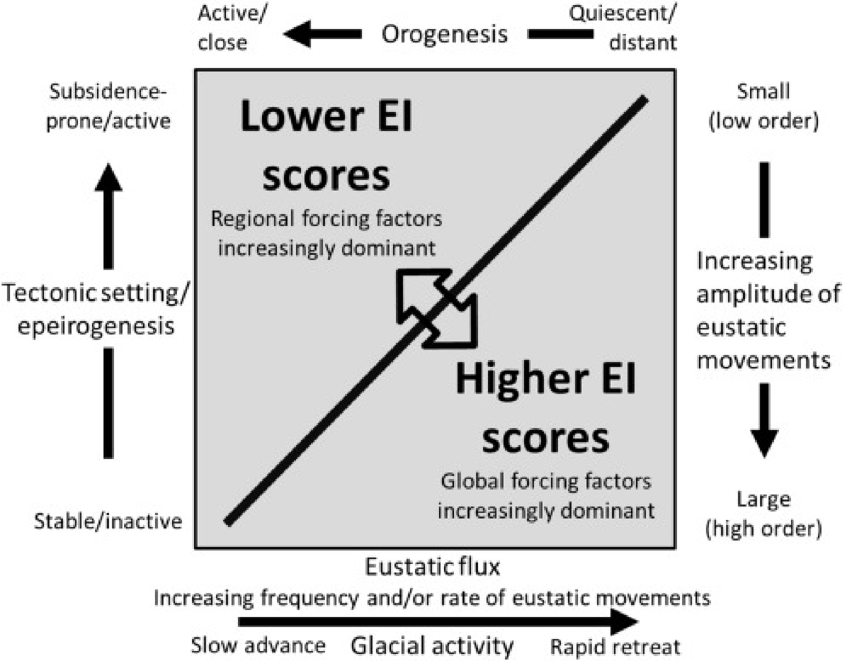
INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
GLACIAL ACTIVITY SOUTH AMERICA after Caputo (1998)
SELECTED ISOTOPE CURVES
GLOBAL after Cramer et al. (2011a)
GLOBAL after Azmy et al. (1998)
IAPETUS after Underwood et al. (1997)
BALTICA after Gouldey et al. (2010)
LAURENTIA after Melchin & Holmden (2006)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
[1]
[2]
[3]
[4]
δ13C carb‰
δ18O‰
δ13C kerogen‰
Point of glacioeustatic maximum low-stand
Increasing lateral extent of glacigenic deposits
negative excursion
positive excursion
for all isotope curves



INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
GRAPTOLITE POPULATION FLUX
after Melchin, Koren & Storch (1998)
after Cooper et al. (2014)
OCEANIC MODEL after Jeppsson (1998)
TEL.
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
p
t
SANDVIKA EVENT
Diversity (Species)
% surviving
Diversity (species)
Rate of extinction
Rate of origination
Rate of turnover
Secundo
Primo
Point of glacioeustatic maximum low-stand



EUSTASY INDEX
REPRESENTATION INDEX
INTERNATIONAL STAGES
UK GRAPTOLITE BIOZONE
TYPE LLANDOVERY THIS STUDY (see Fig 5)
TEL. (part)
AERONIAN
RHUDDANIAN
HIRNANTIAN (part)
guerichi
sedgwickii-halli
convolutus
leptotheca
magnus
triangulatus
revolutus
atavus-acinaces
ascensus-acuminatus
persculptus
Onset of Telychian tectonism in Wales
PUTATIVE BASE LLANDOVERY (= BASE SILURIAN)
Point of glacioeustatic maximum low-stand
MEAN SCORE 43%
p
t
A
B
C
D
E
F
1
2
3
4
5
6
7
8
9
10
80 70 60 50 40 30 20
100 80 60 40 20
Increasing likelihood of eustatic influence
Increasing levels of representation



Active/
close
Orogenesis
Quiescent/
distant
Subsidence-
prone/active
Tectonic setting/
epeirogenesis
Stable/inactive
Lower EI
scores
Regional forcing factors
increasingly dominant
Higher EI
scores
Global forcing factors
increasingly dominant
Small
(low order)
Increasing
amplitude of
eustatic
movements
Large
(high order)
Eustatic flux
Increasing frequency and/or rate of eustatic movements
Slow advance
Glacial activity
Rapid retreat

Palaeogeographical and proxy datasets		**Relevant text figure**	**Number of datasets**
UK (Avalonian & Iapetus)*		7	6
Laurentia		9,10	13
Baltica		10	6
Siberia		11	5
Kazakhstan		11	1
Cathaysia (South China)		11	2
Peri-Gondwana		12	3
Gondwana		12	6
Global		8	7
Proxy datasets	Glacial deposits	13	1
	Isotopes	13	5
	Graptolite flux	14	6
	Oceanic model	14	1
Total number of datasets			62


5 cm

Supplementary data

Biostratigraphical notes and background to correlations used to recalibrate base level and proxy curves; numbers refer to those shown [in square brackets] on Figures 5, 7-13

In Wales, chitinozoans identified as, or comparable to, *Spinachitina taugourdeaui* are present in non-graptolitic strata that underlie the lowest occurrence of *persculptus* Biozone graptolites (Vandenbroucke, 2008; Vandenbroucke *et al*. 2008; Davies *et al*., 2009, 2013; Challands *et al*. 2014). However, published data suggest that the *S. taugourdeaui* Biozone equates with part of the *persculptus* Biozone (Melchin, Holmden & Williams, 2003; Ghienne *et al*., 2014) and that both biozones embrace the upper part of the Late Ordovician glacial maximum and linked HICE event. Taken at face value, this implies that strata (Garth House Formation and its correlatives) deposited during the initial post-glacial maximum transgression (Davies *et al*. 2009) must now be considered to be of *persculptus* Biozone age even though they pre-date the regional first appearance of *persculptus* Biozone graptolites. In post-dating the glacial maximum, the occurrences of *S. taugourdeaui* and *S.* cf. *taugourdeaui* chitinozoans in Wales are higher/younger than elsewhere and in need of further investigation (Challands *et al*. 2014). Late first appearances of *persculptus* Biozone graptolites are a feature of many late Hirnantian successions (e.g. Melchin *et al*., 2013) and it seems that strata assigned to the *persculptus* Biozone in Wales must now be interpreted as spanning only its upper part. Strata that intervene between the glacial maximum low-stand event and the base of the *ascensus-acuminatus* Biozone in Wales are here assigned to an upper *persculptus* biozonal interval equivalent to the Hi2 time slice of Bergström *et al*. (2009) (See Fig. 5, note [20] below). However, for eustasy index assessments (see Section 8), this period has continued to be treated as the equivalent of a single biozone.

Subspecies of the *Stricklandia* brachiopod lineage, *S. lens lens* and *S. lens prima*, previously thought to range into the *revolutus* (*cyphus*) graptolite Biozone, are now known to be restricted to earlier strata. It is their successor, *S. lens intermedia*, that has its FAD at about the base of the *revolutus* Biozone. Critically, key elements of the *Stricklandia* and *Eocoelia* brachiopod lineages co-existed. The ranges of *S. lens progressa* and *E. hemispherica* and their successor species, *S. laevis* and *E. intermedia*, all overlap in the lower *sedgwickii* Biozone. *Stricklandia lens progressa* and *E. hemispherica* range into this interval from the underlying *convolutus* Biozone, whereas *S. laevis* ranges from the *sedgwickii* Biozone into rocks of Telychian age (Fig 5). These finding endorse those of Baarli & Johnson (1988), who established that species and subspecies of *Stricklandia* co-existed within evolving Norwegian populations. This emphasises the importance of last appearances (LADs) of key taxa for Silurian correlation (e.g. Cocks *et al*., 1984) in addition to first appearances (FADs). Noteworthy amongst other brachiopods used for Llandovery correlation are species of the pentamerids *Virgiana*, *Borealis*, *Pentamerus* and *Pentameroides* (e.g. Bassett, 1989; Jin & Copper, 2008) (Fig 5).

The new work shows that the *fisherii* acritarch Biozone is confined to the pre-*revolutus* graptolite Biozone interval and, in contrast to previous reports (Hill & Dorning in Cocks *et al*., 1984), that the *microcladum* Biozone completely, and *estillis* Biozone partly, pre-date the *sedgwickii* Biozone. *Gracilisphaeridium encantador*, the eponymous species of the *G. encantador* acritarch Biozone, has its FAD in the Type Llandovery area in the *guerichi* Biozone, lower than envisaged by Davies *et al*. (1997). An initial study of Type Llandovery chitinozoans by De Permentier & Verniers (2002), and a more detailed assessment of the *electa*, *maennili* and *dolioliformis* biozones by Davies *et al*. (2013), showed in particular that *Eisenackitina dolioliformis* occurred in the upper *convolutus* Biozone at Llandovery and therefore stratigraphically lower than reported in Baltica (e.g. Nestor, 2010).

There is a paucity of information on conodont assemblages from the Type Llandovery area due to facies constraints. The single record of an *I. discreta–I. deflecta* Biozone (= *D. kentuckyensis* Biozone, Aldridge, 1985) assemblage from the Bronydd Formation is consistent with the formation's Rhuddanian age (Cocks *et al*., 1984). For many Llandovery successions around the world, notably those dominated by shallow water carbonates, conodonts provide the principal means of dating and correlation. Hence, to meet the objectives of this paper, it is important briefly to discuss the evolving conodont biozonal scheme for the Llandovery Series, and its shortcomings. Dahlqvist & Bergstom (2005) and Mannik (2007) provided reviews of conodont biostratigraphical research that reflect extensive recent work, particularly in the Baltic region (see also Rubel *et al*., 2007; Loydell, Nestor & Mannik, 2010), but also in North America (e.g. Zhang & Barnes, 2002a; Kleffner, 2004; Kleffner, Barrick & Drachen, 2004). The level of subdivision now achieved in the Telychian is beginning to rival that provided by graptolites, but establishing a detailed conodont biozonation for the Rhuddanian and Aeronian has proved elusive. Until quite recently just two biozones were recognised within this interval, the *D. kentuckyensis* Biozone and the succeeding *D. staurognathoides* Biozone (e.g. Aldridge, 1985). Zhang & Barnes (2002a) put forward a more detailed subdivision based on the succession on Anticosti Island , Québec, but the wider applicability of their scheme has been questioned (e.g. Dahlqvist & Bergstom, 2005). Their *O. hassi* Biozone, spanning the Hirnantian–Llandovery boundary, is applicable in North America (e.g. Mikulic *et al*., 1985), but has not been recognised elsewhere (e.g. Mannik, 2007).

Most relevant to this study has been the erection and widespread acceptance of the *Pranognathus tenuis* Biozone in place of the upper part of the *D. kentuckyensis* Biozone (see Dahlqvist & Bergstom, 2005). The presence of the index taxon distinguishes lower–middle Aeronian rocks. However, the relationship between this conodont biozone and the graptolite biozonal scheme is ambiguous. Melchin, Cooper & Sadler (2004), Cramer *et al*. (2011b) and Melchin, Sadler & Cramer (2012) all located its base within the *triangulatus* Biozone and its top in the *leptotheca* Biozone. However, in an intervening paper, Cramer *et al*. (2011a) placed its base in the *convolutus* Biozone and its top within the *sedgwickii* Biozone, albeit with boundaries that indicated uncertainty with respect to the graptolite biozonation (Cramer *et al.*, 2011a, fig. 3). Discoveries by Loydell, Nestor & Manick (2010) in Latvia confirm that the FAD of *P. tenuis* lies within the *triangulatus* Biozone there. In Norway, Aldridge & Mohamed (1982) recovered the taxon from the same levels that Johnson *et al*. (1991) report *S. lens progressa* (see Fig 10, note [9]) and, in the UK, it is known at different localities to co-occur with *E. hemispherica* and *convolutus* Biozone graptolites, but not with *E. intermedia* or *sedgwickii* Biozone graptolites (Aldridge, 1972, 1975). In the light of the revised brachiopod ranges established in the Llandovery area, these findings suggest that the *P. tenuis* conodont Biozone ranges from the *triangulatus* Biozone into, but not above the *convolutus* Biozone. Below the *P. tenuis* Biozone, the short lived *Aspeludia*? *expansa* conodont Biozone (Armstrong, 1990) spans the *cyphus (revolutus)*–*triangulatus* biozonal boundary (e.g. Loydell, Nestor & Mannik, 2010) (Fig 5).

Following Davies *et al*.'s (2013) re-appraisal of the current GSSPs for the Aeronian and Telychian stages, both erected in the Llandovery area, the base Aeronian GSSP is now known to be in the middle of the *triangulatus* Biozone rather than at its base. Moreover, the FAD of *S. laevis* is now known to be below the Telychian GSSP and significantly below the first appearance of *guerichi* Biozone graptolites. Consequently, it should not now be used as a proxy for the base of the Telychian Stage. In addition, Cocks *et al*.'s (1984) use of the brachiopod *Eocoelia curtisi* and the acritarch *Deunffia monospinosa* in the Type Llandovery succession have been called into question by Davies *et al*.'s (2010, 2011, 2013) discovery that key specimens recorded by Cocks *et al*. (1984) came from a synsedimentary melange. In particular, the presence of *E. curtisi* by itself can no longer be taken as evidence of a post-*sedgwickii* Biozone age, following the work of Doyle, Hoey & Harper (1991), who showed that its FAD at Girvan, southern Scotland, was below beds yielding upper *sedgwickii* Biozone graptolites.

Figure 5. Compilation of selected biostratigraphical ranges and biozonal schemes in use for the late Hirnantian and Llandovery series.

1. The *ascensus-acuminatus* Biozone is recognised as a single biozone in the UK, but is increasingly shown as two separate biozones in other areas and on international charts (e.g. Melchin, Sadler & Cramer, 2012).
2. The *atavus* and *acinaces* biozones are commonly indistinguishable in many regional accounts both in the UK and elsewhere (e.g. Davies *et al*., 1997).
3. The base of the *revolutus* Biozone is commonly shown as slightly younger than the *cyphus* Biozone it replaces (see Zalasiewicz *et al*., 2009).
4. The *halli* Biozone is now well established in the UK, but continues to be conflated with the *sedgwickii* Biozone in many schemes (e.g. Melchin, Sadler & Cramer, 2012).
5. Following the widespread adoption of the *guerichi* Biozone, the terms sensu lato (s.l.) and sensu stricto (s.s.) are used to distinguish the former and modern usages, respectively, of the *turriculatus* Biozone (see Davies *et al*., 2013).
6. See Cocks & Rickards (1969), Baarli (1986) and Davies *et al*. (2013).
7. *Eocoelia hemispherica* is unknown in the Type Llandovery area below the upper *convolutus* Biozone (Davies *et al*., 2013), and Baarli & Johnson (1988) suggested that this is the case worldwide. However, Cocks *et al*. (1984; also Cocks, 1989; Bassett, 1989) placed its FAD in the *leptotheca* Biozone. The earliest record of the genus is from Rhuddanian rocks in South America (Zeigler, 1966).
8. Baarli & Johnson (1988) recognised *Borealis osloensis* as extending into the range of *S. lens progressa*.
9. e.g. Loydell, Nestor & Mannik (2010)
10. See Biostratigraphical notes above.
11. Former base of the *Pterospathodus celloni* Biozone (see Mannik, 2007).
12. Known ranges of *Spinachitina taugourdeaui* and *S.* cf. *taugourdeaui* in Wales, but not internationally; see above and Challands *et al*. (2014) for discussion.
13. Former base of the *Eisenackitina dolioliformis* Biozone (e.g. Loydell, Nestor & Mannik, 2009).
14. See Kiipli *et al*. (2010).
15. Former base of the *Gracilisphaeridium encantador* Biozone (Davies *et al*., 1997).
16. See Davies *et al*. (2011, 2013).
17. See Burgess (1991).
18. Brett *et al.* (1998) recorded *Zygobolba excavata* Biozone ostracodes from the same beds as *Eocoelia intermedia*, the Wallington Limestone Member (Reynales Limestone Formation) and the overlying lower Sodus Shale Formation in the lower part of the Clinton Group, western and central New York State.
19. Brett *et al*. (1998) correlate the interval from the *Zygobolba decoris* Biozone to the *Mastigobolbina lata* Biozone to the *P. celloni* s.l. conodont Biozone, i.e. from the former base of the *P. celloni* Biozone (see [11] above) to the top of the restricted *celloni* Biozone as depicted on Fig. 5.
20. In the absence of published isotope data, the marked facies changes that mark the onset of the late Hirnantian, post glacial maximum transgression at Llandovery and throughout Wales (see Davies *et al*., 2009) are taken to mark the intra-*persculptus* Biozone boundary between the Hi1 and Hi2 times slices of Bergström *et al*. (2009) and, by inference, the end of the HICE excursion.

Figure 7. Other UK datasets

1. The absence of *Eocoelia* indicates a pre-*leptotheca* Biozone age for shelly assemblages from the 'Pentamerus Beds' (= Venusbank Fm. of Cocks *et al*., 1992) in the Hamperley Borehole, Shropshire. Otherwise, Cocks & Rickards (1968) regarded the assemblages from the Hamperley Borehole as being identical to those of the mid–late Aeronian *Eoceolia* Benthic Community. This supports a *magnus* Biozone age (see Fig 5, note [7]) for the underlying flooding event that

introduced marine faunas. The onset of Silurian sedimentation in this region was within the range of *S. lens intermedia* and therefore no older than the *revolutus* Biozone.

2. In the Shelve and Church Stretton areas of Shropshire, Cocks & Rickards (1968) and Zeigler, Cocks & McKerrow (1968) widely recognised forms of *S. lens* that are transitional between *S. lens intermedia* and *S. lens progressa*. The presence of such forms in the Hamperley Borehole, associated with *convolutus* Biozone graptolites but 15 m below a *sedgwickii* Biozone graptolite assemblage (Cock & Rickards, 1968), is consistent with the mid *convolutus* Biozone age now established for that transition, and serves to date the flooding episode recorded by the *Stricklandia* Benthic Community assemblage, to which they belong (Johnson, Rong & Kershaw, 1998).
3. Zeigler, Cocks & McKerrow (1968) recognised *E. intermedia* in the basal beds of the Venusbank Formation along the southern flank of the Shelve Inlier at Norbury, Shropshire, which dates the marine inundation at this locality as *sedgwickii* Biozone in age.
4. Within an otherwise anoxic Rhuddanian succession, Cullum & Loydell (2011; see also Cave & Hains, 1986) reported an oxic interval within the '*cyphus* Biozone' in the Rheidol Gorge, mid Wales.
5. Davies *et al*. (1997, p. 87) reported *halli* Biozone graptolites in the upper part of the '*M. sedgwickii* shales' in mid Wales.
6. Loydell (1991) recognised graptolite assemblages from strata at Dob's Linn, Southern Uplands, previously assigned to the now defunct early Telychian *maximus* Subzone, as being diagnostic of the late Aeronian *halli* Biozone.

Figure 8. Published global sea level curves

1. See note [1] for Fig. 9.
2. See notes [2] and [3] for Fig. 9.
3. Late Aeronian deepening. Long acknowledged as a period of falling sea levels, debate has centred on whether this peaked during the *convolutus* (e.g. Loydell, 1998) or *sedgwickii* biozones (see [4] and [5] below). Based on data presented by Wills & Smith (1922), Loydell (1998) emphasised the anoxic nature of *convolutus* Biozone rocks in North Wales as justification for locating the highstand in this biozone. However, extensive recent work on rocks of this age in mid Wales show this to have been a period during which oxic and anoxic bottom conditions alternated within the Lower Palaeozoic Welsh Basin.
4. Basal *sedgwickii* Biozone highstand. This was first recognised as a 'global' feature by McKerrow (1979) and is now well entrenched in the literature. Graptolite dating was based on the Type Llandovery collections of Jones (1925), which underpinned his original definition of the basal Upper Llandovery C1 interval and which were used in turn to calibrate ranges for the *Stricklandia* (Williams, 1951) and *Eocoelia* (Ziegler, 1966; also Ziegler, Cocks & McKerrow, 1968) brachiopod lineages. Modifications by Cocks *et al*. (1984) did not impact on this early work. Thus, in many areas, the dating of a basal *sedgwickii* Biozone highstand has been based on the calibrated brachiopod biostratigraphy, specifically the presence of *Stricklandia lens progressa*. New work in the type area has since shown, however, that the FAD of *S. lens progressa* and the localities where it is most abundant are stratigraphically below lower *sedgwickii* Biozone graptolites. Hence, the presence of this brachiopod subspecies on its own cannot be used as evidence of a *sedgwickii* Biozone age. Moreover, the ranges of *S. lens progressa* and its successor species, *S. laevis*, overlap in rocks of *sedgwickii* Biozone age, so *S. laevis* cannot be used in isolation as a proxy for the *guerichi* graptolite Biozone (= lower *turriculatus* Biozone of earlier usage). It is also now reasonable to infer the presence of *Eocoelia hemispherica*, *E. intermedia* and *E. curtisi* in rocks of *sedgwickii* Biozone age. It follows that the *sedgwickii* Biozone (or mid Aeronian) deepening phase depicted in many of the key sections used to construct regional and global sea level curves, including those of Johnson (e.g. 1996, 2006; Johnson, Rong & Yang, 1985 and Johnson *et al*., 1991) and Ross & Ross (1996), must be regarded with circumspection as these were commonly dated by brachiopod lineages and lack

independent graptolitic evidence of age. Nevertheless, there is clear evidence at Llandovery that the incoming of *sedgwickii* Biozone graptolites was linked to a marked regional transgression within the overlapping ranges of *S. lens progressa* and *S. laevis*.

5. Late Aeronian lowstand. Based on his analysis of graptolitic facies, Loydell (1998) rejected the evidence for a deepening event of early *sedgwickii* Biozone age. He suggested that the presence of oxic facies in many areas, bracketed by dark graptolite-bearing units of *convolutus* Biozone age below and *guerichi* Biozone age above, showed that the *sedgwickii-halli* biozonal interval was a period of sustained regression. In other areas, he cited the absence of *sedgwickii* Biozone aged rocks as evidence of contemporary emergence and erosion. The overstepping nature of *sedgwickii* Biozone rocks at Llandovery and in the Welsh Borderland counters this assessment. At Llandovery, lower *sedgwickii* Biozone transgressive facies (Ydw Member; Davies *et al*., 2013) are preserved beneath a thick, shoaling upwards sequence. In other areas, above their transgressive base, rocks of the *sedgwickii-halli* biozonal interval record deposition only under shoal conditions, but the evidence overall suggests that these form part a single T-R cycle. On Baltica, in Danish and Swedish sections where *sedgwickii* Biozone graptolites are unrecorded, bioturbated mudstones succeed graptolitic facies that yield the upper *convolutus* Biozone marker *Cephalograptus cometa extrema*, and underlie beds with 'lower' *turriculatus* (= *guerichi*) Biozone graptolites (Johnson, Kaljo & Rong, 1991). Loydell (1998) cited this as evidence against a basal *sedgwickii* Biozone highstand. Oxic facies also succeed *C. c. extrema*-bearing graptolitic facies in the Welsh Basin (e.g. Cave & Hains, 1986; Davies *et al*., 1997), but there they underlie the FAD of lower *sedgwickii* Biozone assemblages within the basin-wide *M. sedgwickii* Shales Member. Loydell (1994, 1998) invoked basin isolation to explain the presence of organic-rich graptolitic mudstones at this level in Wales, despite evidence on the adjacent platform for a coeval marine transgression (see Fig. 7, note [3]). It is arguably the Danish and Swedish sections that are aberrant. There, within condensed successions, the absence of *sedgwickii* Biozone graptolites could indicate either omission, or bioturbation or erosion of an attenuated graptolite-bearing transgressive unit as sea level fell during the later part of the interval (i.e. regressive submarine erosion), or enhanced tectonic activity in basins adjacent to an advancing Scandian orogenic front (see Section 8).

Figure 9. Published circum-Iapetus sea level curves: Laurentian interior and Appalachian Foreland Basin

1. Ross & Ross (1996) recognised a lowstand event linked to the Mosalem Formation of Iowa and the equivalent Schweizer Member (Wilhelmi Fm.) of Illinois that they considered to be mid Rhuddanian ('*vesiculosus*' Biozone), but reassessments of age discussed below now suggest that it is of *persculptus* Biozone age. Graptolites from these units were assigned by Ross (1962, 1964) to the late *acuminatus* or early *vesiculosus* (= atavus–acinaces, see Fig. 5) biozones (= mid Rhuddanian). Berry & Boucot (1970) reassigned the fauna to the mid Rhuddanian–lower Aeronian interval. Ross & Ross (1996) implied that the graptolite bearing beds marked a deepening event, but accounts of sections in Illinois by Willman (1973; Willman & Atherton, 1975) and in Iowa by Johnson, Rong & Yang (1985; Johnson, 1987) and Witzke (1992) provided no evidence of a subsequent shallowing. The contact with the succeeding Tete des Morts Formation (= Birds Member, Wilhelmi Fm) was described as gradational and the Mosalem and Tete des Morts formations were reported by Witzke (1992) to form part of an uninterrupted period of deepening. Witzke & Bunker (1996) gave an alternative view, suggesting that the Mosalem Formation might form a 'discrete T-R cycle'. The top of the shoaling phase shown by Ross & Ross (1996) was subsequently adopted and widely correlated by subsequent workers in the US as an intra-Rhuddanian sequence (or sub-sequence) boundary (e.g. Harris *et al*., 1998), despite a lack of firm biostratigraphical evidence to support the correlation. Loydell *et al*. (2002) recognised the graptolite fauna as being *persculptus* Biozone or, at the youngest, early *ascensus-acuminatus* Biozone in age. The implications of this revised dating were apparently not fully digested by Page *et al*. (2007), who seem to have followed Ross & Ross (1996) closely in the

construction of their global curve. The event must be significantly older than first thought and is perhaps more likely to compare with one of the intra-*persculptus* Biozone events seen at Llandovery (Davies *et al*., 2009).

2. Johnson, Rong & Yang (1985) associated the earliest of their Llandovery deepening episodes with the Blanding Formation of Illinois and Iowa, considered by them to be basal Aeronian in age. Johnson (1996) subsequently matched this highstand with the older Tete des Morts Formation (see above), a unit previously included in the Rhuddanian but shown by Johnson (1996) as spanning the Rhuddanian-Aeronian boundary in accord with Berry & Boucot (1970; see above). The pitting and erosion displayed by the top of the Tete des Morts Formation (Willman, 1973) justified its recognition by Ross & Ross (1996) as indicating a stage boundary lowstand event. Loydell *et al*.'s (2002) graptolite revisions (see above) called both of these interpretations into question. Llandovery rocks in both Iowa and Illinois comprise condensed dolomitic carbonate successions. Erosional diastems and hardgrounds have been recognised and cryptic omission surfaces are likely to be present. However, the Tete des Morts Formation and its equivalents are widely shown to succeed the Mosalem Formation conformably (e.g. Ross & Ross, 1996) and the revised dating suggests that it is unlikely to extend above the lower Rhuddanian. The pitted top of the Tete des Morts Formation might record the effects of an intra-Rhuddanian lowstand widely recognised in other North American successions rather than a stage boundary lowstand as argued by Ross & Ross (1996). This implies a significant non-sequence beneath the transgressive base of the Blanding Formation (= Elwood Fm), and suggests that the latter unit was deposited during a late Rhuddanian highstand (Witzke, 1992; also Metzger, 2005). In Illinois, Mikulic *et al*. (1985) recorded the conodont *Ozarkodina hassi* in both the Bird Member (see [1] above) and overlying Elwood Formation. Zhang & Barnes (2002b) recognised an *O. hassi* Biozone as spanning the Hirnantian–Rhuddanian boundary, but *O. hassi* itself is known to range into the early Aeronian (e.g. Loydell, Nestor & Mannik, 2010).
3. FAD of *S. lens intermedia*. Johnson's (1987) and Johnson, Kaljo & Rong's (1991) designation of a global highstand at or just above the Rhuddanian–Aeronian boundary owed much to its recognition and dating in the Iowa area at a time when the FAD of *S. lens intermedia* was linked to the base of the *triangulatus* Biozone. Following work in Norway by Baarli (1986), who placed the FAD of *Stricklandia lens intermedia* in the *cyphus* (= *revolutus*) graptolite Biozone, Johnson *et al*. (1991) favoured an older placement (i.e. pre-*triangulatus* Biozone) for this deepening episode in Iowa (Laurentia) and globally. However, in all subsequent reviews, Johnson (1996, 2006) continued to refer to a highstand peak 'at or near' to the stage boundary. Davies *et al*. (2013) confirmed the biostratigraphical recalibration of the FAD of *S. lens intermedia* in the Llandovery area. In Iowa, *Stricklandia lens intermedia* is first recorded in the Blanding Formation (Witzke, 1992), possibly deposited during a late Rhuddanian highstand (see [2]).
4. FAD of *S. lens progressa*. Following on from [3], the stratigraphy spanning the Rhuddanian–Aeronian stage boundary subsequently became linked to a shallowing episode associated with a period of glacial re-advance in South America (Johnson, 1996, 2006; see Section 7.a). However, the position of the Rhuddanian–Aeronian contact is poorly constrained in many areas, including the critical successions in Iowa and Illinois. Above the deepening event recorded by the Blanding Formation, the presence of *Stricklandia lens progressa* mid-way through the overlying Sweeny Member (Hopkinton Fm.) has been taken as evidence of a *sedgwickii* graptolite Biozone age (e.g. Johnson, Rong & Yang, 1985; Johnson, 1987). However, the revised range of this subspecies at Llandovery now suggests that the earliest Iowan assemblages likely equate with the *convolutus* Biozone (see also Baarli, 1986). The base of the Sweeny Member (= base Drummond Mbr, Kankakee Fm) is recorded as a marked unconformity in the Illinois Basin and in Wisconsin by Ross & Ross (1996). The erosive lowstand event recorded by the unconformity appears to have been widely recognised as a sequence boundary (e.g. Brett *et al*., 1998) and could account for the removal of late Rhuddanian to early Aeronian strata in Iowa, Illinois and more widely in North America. However, Ross (1962), Willman (1973), Mikulic *et al*. (1985) and Witzke (1992) recognised the contact between the Blanding Formation and the Sweeny Member, and their equivalents, as gradational. If this is the case, the Blanding Formation together with the lower levels of the Sweeny Member must span the whole of the *revolutus*–*leptotheca* biozonal interval.

It follows that the lower to mid Aeronian would have been a protracted period of condensed shoal facies deposition bracketed by well-constrained highstand events. Therefore, and contrary to Ross & Ross (1996), Page *et al*. (2007) and Haq & Schutter (2008), evidence for a discrete early Aeronian shallowing phase is considered to be lacking in these key sections.

5. FAD of *S. laevis*. Johnson, Rong & Yang (1985; Johnson, 1987) considered the appearance of *S. laevis* in the Iowan Farmers Creek Member to establish an early Telychian *guerichi* (= lower *turriculatus* s.l.) Biozone highstand. However, the FAD of this species at Llandovery is now established as occurring within the *sedgwickii* Biozone. In the absence of other dating constraints, the assumption must be that this is also true in Iowa and throughout the circum-Iapetus realm (e.g. Johnson, Cocks & Copper, 1981; Johnson *et al*., 1991; Brett *et al*., 1998).
6. Following Kluessendorf & Mikulic (1996), Witzke & Bunker (1996) recognised the top of the Picture Rock Member as a regional unconformity (disconformity). The Farmers Creek Member (below the Picture Rock Member) bears *Stricklandia laevis* whereas the overlying Johns Creek Quarry Member (basal Scotch Grove Formation) contains the late Llandovery genera *Costistricklandia* and *Pentameroides*. The unconformity could therefore account for the removal or non-deposition of early to mid Telychian strata in Iowa. However, Kluessendorf & Mikulic (1996) contended that erosion pre-dated the first appearance of *celloni* Biozone conodonts in the Brandon Bridge Member (Joliet Formation) of Illinois and Wisconsin, and since Witzke (1992) recorded conodonts of the *celloni* Biozone in the upper Picture Rock Member, it seems more likely that the level of the erosive event/lowstand? in Iowa is within or at the base of the Picture Rock Member rather than at the top. In either case, unambiguous evidence for an early Telychian highstand is lacking throughout these states.
7. It follows that the rocks immediately below this regional disconformity in Illinois (Plaines Member, Kankakee Formation), placed by Ross & Ross (1996) in the *griestoniensis* Biozone, are also much older. Traditionally the *Pentamerus*-rich Plaines Member has been correlated with the upper part of the Iowan Sweeny Member, distinguished locally as the Marcus Formation, implying that it lies within the range (*convolutus*–*sedgwickii* biozones) of *S. lens progressa* (Witzke, 1992).
8. The *Ozarkodina hassi* conodont Biozone of Zhang & Barnes (2002a) spans the Hirnantian–Rhuddanian stage boundary.
9. *S. lens* is first recorded in the Merrimack Formation on Anticosti Island (Jin & Copper, 2010).
10. Graptolites no younger than the *triangulatus* Biozone have been reported from the lower part of the Gun River Formation (Johnson, Cocks & Copper, 1981; Jin & Copper, 1999; Zhang & Barnes, 2002).
11. Upper levels of the Gun River Formation were reported to contain *D. staurognathoides* Biozone conodonts by Zang & Barnes (2002a). This implies an age no older than the *sedgwickii* Biozone, but see discussion by Dahlqvist & Bergstom (2005) and Biostratigraphical Notes above.
12. Graptolites in the succeeding Jupiter Formation, from below the distinctive *Panderodus* conodont-bearing interval of the Goeland Member (= Member 3 of Zhang & Barnes, 2002b), are consistent with the *convolutus* Biozone (Johnson, Cocks & Copper, 1981; Jin & Copper, 1999).
13. The FAD of *sedgwickii* Biozone graptolites coincides with the transgressive base of the East Point Member (Johnson, Cocks & Copper, 1981; Jin & Copper, 1999; Zhang & Barnes, 2002b). Johnson, Cocks & Copper (1981) also reported *E. curtisi* and t*urriculatus* s.l. Biozone graptolites close to the top of the Jupiter Fm.
14. Age of the Medina Group. The upper Whirlpool, Power Glen and lower Cabot Head formations are said to contain diverse Silurian shelly assemblages suggestive of an 'early–middle Rhuddanian' age (Brett *et al*., 1998).
15. Age of lower Clinton Group. Kleffner (2004; quoted in Dahlqvist & Bergstrom, 2005 and Cramer *et al*., 2011a) reported *tenuis* Biozone conodonts from the upper Neahga Shale Formation and the overlying Reynales Limestone Formation (Hickory Corner Member). Current understanding suggests that this conodont biozone spans the 'mid' *triangulatus*- *convolutus* biozonal interval (see Section 2 for background and discussion).
16. Following on from [11], the overstepping base of the Reynales Limestone (Furnaceville Hematite Member and its lateral equivalents) is recognised as a significant non-sequence (Brett *et al*.,

1998). This can now be seen to separate the level of the first appearance of *tenuis* Biozone conodonts (upper Neahga Shale) from the overlying *tenuis*-bearing levels of the Reynales Limestone. If the occurrence of *tenuis* Biozone conodonts within the lower Clinton Group is taken to encompass the total range of the biozone, the basal Reynales Limestone non-sequence likely spans much or all of the late *triangulatus*-early *convolutus* biozonal interval.

17. The uppermost beds of the Reynales Limestone (Wallington Member), in common with the succeeding lower Sodus Shale Formation, contain *E.* cf. *intermedia* (Brett *et al*., 1998), suggestive of a *sedgwickii* Biozone age.
18. Brett *et al*. (1998) noted the presence of a 'shale-on-shale unconformity' at the contact between the lower and upper members of the Sodus Shale Formation. The presence above this contact of *E. curtisi*, *decora* Biozone ostracodes and *celloni* Biozone conodonts shows that the boundary marks a further significant non-sequence that accounts for the local absence of strata of upper *sedgwickii* to *turriculatus* s.s. biozone age, comparable to that recognised in Illinois by Kluessendorf & Mikulic (1996) (see [8] above).
19. The FAD *S. lens progressa*, reported by Baarli, Brande & Johnson (1992) to occur above the Big Seam.
20. The presence of forms transitional between *Pentamerus oblongus* and *Pentameroides suberectus* in the S. *laevis*-bearing Ida Seam suggests that a significant non-sequence, accounting for the local absence of much of the late Aeronian and early Telychian, is present at the base of this unit.

Figure 10. Published circum-Iapetus sea level curves: Laurentian (continued) and Baltica

1. Harris *at al*. (1998) cited the presence of *Virgiana mayvillensis* in the uppermost Mayville Formation to infer a late Rhuddanian age for the associated high-stand event. This is based on the restricted occurrence of the species in Canada, notably in the Merrimack Formation on Anticosti Island as confirmed by Jin & Copper (2010).
2. LAD of *D. kentuckyensis* Biozone conodonts. Harris *et al*. (1998) reported conodont assemblages ranging from the upper part of the Byron Dolostone and throughout the overlying Hendricks Formation of the Door Peninsula, Wisconsin, as being indicative of the upper part of the *I. discreta–I. deflecta* Biozone (= *D. kentuckyensis* Biozone, Aldridge, 1985). Though this was prior to the erection of the *tenuis* conodont Biozone, it can now be inferred that these too pre-date the *sedgwickii* graptolite Biozone (see Fig. 5 and Biostratigraphical notes above).
3. Harris *et al*. (1998) recognised the regional unconformity identified in Illinois by Kluessendorf & Mikulic (1996) [see note 6 for Fig. 9? above] as forming the boundary between the Wisconsin Manistique and Waukesha formations. However, their report of both *Pentamerus* and *Pentameroides* in the Manistique Formation suggests that this unit contains strata of mid Telychian (*griestoniensis* Biozone) age that postdate the regional unconformity. Consequently, the regional hiatus is more likely to be either within or at the base of the Manistique Formation.
4. FAD of *Pentamerus* (Sheehan, 1980). *Virgiana*-bearing assemblages present in the lower part of the High Lake Member (Laketown Dolomite Fm) can now be regarded as no younger than the *magnus* Biozone (e.g. Johnson, 1987). Their replacement in the upper part of the member by assemblages containing *Pentamerus*, above a non-sequence that Harris & Sheehan (1996, 1998) associated with their S2/3 sequence boundary, implies a flooding episode within the *convolutus* Biozone.
5. Hurst, Sheehan & Pandolfi (1985) recognised major facies changes at the base of the Gettel Member and its correlatives within the Laketown Dolomite Formation, associated with the FAD of the mid–late Telychian genus *Pentameroides* (Sheehan, 1980). This implies that a significant hiatus separates these units from the underlying *Pentamerus*-bearing High Lake Member, regarded by Harris & Sheehan (1996, 1998) as being exclusively Aeronian in age.
6. FAD *S. lens intermedia* according to Baarli (1986).
7. LAD *Borealis borealis* according to Johnson *et al*. (1991).
8. FADs *S. lens progressa* and *tenuis* Biozone conodonts according to Aldridge & Mohamed (1982), Baarli (1986) and Johnson *et al*. (1991). Though previously taken to indicate a *sedgwickii*

Biozone age, Davies *et al*. (2013) placed the FAD of *S. lens progressa* in the *convolutus* Biozone.

9. Norwegian Oslo succession. In the Asker area, on which the Norwegian curve is based, Aldridge & Mohamed (1982) recorded a primitive form of *D. staurognathoides* just below the top of the Solvik Formation. In the light of these findings, Dahlquist & Bergstrom (2005) placed the base of the *D. staurognathoides* conodont Biozone at the same level as the boundary between the Solvik Formation and the overlying Rytteråker Formation, within the local range of *S. lens progressa* (Baarli & Johnson, 1988; Johnson *et al*. 1991). Following Davies *et al*. (2013), this suggest that the base of the *S. laevis*-bearing Rytteråker Formation, and the deepening event associated with it in the Asker area (e.g. Johnson *et al*. 1991), though not marking the local FAD of *S. laevis*, lies at or very close to the *convolutus–sedgwickii* biozonal boundary (in agreement with Worsley *et al*., 1983). Baarli & Johnson (1988) recognised the range of *E. hemispherica*, found in the Skien district, as overlapping the lower part of the range of *S. lens progressa*.
10. The earliest examples of definite *S. laevis* occur in the top of the Rytteråker Formation and basal Vik Formation, in transgressive strata that Baarli & Johnson (1988) correlated with the base of the *turriculatus* s.l. (*guerichi*) Biozone. However, Johnson *et al*. (1991) suggested that the transition from *S. lens progressa* occurred at a lower level in the Rytteråker Formation of the Asker and Syling areas, suggesting that the top Rytteråker–basal Vik occurrences there lay within and not at the base of the range of *S. laevis*.
11. FAD *triangulatus* Biozone graptolites in the lower part of the Saarde Formation in the Ikla borehole (Rubel, 1977; Johnson *et al*., 1991).
12. FAD *S. lens progressa* in the Saarde Formation, at a depth of 355 m in the Ikla borehole (Rubel, 1977). This was taken by Johnson *et al*. (1991; also Nestor & Nestor, 2002) to indicate a *sedgwickii* Biozone age, but the taxon is now known to have its FAD in the *convolutus* Biozone (Davies et al., 2013).
13. FADs of *S. laevis* and *E. dolioliformis* and the age and relationships of the Rumba Formation. Nestor (1976) recognised that the base of the Rumba Formation overlay a regional unconformity in Estonia, but that the magnitude of the unconformity was reduced in the distal succession proved in the Ikla borehole. Gouldey *et al*. (2010) suggested that this non-sequence was formed in a submarine setting. Most authors appear to recognise the base of the Rumba Formation as marking the abrupt onset of a deepening episode, which has been interpreted as a *sedgwickii* Biozone event (e.g. Nestor, 1997; Kaljo & Martma, 2000). In contrast, Johnson *et al*. (1991), Nestor & Nestor (2002; also Nestor, *et al*., 2003) and Loydell, Nestor & Mannik (2010; and references therein) regarded the base of the Rumba Formation as a basal Telychian flooding episode. This appears to have been based, in part, on the understanding, no longer valid, that the FAD of *S. laevis*, 1.2 m above the base of the Rumba Formation (Rubel, 1977), equated with the FADs of *guerichi* Biozone graptolites and *dolioliformis* Biozone chitinozoans. At the top of the Rumba Formation, Mannik (2007) recorded the base of the *P. eopennatus* conodont Superbiozone (base of the *P. eopennatus* ssp. n. 1 Biozone) in the top metre of the formation in the Estonian Viki core. This biozone was unproven in the Latvian Kolka-54 core, where graptolite assemblages suggest a non-sequence and the possible removal or non-deposition of strata equivalent to the uppermost Rumba Fm (Loydell, Nestor & Mannik, 2010). Rubel *et al*. (2007) also noted that the *P. eopennatus* ssp. n 1 Biozone had not been identified in the Estonian Viirelaid core, and suggested a possible gap or condensed interval in the upper part of the Rumba Formation there. The top of the formation in the Ikla core, Estonia, was identified as an unconformity that Gouldey *et al*. (2010) again considered to be submarine in origin. Geochemical fingerprinting by Kiipli, Kiipli & Kallaste (2006) of the 'O' Bentonite in the upper part of the Rumba Formation showed its equivalence to the widespread Osmundsberg Bentonite, which is known elsewhere in the Baltic region to overlie *turriculatus* s.s. Biozone graptolites. In her review of east Baltic chitinozoan assemblages, Nestor (2012) showed the Rumba Formation as spanning the *turriculatus-crispus* biozonal boundary, and the current consensus places the base of the formation at the local base of the *turriculatus* s.l. (*guerichi*) Biozone (e.g. Kaljo & Martma, 2000; Gouldey *et al*., 2010). These correlations are reflected in Figure 10. However, from the revised Llandovery area data, the reported occurrences of *dolioliformis* Biozone

chitinozoans and *S. laevis* in the Rumba Formation are compatible with an age as early as the *sedgwickii* Biozone. Hence, it is possible that the formation represents a highly condensed succession, bounded by and possibly containing non-sequences, that spans much or all of the *sedgwickii - guerichi - turriculatus* biozonal interval.

14. Following on from [12] and [13], many authors have associated the widespread non-sequence seen below the Rumba Formation throughout much of Estonia with a late Aeronian (*sedgwickii* Biozone) shoaling episode and also with glacioeustatic forcing (e.g. Nestor & Nestor, 2002). However, if the current consensus placing the base of the Rumba Formation at the base of the *turriculatus* s.l. Biozone is accepted, and given that *S. lens progressa* can no longer be regarded as indicative of the *sedgwickii* Biozone (see [12] above), the possibility emerges that the whole of the *sedgwickii* Biozone is unrepresented in the Ikla section. The likely presence of a stratigraphical break at the base of the Rumba Formation in the Ikla drill core is additionally significant as the C^{13} isotope curve obtained for this borehole is widely used in texts assessing Llandovery isotope trends, yet an equivalent gap in the isotope record is commonly not shown (e.g. Munnecke & Mannik, 2009; Gouldey *et al*., 2010) (see Fig. 13).

Figure 11. Published curves for Siberia, Kazakhstan and Cathaysia (South China)

1. Tesakov *et al*. (1998) located the post-glacial deepening maximum in Siberia above the base of the *acuminatus* Biozone and below the FAD of *cyphus* Biozone graptolites. However, they provided inconsistent and in places contradictory data for the dating of younger flooding events, which undermines the reliability of their sea level curve.
2. Tesakov *et al*. (1998) recognised a high-stand event associated with the *convolutus* Biozone, but which they also recognised as basal Aeronian.
3. Tesakov *et al*. (1998) recognised a high-stand event that significantly precedes the FAD of *turriculatus* Biozone graptolites. They associated it with the FAD of *celloni* Biozone conodonts, but Artyushkov & Chekhovich (2001) placed this event within the *staurognathoide*s conodont Biozone.
4. In the Hanjiadian district of the Yangtze Platform, south China, Johnson, Rong & Yang (1985) recognised a graptolite diversity maximum spanning the *cyphus* and *gregarius* biozones as an evidence of a deepening episode.
5. Mu, Chen & Rong (1989) recognised the Shihniulan Formation of the Hanjiadian district as spanning the *sedgwickii* Biozone.
6. The northwards younging base of the Xiangshuyuan Formation, of *cyphus* Biozone age in the Leijatun district, must be significantly younger in the more northern Longjingopo district (Johnson, Rong & Yang, 1985; Mu, Chen & Rong, 1989).
7. Johnson, Rong & Yang (1985) associated the FAD of *Stricklandia traversa*, a species endemic to China, with the base of the *turriculatus* s.l. Biozone. Consequently, this does not correlate with the FAD of *S. laevis* in the UK and more widely, as they contended.

Figure 12. Published curves for Peri-Gondwana and Gondwana

1. Jell & Tallent (1989) presented graptolite dates and facies descriptions for the Cadia Group. These imply the presence of a high-stand event linked to the Bridge Creek Limestone, which spans the *cyphus (revolutus)–triangulatus* biozonal boundary, and of a subsequent shallowing linked to the 'Upper Clastic Member'. The post glacial deepening maximum appears to have been reached during the *magnus* Biozone, marked by the maximum extent of the Cadia Shale Formation.
2. Jell & Tallent (1989) recognised a significant hiatus separating levels of the Cadia Shale of *leptotheca* and possible early *convolutus* biozone age from the transgressive, early Telychian Cobbler's Creek Limestone Formation.

Figure 13. Proxy datasets

1. DiazMartinez & Grahn (2007) report the Rhuddanian chitinozoan *Belonechitina* cf. *postrobusta* from marine sediments underlying Llandovery glacigenic deposits in Peru and Bolivia.
2. Caputo (1998) reported early Aeronian '*Monograptus gregarius'* Biozone graptolites from marine sediments immediately overlying glacigenic deposits in the Amazon Basin.
3. Caputo (1998) viewed the presence of early Telychian chitinozoans in marine rocks 'lateral to tillites' as evidence for a glacial advance that peaked during the late Aeronian (see also Johnson, 2006).
4. Marked negative C isotope excursions coincide with the Rumba Formation (e.g. Munnecke & Mannik, 2009), and Kaljo & Martma (2000) recognised a non-sequence beneath the lowest of these excursions, which coincides with the base of the Rumba Formation. They associated the onset of this excursion and the base of the Rumba Formation with the base of the *sedgwickii* Biozone, but the consensus view now places the base of the Rumba Formation and therefore the negative δ^{13}C excursion at the base of the Telychian Stage. See notes [13] and [14] for Figure 10.

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UK Graptolite Biozone	Biozonal subdivisions*	Fig 7				Fig 8				Fig 9				Fig 10			
		R (6 max)	Low order	High order	EI raw score	R (7 max)	Low order	High order	EI raw score	R (9 max)	Low order	High order	EI raw score	R (10 max)	Low order	High order	EI raw score
guerichi	36	4	3	0	**3**	7	2	0	**2**	2	0	0	**0**	7	3	0	**3**
	35	6	4	0	**4**	7	5	0	**5**	2	0	0	**0**	7	3	0	**3**
	34	6	4	0	**4**	7	5	0	**5**	2	1	0	**1**	8	5	0	**5**
sedgwickii-halli	33	6	6	0	**6**	7	2	1	**2.5**	2	2	0	**2**	9	3	2	**4**
	32	6	5	0	**5**	7	2	2	**3**	2	1	0	**1**	8	3	2	**4**
	31	6	6	0	**6**	7	2	0	**2**	2	2	0	**2**	9	3	2	**4**
	30	6	4	0	**4**	7	3	0	**3**	4	4	0	**4**	9	3	2	**4**
	29	6	4	0	**4**	7	3	0	**3**	4	4	0	**4**	9	1	2	**2**
	28	6	6	0	**6**	7	4	2	**5**	5	5	0	**5**	9	6	1	**6.5**
convolutus	27	6	4	0	**4**	7	3	3	**4.5**	7	5	2	**6**	10	3	3	**4.5**
	26	6	6	0	**6**	7	0	4	**2**	8	3	3	**4.5**	10	3	3	**4.5**
	25	6	6	0	**6**	7	0	2	**1**	8	3	2	**4**	10	3	1	**3.5**
leptotheca	24	6	6	0	**6**	7	1	2	**2**	8	2	2	**3**	9	3	1	**3.5**
	23	5	5	0	**5**	7	0	3	**1.5**	8	3	2	**4**	9	3	1	**3.5**
	22	5	5	0	**4**	7	1	3	**2.5**	8	3	2	**4**	9	3	1	**3.5**
magnus	21	5	5	0	**5**	7	1	3	**2.5**	8	4	2	**5**	9	3	1	**3.5**
	20	6	6	0	**6**	7	2	2	**3**	8	2	3	**3.5**	9	1	4	**3**
	19	6	6	0	**6**	7	3	2	**4**	8	1	3	**2.5**	9	2	4	**4**
triangulatus	18	6	3	3	**4.5**	7	0	4	**2**	8	2	3	**3.5**	10	2	4	**4**
	17	6	2	4	**4**	7	0	3	**1.5**	8	2	3	**3.5**	10	3	3	**4.5**
	16	6	6	0	**6**	7	3	0	**3**	8	4	2	**5**	10	4	2	**5**
revolutus	15	6	6	0	**6**	7	4	2	**5**	9	5	3	**6.5**	10	4	4	**6**
	14	5	2	3	**3.5**	7	1	6	**3**	9	4	5	**6.5**	10	2	7	**5.5**
	13	5	5	0	**5**	7	1	6	**3**	6	4	1	**4.5**	10	4	4	**6**
atavus-acinaces	12	5	1	0	**1**	7	0	0	**0**	6	3	1	**3.5**	10	4	0	**4**
	11	5	1	0	**1**	7	0	0	**0**	7	2	1	**2.5**	10	4	0	**4**
	10	5	1	0	**1**	7	0	0	**0**	7	4	1	**4.5**	10	5	0	**5**
	9	5	1	0	**1**	7	0	0	**0**	7	3	1	**3.5**	10	3	0	**3**
	8	4	1	0	**1**	7	0	0	**0**	7	3	1	**3.5**	10	2	0	**2**
	7	4	1	0	**1**	7	0	0	**0**	7	4	1	**4.5**	10	4	0	**4**
acensus-acuminatus	6	4	4	0	**4**	7	0	0	**0**	7	4	1	**4.5**	9	2	0	**2**
	5	4	3	0	**3**	5	0	0	**0**	7	3	1	**3.5**	6	2	0	**2**
	4	4	4	0	**4**	4	0	0	**0**	9	5	1	**5.5**	5	2	0	**2**
upper** *persculptus*	3	3	3	0	**3**	3	0	1	**0.5**	8	3	2	**4**	2	2	0	**2**
	2	3	2	2	**3**	3	0	1	**0.5**	7	5	1	**5.5**	1	1	0	**1**
	1	3	1	2	**2**	1	1	0	**1**	6	4	1	**4.5**	1	0	0	**0**

UK Graptolite Biozone	Biozonal subdivisions*	Fig 11				Fig 12				Fig 13				Fig 14				Representation raw score per subdivision (tR)	Representation Index	Eustasy Index raw score per subdivision	EUSTASY INDEX (EI)	UK Graptolite Biozone
		R (8 max)	Low order	High order	EI raw score	R (9 max)	Low order	High order	EI raw score	R (6 max)	Low order	High order	EI raw score	R (7 max)	Low order	High order	EI raw score	Max = 62	(tR/Max)%	EIr	(EIr/tR)%	
guerichi	36	8	1	3	**2.5**	5	3	2	**4**	5	0	1	**0.5**	7	0	5	**2.5**	45	**73**	17.5	39	*guerichi*
	35	8	0	3	**1.5**	7	2	2	**3**	5	2	1	**2.5**	7	0	2	**1**	49	**79**	20	**41**	
	34	8	5	3	**6.5**	7	3	2	**4**	5	3	1	**3.5**	7	3	2	**4**	50	**81**	33	**66**	
sedgwickii-halli	33	8	5	0	**5**	7	2	2	**3**	5	0	0	**0**	7	0	3	**1.5**	51	**82**	24	**47**	*sedgwickii-halli*
	32	8	4	0	**4**	7	1	2	**2**	5	0	0	**0**	7	0	3	**1.5**	50	**81**	20.5	**41**	
	31	8	4	0	**4**	7	2	2	**3**	5	1	2	**2**	7	0	3	**1.5**	51	**82**	24.5	**48**	
	30	8	3	0	**3**	7	2	2	**3**	5	1	2	**2**	7	0	3	**1.5**	53	**85**	24.5	**46**	
	29	8	2	1	**2.5**	7	0	3	**1.5**	5	1	2	**2**	7	0	4	**2**	53	**85**	21	**40**	
	28	8	3	2	**4**	7	2	2	**3**	5	3	0	**3**	7	3	4	**5**	54	**87**	37.5	**69**	
convolutus	27	8	2	4	**4**	7	0	4	**2**	5	1	1	**1.5**	7	0	6	**3**	57	**92**	29.5	**52**	*convolutus*
	26	8	1	3	**2.5**	7	2	3	**3.5**	5	3	1	**3.5**	7	1	5	**3.5**	58	**94**	30	**52**	
	25	8	1	3	**2.5**	7	1	2	**2**	5	0	0	**0**	7	0	4	**2**	58	**94**	21	36	
leptotheca	24	8	0	4	**2**	8	2	2	**3**	5	0	0	**0**	7	0	4	**2**	58	**94**	21.5	37	*leptotheca*
	23	8	0	4	**2**	8	2	2	**3**	5	0	0	**0**	7	0	3	**1.5**	57	**92**	20.5	36	
	22	8	0	4	**2**	8	2	2	**3**	5	0	0	**0**	7	0	2	**1**	57	**92**	20	35	
magnus	21	8	0	4	**2**	8	1	2	**2**	5	0	0	**0**	7	0	3	**1.5**	57	**92**	21.5	38	*magnus*
	20	8	0	5	**2.5**	8	1.0	3	**2.5**	5	0	0	**0**	7	0	4	**2**	58	**94**	22.5	39	
	19	8	0	5	**2.5**	8	1	3	**2.5**	5	2	0	**2**	7	0	4	**2**	58	**94**	25.5	**44**	
triangulatus	18	8	3	3	**4.5**	8	1	4	**3**	5	0	0	**0**	7	1	4	**3**	59	**95**	24.5	**42**	*triangulatus*
	17	8	3	3	**4.5**	8	1	4	**3**	6	4	0	**4**	7	2	5	**3.5**	60	**97**	28.5	**48**	
	16	8	2	2	**3**	8	5	1	**5.5**	6	3	1	**3.5**	7	3	3	**4.5**	60	**97**	35.5	**59**	
revolutus	15	8	3	1	**3.5**	8	4	2	**5**	6	4	1	**4.5**	7	3	4	**5**	61	**98**	41.5	**68**	*revolutus*
	14	8	2	1	**2.5**	8	1	5	**3.5**	6	5	1	**5.5**	7	1	5	**2.5**	60	**97**	32.5	**54**	
	13	8	2	1	**2.5**	8	1	5	**3.5**	6	5	1	**5.5**	7	2	3	**3.5**	57	**92**	33.5	**59**	
atavus-acinaces	12	8	0	1	**0.5**	9	1	0	**1**	6	0	0	**0**	7	1	2	**2**	58	**94**	12	**21**	*atavus-acinaces*
	11	8	0	1	**0.5**	9	1	0	**1**	6	1	0	**1**	7	1	2	**2**	59	**95**	12	**20**	
	10	8	0	0	**0**	9	0	0	**0**	6	2	0	**2**	7	1	3	**2.5**	59	**95**	15	**25**	
	9	8	0	0	**0**	9	1	0	**1**	6	1	0	**1**	7	1	3	**2.5**	59	**95**	12	**20**	
	8	8	0	0	**0**	9	2	0	**2**	6	1	0	**1**	7	2	2	**3**	58	**94**	12.5	**22**	
	7	8	0	0	**0**	8	2	0	**2**	6	1	0	**1**	7	2	2	**3**	57	**92**	15.5	**27**	
acensus-acuminatus	6	8	0	0	**0**	8	2	0	**2**	6	1	0	**1**	7	2	1	**2.5**	56	**90**	16	**29**	*acensus-acuminatus*
	5	7	0	1	**0.5**	7	2	0	**2**	6	1	0	**1**	6	2	1	**2.5**	48	**77**	14.5	**30**	
	4	4	0	2	**1**	4	1	0	**1**	4	1	0	**1**	5	2	1	**2.5**	39	**63**	17	**44**	
upper** *persculptus*	3	0	0	0	**0**	1	1	0	**1**	2	2	0	**2**	4	3	0	**3**	23	**37**	15.5	**67**	upper** *persculptus*
	2	0	0	0	**0**	1	1	0	**1**	2	0	2	**1**	4	0	3	**1.5**	21	**34**	13.5	**64**	
	1	0	0	0	**0**	1	0	0	**0**	2	1	0	**1**	4	2	1	**2.5**	18	**29**	11	**61**	

Representation MAX (all datasets)	**2232**	**Mean EI score**	**43**
Total Representation score (TR)	**1886**		
Total Representation Index (TR/MAX)%	**84.5**		

Notes: * As shown un-numbered on Figures 7-15. **see text & Supplementary Data for explanation of usage. 'R' referes to level of representation of each subdivision within each dataset (see text). Numbers in 'Low order' columns refer to time slices indicated by solid colours on Figures 7-14 allocated a eustasy index raw score of 1.0 that show similarities with the low order (red) Type Llandovery base level curve. Numbers in 'High order' columns refer to time slices indicated by diagonal ornament that show closer similarities with the (blue) high order Type Llandovery base level curve and allocated a eustasy index raw score of 0.5. Colours in EI column show subdivisons that have scores incrementally higher than the mean (grouped arbitrarily into >43, >50 and >60).

Eustasy Index scores for the Type Llandovery succession (see text for explanation and interpretation)