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Survival of Burgess Shale-type animals in a Middle Ordovician deep-water setting

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Abstract: Exceptional preservation of non-biomineralized arthropods, sponges and vermiform taxa occurs in the Darriwilian (Middle Ordovician) Llanfallteg Formation of South Wales, UK. The assemblage contains elements typical of Ordovician communities juxtaposed with those more commonly associated with Cambrian Konservat-Lagerstätten. This assemblage is preserved in rocks of a deep-marine succession dominated by fine-grained siliciclastic and volcaniclastic density-current deposits. Non-biomineralized taxa of Cambrian aspect are preserved as pyritized carbonaceous compressions on the spectrum of Burgess Shale-type preservation. Trilobites with phosphatized digestive structures have also been recovered. The assemblage of the Llanfallteg Formation Konservat-Lagerstätte demonstrates that some Burgess Shale-type faunal elements survived into the Middle Ordovician within cool, deep-water refugia in the Welsh Basin, offshore from communities dominated by typical Ordovician taxa.

Supplementary material: Assemblage composition data and sedimentological images can be found at https://doi.org/10.6084/m9.figshare.c.2182218.

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The Great Ordovician Biodiversification Event (GOBE) was a global increase in the ecological complexity and diversity of skeletal fossils at the generic, familial and ordinal levels during the Ordovician Period (Sepkoski 1981, 1995; Harper 2006; Servais *et al*. 2010; Harper *et al*. 2015). Groups typical of the later Palaeozoic (e.g. rhynchonelliform brachiopods, bryozoans, crinoids, corals) flourished, whereas typical Cambrian groups seemingly declined (e.g. Sepkoski & Sheehan 1983; Harper *et al.* 2015). Although many groups began to diversify during the Floian (Servais *et al*. 2010), the spatial and temporal patterns of the GOBE differed markedly for different organisms; for example, phytoplankton diversification appears to have begun during the late Cambrian (Servais *et al*. 2016), but corals did not diversify until the Late Ordovician (Webby *et al*. 2004*a*). Most groups show several peaks of diversification at different times; for example, during the early Floian, Darriwilian and late Katian for brachiopods, but during the early Sandbian, early Katian and late Katian for trilobites (Harper *et al*. 2015). Diversification patterns for some groups, such as brachiopods (Zhan & Harper 2006) and chitinozoans (Achab & Paris 2007), were different on different palaeocontinents. The potential drivers for these changes have been widely debated (Webby *et al*. 2004*b*) and were probably complex (Botting & Muir 2008).

Biomineralizing taxa form only a minority of ancient and Recent marine communities (e.g. Schopf 1978; Conway Morris 1986). However, the paucity of non-biomineralized fossils from Ordovician rocks has led to understanding of the GOBE being derived almost exclusively from these biomineralized and other easily preserved taxa, such as trilobites, brachiopods and fossil plankton (Servais *et al*. 2010). Ideally, these data must be combined with information derived from Konservat-Lagerstätten: deposits with exceptionally preserved fossils, which usually include non-biomineralized organisms and anatomical details that are not preserved under normal taphonomic conditions. As taphonomic windows revealing the rarely preserved non-biomineralizing majority of faunas, these deposits are critical to understanding the evolution of ecosystems.

Only a few Ordovician Konservat-Lagerstätten are currently known, and only two from the Middle Ordovician, both of which are unusual, shallow-water assemblages (Botting 2005; Liu *et al.* 2006). Ordovician Konservat-Lagerstätten in general represent a diverse range of communities, from shallow-water arthropod-dominated assemblages (e.g. Young *et al.* 2007) to diverse open-marine assemblages (Van Roy *et al*. 2010; Botting *et al*. 2015) and to a deep-water sponge- and hydroid-dominated community resembling certain modern abyssal faunas (Botting *et al*. 2011). The rarity of these deposits and their disparate community types currently makes it difficult to build a coherent picture of the diversification of non-biomineralized organisms during the GOBE.

A new exceptionally preserved fauna has been recovered from the Darriwilian (Middle Ordovician) Llanfallteg Formation, predominantly at Cat's Hole Quarry, near Clarbeston Road, Pembrokeshire (Fig. 1a). From this site, Whittington (1993) described a single specimen of a trilobite, *Placoparia (Placoparia) cambriensis*, with preserved antennae and axial tendinous nodes, and Legg & Hearing (2015) recently described a new xenopod arthropod, *Etainia howellsorum*. Herein we report further exceptionally preserved material collected by Cedric Conolly over 30 years, plus material collected by the authors from a large excavation in August 2013.

Geological setting

The Llanfallteg Formation crops out within several fault-bounded blocks across northern Pembrokeshire, near the village of Clarbeston Road. Exposures are limited to disused quarries and some small road cuttings. The beds were folded during the Caledonian orogeny and dip steeply at 80–90° south with a local strike of *c.* 63° (Fig. 1b). The sites are located south of the ENE–WSW-trending Penfford Fault.

British Ordovician regional stratigraphy has been defined principally by trilobite and graptolite biostratigraphy (e.g. Fortey & Owens 1987; Zalasiewicz *et al*. 2009). The local stratigraphy is integrated with the international scheme by both biostratigraphic correlation and a wealth of radiometric dates (e.g. Fortey *et al*. 2000; Brenchley *et al.* 2006). The Llanfallteg Formation mudstones contain the graptolites *Didymograptus* ex gr. *artus* and *Glossograptus armatus*; these fossils constrain the principal fossiliferous locality to the *D. artus* Biozone (Zalasiewicz *et al.* 2009). This places the Llanfallteg Formation in the earliest Llanvirn Stage of British regional stratigraphy (Fortey & Owens 1987),

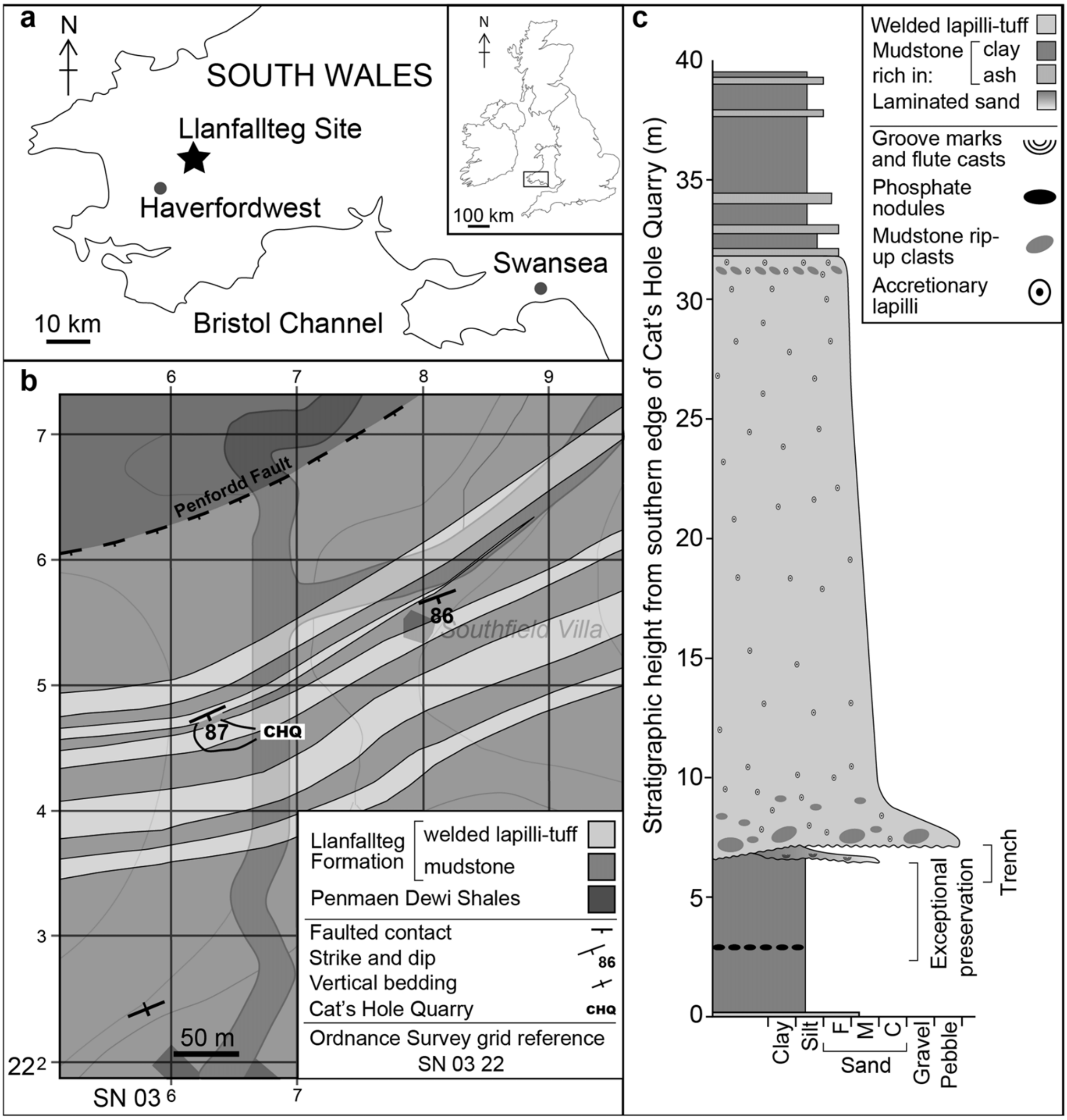

Fig. 1. Location and sedimentology of the Llanfallteg assemblage site. (**a**) Location map. (**b**) High-resolution geological map of the area surrounding the Llanfallteg assemblage site, with Ordnance Survey grid references. (**c**) Sedimentary log through Cat's Hole Quarry (CHQ), the main exposure investigated in this study.

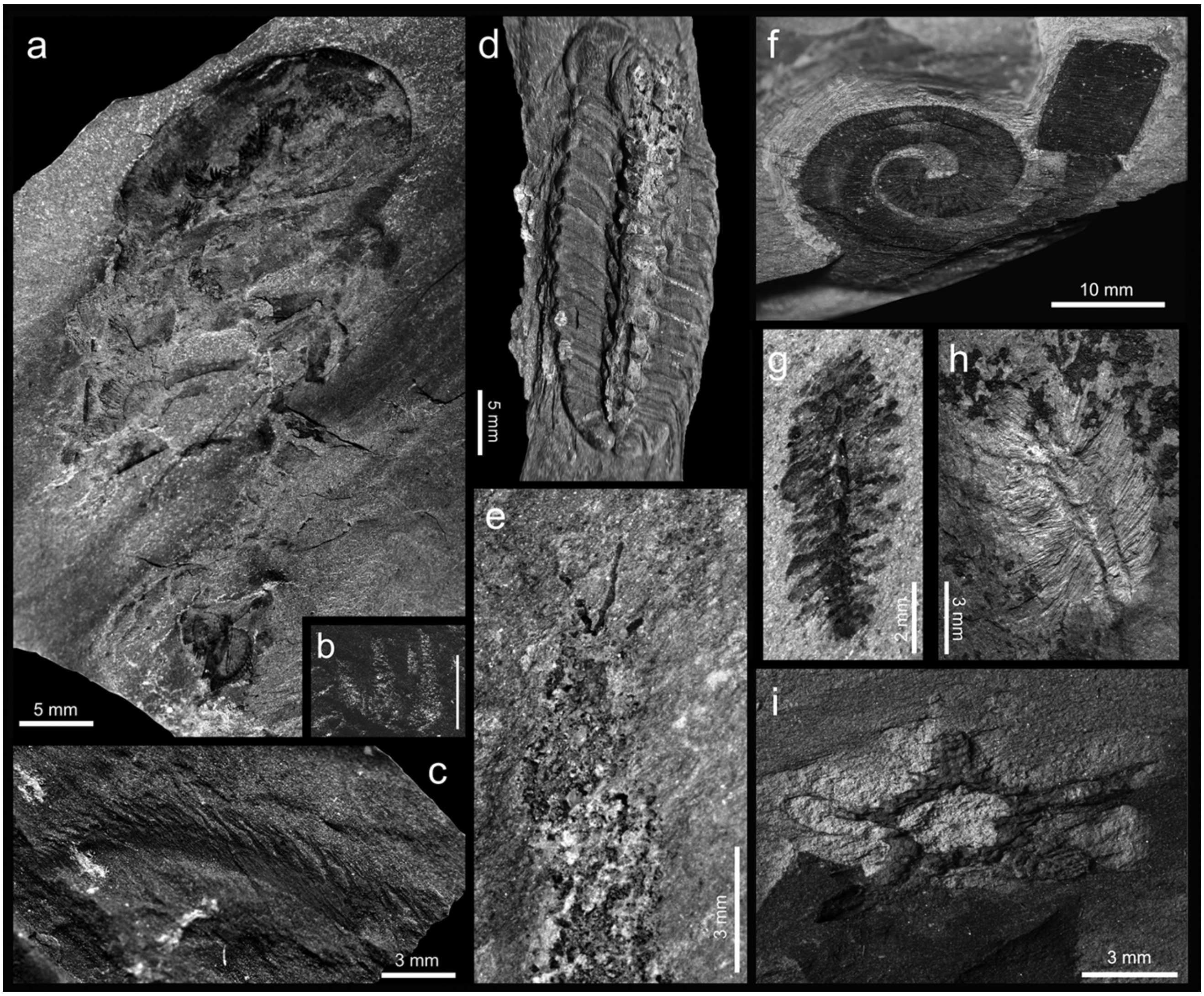

Fig. 2. Selected exceptionally preserved fossils from the Llanfallteg Formation. (**a**) *Etainia howellsorum* (xenopod), OUMNH (Oxford University Museum of Natural History) B 4615. (**b**) Energy-dispersive X-ray spectrograph showing carbon distribution in the appendages of OUMNH B 4615. (Scale bar represents 600 µm.) (**c**) Isolated medial spine of a *Furca*-like marrellomorph, NMW (National Museum of Wales) 2016.7G.1. (**d**) Trilobite (*Selenopeltis*) with phosphatized gut, NMW 2016.7G.2. (**e**) Probable annelid with anterior cephalic appendages, NMW 2016.7G.3. (**f**) Near-complete palaeoscolecidan worm, NMW 2016.7G.4. (**g**) Putative lobopodian, NMW 2016.7G.5. (**h**) Sponge (*Pirania*) NMW 00.17G.113. (**i**) Asterozoan echinoderm, NMW 2016.7G.6.

globally correlated to the international Middle Ordovician Darriwilian Stage (Fortey *et al.* 2000).

The Llanfallteg Formation contains siliciclastic and volcaniclastic sediments interbedded with welded lapilli-tuffs. The siliciclastic units comprise massive lenticular or discontinuously laminated blue-grey clay-rich siltstones interleaved with moderately sorted millimetre-scale laminae of light grey fine sand and silt. The coarser laminae display unidirectional flow structures and can include clusters of graptolites, conodont elements and arthropod fragments. The clay-rich silty sediment locally includes small phosphatic nodules, generally in isolation, with one nodule-rich band 3.5 m below the base of the main tuff (Fig. 1c). The mixed sandy and silty laminae are interpreted as distal fine-grained density currents deposited against a background of hemipelagic silty sedimentation.

The volcaniclastic laminae are commonly wrinkled and often include soft-sediment deformation and water-escape structures. The dominance of amorphous silica and small quartz grains supports an interpretation of rapid deposition as ash-fall laminae from nearby volcanic eruptions.

Local quarries contain exposures of well-indurated, finely crystalline, acidic volcaniclastic units up to 25 m thick (Fig. 1). These units have a groundmass of amorphous silica with fiamme structures alongside accretionary lapilli and subhedral feldspar phenocrysts. The tuffs fine upwards from an erosive base with centimetre-scale subrounded to angular mudstone clasts. These welded lapilli-tuffs were energetically emplaced when hot (e.g. Boulter 1987), consistent with deposition from subaqueous pyroclastic flows after subaerial eruptions (e.g. Carey & Schneider 2011, and references therein).

The Llanfallteg assemblage

Approximately 450 body fossils were examined in this study. The assemblage includes skeletal and non-biomineralized taxa characteristic of both Cambrian and Ordovician communities. Ordovician elements, particularly graptolites and trilobites, form the majority of the preserved assemblage; ‘Cambrian-type’ organisms are rarer. The trilobites recovered are all taxa typical of Middle Ordovician moderate-depth to deep-water environments (Fortey & Owens 1987; Whittington 1993). They include taxa characteristic of an atheloptic assemblage, which are either blind or have very reduced eyes, such as *Placoparia*, *Ormathops*, *Selenopeltis* and several trinucleids, nileids and raphiophorids (Fortey & Owens 1987). Non-atheloptic trilobite taxa have also been found, but are less abundant.

One of the most striking specimens is a xenopod arthropod, *Etainia howellsorum* (Fig. 2a and b), with preserved appendages, including soft lamellar exopod setae, which is regarded as a member of an otherwise exclusively Cambrian clade (Legg & Hearing 2015). Other non-biomineralized arthropod specimens include some resembling the marrellomorph *Furca* (Fig. 2c), which is also known from other Ordovician sites (Van Roy *et al*. 2010; Rak *et al*. 2013).

Ceratiocaridid and trilobite carapaces dominate the remaining arthropod fauna. Ceratiocaridids are common elements in some Ordovician and Silurian marine deposits (e.g. Braddy *et al*. 2004) and at this site are represented by mostly fragmentary remains. The majority of trilobites from this deposit are benthic, with either no or greatly reduced eyes, typical of an atheloptic assemblage (Fortey & Owens 1987). Trilobite preservation here is three-dimensional and can be remarkable (Whittington 1993). Newly recovered nileid (*Barrandia*) and dalmanitid (*Ormathops*) specimens preserve traces of antennae, and numerous specimens, including of *Placoparia*, *Ormathops* and *Selenopeltis*, have phosphatized digestive structures (Fig. 2d). Only two pelagic trilobite specimens were recorded: a cyclopygid compound eye and *Corrugatagnostus* sp. (but see Fatka *et al*. 2009).

Vermiform fossils of the Llanfallteg assemblage include soft-bodied annulated forms, one with apparent cephalic appendages (Fig. 2e), and weakly biomineralized palaeoscolecids (Fig. 2f). There is also a putative lobopodian (Fig. 2g) with a possible digestive structure.

The sponge fauna is of unusually low diversity compared with other Ordovician faunas from Wales (Botting *et al*. 2015; Muir & Botting 2015). An undescribed reticulosan with a perforated body wall is the only common species; a single specimen of the Burgess Shale protomonaxonid genus *Pirania* was also recovered (Fig. 2h).

The remaining faunal elements are skeletonized taxa typical of Ordovician communities, without evidence for soft tissue preservation. Echinoderms are represented by a single specimen each of a mitrate (B. Lefebvre, pers. comm. 2015), an asterozoan (Fig. 2i), an edrioasteroid and an isolated pelmatozoan columnal. The brachiopods are almost entirely lingulates, including a finely ribbed species resembling the common Ordovician genus *Monobolina* and a few other lingulid specimens. Bivalve molluscs, gastropods and nautiloids are present but rare. Most skeletonized taxa show damage consistent with moderate transport (e.g. separated or broken brachiopod valves, truncated asterozoan arms). Both graptoloid and dendroid graptolites are present. Graptoloids are the most abundant group (one-third of specimens) within the assemblage. Trace fossils are scarce, limited to infaunal burrowing of restricted morphology. The lack of observed epibenthic trace fossils may reflect the difficulty of identifying non-event bedding. Burrows are simple, unbranched or occasionally branching, of constant diameter, never wider than 5 mm, and preserved as clusters of framboidal pyrite. Single burrows may extend at least 100 mm horizontally but are restricted to less than 10 mm in vertical extent.

Exceptional preservation

Soft-tissue preservation in the Llanfallteg Formation Konservat-Lagerstätte assemblage is characterized by two principal modes: pyritized carbonaceous compressions of non-biomineralized taxa and phosphatization of arthropod digestive structures. Digestive-tract preservation in *Selenopeltis* (Fig. 2d) shows the serial paired digestive caeca described by Fatka *et al.* (2013). The non-biomineralized taxa are preserved as pyritized carbonaceous compressions (Fig. 2b), possibly with some aluminosilicate replacement. Anatomical detail including appendages, gills and oral apparatus is preserved in *E. howellsorum* (Legg & Hearing 2015) and in some other specimens. Scanning electron microscopy reveals clusters of 1–5 μm diameter pyrite framboids in the flattened fossils. Although much of the pyrite has been oxidized, energy-dispersive X-ray spectroscopy demonstrates that both iron and carbon are concentrated in the fossils.

The taphonomic pathways at play in the Llanfallteg Formation Konservat-Lagerstätte are to be the subject of further work, but initial comparison can be made with Burgess Shale-type preservation in the eponymous Canadian deposit and the Chengjiang Konservat-Lagerstätte, which form a spectrum of Burgess Shale-type preservation (*sensu* Cai *et al*. 2012, fig. 6). However, it should be noted that the carbonate cement seal considered by some an essential component of Burgess Shale-type preservation (Gaines *et al*. 2012) has not been observed.

Discussion

Both sedimentological and palaeontological evidence support the deep-water, subphotic character of this assemblage. The fine-grained sediments, including distal turbidites, lack any evidence of wave or storm influence. The dominance of atheloptic forms among the trilobites implies subphotic, deep-water conditions, supporting previous work in the area (Fortey & Owens 1987). The diminutive, low-diversity ichnofauna is also characteristic of a mud-dominated deep-water setting (McIlroy 2004). Many skeletal elements of the Llanfallteg assemblage, such as bivalve, brachiopod and echinoderm remains, are disarticulated or otherwise physically damaged, and are commonly incorporated within the density current deposits. This is consistent with transport of an exogenous fauna from the shallow-water habitats generally occupied by these taxa elsewhere in the Welsh Basin at this time (Cope 1999; Botting & Muir 2008; Botting *et al*. 2013).

The recovered biota is, therefore, not a single community, but a mixed assemblage combining elements from different ecosystems. In addition to transporting exogenous elements from shallower-water ecosystems, distal density currents also entrained organisms of an indigenous deep-water community, some of which were exceptionally well preserved. Swift burial can enhance preservation by suppressing sediment column chemoclines and raising the redox boundary, retarding the degradation of organic matter (e.g. Gaines *et al*. 2012; Garson *et al*. 2012). Rapid entombment could therefore have played a major role in the exceptional preservation here.

Even allowing for the mixing of communities within the Llanfallteg assemblage, the fauna demonstrates that taxa of Middle Ordovician aspect (e.g. the trilobites *Placoparia*, *Barrandia* and *Ormathops*) lived in the same area as taxa more typical of Cambrian Konservat-Lagerstätten (e.g. marrellomorph and xenopod arthropods, and piraniid sponges). The juxtaposition of these taxa is unusual, but invites four clear comparisons: the Early Ordovician Fezouata (Van Roy *et al*. 2010) and Afon Gam biotas (Botting *et al*. 2015), the Middle Ordovician Winneshiek Lagerstätte (Liu *et al*. 2006) and the Upper Ordovician Beecher's Trilobite Bed (Briggs *et al*. 1991).

The Fezouata Biota contains taxa typical of both Cambrian and Ordovician communities, alongside early examples of more modern groups (Botting 2007; Van Roy *et al*. 2010, 2015), which the Llanfallteg assemblage notably lacks. However, it remains unclear whether all these elements were derived from a single community or represent separate assemblages. The Fezouata sediments were deposited in much shallower water than the Llanfallteg Formation but nearer the Ordovician South Pole (e.g. Martin *et al*. 2016); hence, both the Llanfallteg and Fezouata assemblages could have been adapted to cool water, at depth and nearshore, respectively. The Tremadocian Afon Gam Biota of North Wales has been recovered from a series of mass-flow units deposited at around storm wave base. The Afon Gam community is similar to the Llanfallteg assemblage in the presence of Cambrian-type arthropods, sponges and other taxa (Botting *et al*. 2015). In contrast, the Afon Gam Biota contains abundant algae and sponges, whereas arthropods (including trilobites) are relatively much scarcer; it also lacks the unexpectedly derived taxa observed in the Fezouata Biota (Botting *et al*. 2015).

The Llanfallteg assemblage contrasts with other exceptionally preserved faunas from Middle and Upper Ordovician strata in Wales, which represent shallower-water environments and are generally dominated by sponges. These contain some Burgess Shale sponge genera but lack non-poriferan Cambrian-type taxa (Botting *et al*. 2011; Botting & Muir 2012; Muir & Botting 2015).

The Winneshiek Lagerstätte from the Darriwilian St Peter Formation, IA, USA (Liu *et al*. 2006), is the only Middle Ordovician Konservat-Lagerstätte known outside Wales. Fossils of the Winneshiek Lagerstätte include articulated conodont assemblages, articulated jawless fish head-shields, eurypterids and phyllocariids, but lack common Ordovician marine fossils such as trilobites and graptolites (Liu *et al*. 2006). As well as differences in fauna, the Llanfallteg and Winneshiek Konservat-Lagerstätten differ in depositional environment and modes of preservation. The St Peter Formation sandstones and shales were deposited in a shallow-water brackish to marine setting and the soft-bodied Winneshiek fossils are preserved as stains (Liu *et al*. 2006). This contrasts with the pyritized carbonaceous compression preservation and digestive tract phosphatization observed in the deep-water Llanfallteg Formation Konservat-Lagerstätte.

Of the Ordovician Konservat-Lagerstätten, the Katian (Upper Ordovician) Beecher's Trilobite Bed and its equivalents from the Lorraine Group, NY, USA, have the most comparable depositional environment to the Llanfallteg Formation Konservat-Lagerstätte. Exceptional preservation in the Lorraine Group is restricted to a few thin horizons, traceable over *c.* 100 m, each preserving a mass mortality event caused by sediment influx as a fine-grained turbidite (Cisne 1973; Farrell *et al*. 2009). Both are therefore settings of deep-water fine-grained turbidite deposition, but the Llanfallteg Formation sedimentary packages are lenticular and difficult to trace over more than a few metres. The exceptional Lorraine Group faunas are dominated by the Late Ordovician atheloptic trilobite genus *Triarthrus* (Farrell *et al*. 2009) and non-biomineralized taxa are rare. The styles of preservation are also different between the Lorraine Group and Llanfallteg Formation Konservat-Lagerstätten, with Beecher's Trilobite Bed involving more complete pyritization of biomineralized and non-biomineralized tissues, with all the organic matter metabolized by sulphate-reducing bacteria (Briggs *et al*. 1991). In contrast, there has only been partial pyritization of the exceptionally preserved fauna from the Llanfallteg Formation Konservat-Lagerstätte, as some organic matter has been retained (Fig. 2b). Despite these differences, Beecher's Trilobite Bed and its equivalents record a similar, trilobite-dominated deep-water assemblage with other rarer elements, but have not yielded any surviving Burgess Shale-type taxa.

Conclusions

The Llanfallteg Formation Konservat-Lagerstätte contains a range of exceptionally preserved taxa with both Cambrian and Ordovician faunal elements. The indigenous fauna of the Llanfallteg assemblage represents a largely Cambrian-type assemblage living in deep water and contains some taxa typical of the Burgess Shale. Some of the Ordovician-type taxa show evidence of downslope transport from shallower environments.

The Llanfallteg assemblage supports a growing body of evidence that Burgess Shale-type taxa persisted into post-Cambrian communities, but became increasingly restricted to deep- and/or cold-water settings (Conway Morris 1989; Van Roy *et al*. 2010). These faunas were contemporaneous with animal communities evolving in shallow-water environments during the GOBE. The length of time that Cambrian-type taxa survived in deep-water refugia is not yet known: exceptional preservation in deep, aphotic habitats is rare, and their subsequent history may have been much longer than currently suspected.

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