The Herefordshire Lagerstätte: fleshing out Silurian marine life

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Abstract: The Herefordshire Lagerstätte (c. 430 Ma) from the UK is a rare example of soft-tissue preservation in the Silurian. It yields a wide range of invertebrates in unparalleled three-dimensional detail, dominated by arthropods and sponges. The fossils are exceptionally preserved as calcitic void infills in early diagenetic carbonate concretions within a volcaniclastic (bentonite) horizon. The Lagerstätte occurs in an outer shelf/upper slope setting in the Welsh Basin, which was located on Avalonia in the southern subtropics. The specimens are investigated by serial grinding, digital photography and rendering in the round as ‘virtual fossils’ by computer. The fossils contribute much to our understanding of the palaeobiology and early history of the groups represented. They are important in demonstrating unusual character combinations that illuminate relationships; in calibrating molecular clocks; in variously linking with taxa in both earlier and later Palaeozoic Lagerstätten; and in providing evidence of the early evolution of group representatives of several groups.

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The Herefordshire Lagerstätte is unique in preserving representatives of many major invertebrate groups in high-fidelity 3-D, as calcite in-fills within concretions in a marine volcaniclastic deposit. The Herefordshire fossils are unimpressive at first sight, yet they yield univalved evidence about the palaeobiology and evolutionary significance of Silurian animals. They provide, for example, the earliest evidence for the time of origin of certain major crown-groups (i.e. the living biota), for instance sea spiders (pycnogonids).

The locality lies in the Welsh Borderland, a historic region central to R. I. Murchison’s pioneering research which established the Silurian System in the 1830s. In 1990 Bob King, mineralogist and retired Curator in the Department of Geology at the University of Leicester, collected concretions in float from the locality and presented nine of them to the Leicester collections. Curator Roy Clements asked David Siveter to examine one of the concretions when he was accessioning the material in 1994. What David recognized under the microscope, an arthropod with preserved limbs (later named *Officulus kingi*), was confirmed by Derek Siveter and, together with Bob King, they identified the stratigraphic horizon and collected more concretions. In 1995 Derek Briggs joined the team and, following more visits to the locality, we published an initial paper flagging the significance of the discovery (Briggs et al. 1996). NERC and Leverhulme Trust funding enabled Patrick Orr and later Mark Sutton to work on the Lagerstätte, initially as postdoctoral researchers. The support and co-operation of the site owners and help from English Nature has been crucial in realizing its scientific potential.

Locality, age and palaeogeographical setting

The Herefordshire site lies in the Old Radnor to Presteigne area of the Welsh Borderland (Fig. 1a) in the vicinity of the Church Stretton Fault Zone. The fossil-bearing concretions (Fig. 1b and c) occur in a soft, fine-grained, cream-coloured, weathered and largely unconsolidated bentonite (Fig. 1b) that crops out over about 30 m. The bentonite is unique in the British stratigraphic record, at least, in reaching a thickness of more than 1 m in places. The bentonite was deposited within mudstones of the Wenlock Series Coalbrookdale Formation (Fig. 1d), which rests on the slightly older Dolyhir and Nash Scar Limestone Formation. In the Dolyhir region these coral and algal-rich limestones lie with angular unconformity on the limonites (Currie et al. 1974). The Sheinwoodian and Homerian stages (Fig. 1d), which is radiometrically constrained to 430.5 ± 0.7 Ma (Cohen et al. 2013, updated 2018). Various evidence from brachiopods, graptolites and conodonts indicates a Wenlock age for the Dolyhir and Nash Scar Limestone Formation in addition to the overlying Coalbrookdale Formation (Bassett 1974; Cocks et al. 1992). The Sheinwoodian conodont *Ozarkodina sagittata rhenana* has been recovered from the limestones at Dolyhir and Nash Scar (Bassett 1974; Aldridge et al. 1981). The presence of Homerian Cyrtograptus lundgreni Biozone graptolites in the Coalbrookdale Formation mudstones immediately above the limestones at Nash Scar (Bassett 1974) suggests that deposition of these mudstones did not commence locally until *C. lundgreni* times (Hurst et al. 1978). This is consistent with the presence of the limestone hardground that presumably formed during a hiatus in deposition in the late Sheinwoodian.

The recovery of the chitinozoans *Margaritina margaritana*, *Ancyrocithina plurispinosa* and *Cingulochitina cingulata* from 20 to 50 cm below the bentonite also indicates an upper Sheinwoodian to Homerian age for the Coalbrookdale Formation (G. Mullins, pers. comm. 2000; see also Steeman et al. 2015). That age is unchallenged by ostracods (David Siveter, unpublished information) and radiolarians (Siveter et al. 2007a) recovered from concretions in the bentonite.
Fig. 1. Provenance and palaeogeography. (a) Welsh Borderland location of the Herefordshire Lagerstätte with regional geology. (b) The volcanic ash (bentonite), with concretions in situ, in contact with Coalbrookdale Formation shales above. (c) Typical concretion, 6 × 4 cm, concentrically weathered, lacking the blue-grey-hearted centre of calcium carbonate that is present in partially weathered examples, and incorporating an eccentric specimen of the aplacophoran *Acaenoplax*. (d) Local stratigraphy of the Dolyhir–Presteigne area. Radiometric dates are those given in Cohen et al. (2013, updated 2018), the International Commission on Stratigraphy (ICS) Chronostratigraphic Chart. Cramer et al. (2012) give marginally different radiometric dates for some of the boundaries based on sampling from Gotland and the West Midlands, UK, for example 429.5 Ma for the Sheinwoodian–Homerian boundary. However, the majority margin of error on these dates (±0.7 Ma) provides overlap with the dates given in the ICS Chronostratigraphic Chart. (e) Welsh Basin palaeogeography at approximately the Sheinwoodian–Homerian boundary (modified from Cherns et al. 2006, fig. 4.13a). (f) Eastern Laurussian palaeogeography during the Wenlock (modified from Cocks & Torsvik 2005, fig. 9).
The volcanic ash in which the Herefordshire Lagerstätte is preserved accumulated in the Welsh Basin (Fig. 1c). This lay on the microcontinent of Avalonia, which included southern Britain (Fig. 1f; Cocks & Torsvik 2011). Avalonia and adjacent Baltica were in southern tropical/subtropical palaeolatitudes in the mid-Silurian, separated from Laurentia by a remnant Iapetus Ocean. Shallow-water muds characterized much of the Welsh Borderland and central England east of the Church Stretton Fault Zone (Bassett et al. 1992; Cherns et al. 2006). Coeval fine clastics and turbidites accumulated to the west in the deepest parts of the Welsh Basin. Palaeogeographical and sedimentological evidence indicates that the Coalbrookdale Formation in the Dolyhir–Nash Scar area of the Church Stretton Fault Zone accumulated in a moderately deep, outer shelf/shelf slope environment (Briggs et al. 1996); the presence of the Visbyella brachiopod community suggests water depths of 100–200 m (Hurst et al. 1978; Brett et al. 1993). Geochemical analyses suggest a destructive plate margin as the source of the volcanic ash (Riley 2012). The closest known volcanic centres of Wenlock age (Cocks & Torsvik 2005) are the Mendip Hills in SW England (Avalonia) and the Dingle peninsula in SW Ireland (Avalonia). The Herefordshire bentonite is geochemically similar to volcanic rocks in both areas (Riley 2012). A more distant candidate is the Czech Republic, then on Perunica, a microcontinent in the centre of the Rheic Ocean (Fig. 1f).

Taphonomy

The volcanic ash that hosts the Herefordshire biota was deposited on an erosion surface on massive limestone and, in places, muds; the uneven topography likely reflects the original Wenlock seafloor. The ash layer varies from a few tens of centimetres to over 1 m thick and is highly weathered at least in outcrop: no evidence for primary sedimentary structures is preserved. Thus, it is unclear whether the ash represents in situ settling or was reworked, or whether there was one or several ashfalls. Occasional examples of unsuccessful escape traces (Orr et al. 2000) indicate that at least some of the animals were buried alive, which is consistent with the remarkable preservation. The bentonite has yielded at least five thousand randomly distributed calcite-cemented concretions 2–25 cm in diameter (Orr et al. 2000; Fig. 1b and c). Unusually for fossils preserved in this way, the organisms do not appear to have influenced the size or shape of the concretions, nor are they usually in the centre (Fig. 1c). Fossils are only preserved where they were incorporated into concretions but it is not clear what determined the locus of concretion formation. The timing and nature of the growth of the Herefordshire concretions merits further investigation.

The fossils show high-fidelity three-dimensional preservation – the threads that attach the juveniles to the arthropod Aquilonerfer (Briggs et al. 2016), for example, are less than 50 µm in diameter (Fig. 4h). About half the taxa lacked bimineralyzed hard parts and the bimineralized taxa preserve remarkable details in addition to features preserved in the normal fossil record. The soft tissues show negligible collapse (Fig. 3a and d) indicating that the ash stiffened and recorded the outer morphology of the animals before significant decay took place. The spherical morphology of the concretions suggests that they formed rapidly, before sediment compaction. The fossils are preserved as voids that were infilled with calcite (Fig. 3) which also dominates the concretion cement (Orr et al. 2000). The bimineralized skeletons of brachiopods, gastropods, trilobites and ostracods are preserved, but organic remains, even non-bimineralized arthropod cuticles, are lost – the periderm of the rare graptolites is an exception. Preservation was investigated in detail in the arthropod Offacolus (Orr et al. 2000). Sparry calcite infilled the external mould of Offacolus, sometimes with an initial phase of finer fibrous calcite around the periphery (Figs 3a, 4c and f). Pyrite precipitated on the boundary between calcite crystals but as a minor constituent of the void fill. Clay minerals precipitated on and underneath the exoskeleton, and in some examples the gut trace was replicated in calcium phosphate. Ferroan dolomite (ankerite) formed at a later stage perhaps coincident with the transformation on burial of smectite to illite. Abundant radiolarians are evident on the surface of split concretions (Siveter et al. 2007a; Fig. 5x). Their preservation shows parallels to that of Offacolus (Orr et al. 2002).

The precipitation of calcite retained the shape of the test when the opaline silica that formed it was replaced during diagenesis by a mixture of ankerite and diagenetic clay minerals; replacement of silica by ankerite has also been observed in siliceous spongopleurans (Nadhira et al. 2019). Although there are similarities with the diagenetic sequence displayed by radiolarians in concretions elsewhere (Holdsworth 1967; Orr et al. 2002), the nature of the preservation of soft tissue morphology at the Herefordshire site remains unique.

Releasing the information from the fossils

The Herefordshire concretions are collected in bulk using earth moving equipment. Each scoop is tipped slowly on to a waste-pile; concretions roll out and are collected manually. The concretions are split repeatedly in the laboratory with a manual rock-splitter; the process is halted if a fossil is found (Fig. 3; c. 50% of concretions). Specimens are identified provisionally, photographed with a Leica DFC420 digital camera mounted on a Leica MZ8 binocular microscope with a thin layer of water over the specimen to enhance contrast, and catalogued in a custom online database.

The fossils record copious anatomical information but present challenges for its extraction. Manual or chemical preparation of specimens (see e.g. Sutton 2008) is impractical. Study of the Herefordshire fauna is unique among invertebrate Lagerstätten in relying almost exclusively on virtual reconstructions. Indeed, research on the fossils has played an important role in the development of such techniques and their wider application (Sutton et al. 2001b, 2014). Non-destructive approaches to data-capture, such as X-ray computed tomography, are clearly preferable as a basis for virtual reconstructions but are largely ineffective for Herefordshire fossils: X-ray absorption contrast between fossil and matrix is very low. Limited success has been achieved with some specimens by using phase-contrast synchrotron tomography (see Sutton et al. 2014, p. 78), but a destructive yet highly effective physical-optical tomography ‘serial grinding’ technique is, of necessity, our method of choice. This takes advantage of the strong optical contrast between specimen and matrix and has been used to reconstruct over 100 specimens.

Specimens for reconstruction are trimmed with a fine rock-saw to c. 10 mm cuboids and mounted on a Buehler ‘slide holder’ which consists of an inner metal cylinder which can be adjusted to elevate specimens a precise distance above a hard outer ceramic disc. Specimens are ground to remove a consistent thickness (20–50 µm), washed, and photographed. This process is repeated until the entire specimen has been digitized, typically in 200–400 increments. Part and counterpart are ground separately, and large specimens are processed in several pieces which are re-united digitally, following reconstruction, using the custom SPIERS software suite (Sutton et al. 2012b).

Reconstruction begins with manual or semi-automatic registering (aligning) of photographs using the cut edges of cuboids as a guide. Data are then prepared for reconstruction by carefully distinguishing pixels representing the fossil from those corresponding to matrix. Software exists to automate this process but an understanding of the taphonomy and likely anatomy of the specimen, and of artefacts generated by the process (e.g. ‘out-of-plane’ structures visible through bubbles in the encasing resin), is
Box 1. The faunal composition of the Herefordshire Lagerstätte

Thirty-two species, including two under open nomenclature, have been described from the Herefordshire Lagerstätte, and at least 29 await description (Table 1). Some 75% of Herefordshire species (excluding radiolarians) are non-biomineralized but this reflects bias in initial taxa selected for study and may fall to c. 50% when other biomineralized taxa, including trilobites and the extensive sponge fauna, are described. Arthropods are diverse (Fig. 2b): 19 species have been recorded, 17 of which have been fully described. They include representatives of most major euarthropod groups: megacheirans, pycnogonids, chelicerates, trilobites, marrellomorphs, stem mandibulates and pancrustaceans (this last by far the most species-rich, with 9 described species) as well as one lobopodian. Sponges are the most abundant and diverse of the other major groups, probably comprising at least 20 species, although all but one await detailed investigation. Molluscs are represented by two species of aplacophorans and two gastropods (one uninvestigated), one bivalve and an orthoconic nautiloid (uninvestigated). There are at least four echinoderm species, an asteroid, edrioasteroid, ophiocistioid and a crinoid (the last uninvestigated), at least two brachiopods (one an uninvestigated lingulid), an annelid, possibly two cnidarians (a coral and a possible hydrozoan, both uninvestigated), and two nanomiaids (uninvestigated). Sponges are the most abundant and diverse of the other major groups, probably comprising at least 20 species, although all but one await detailed investigation. Molluscs are represented by two species of aplacophorans and two gastropods (one uninvestigated), one bivalve and an orthoconic nautiloid (uninvestigated). There are at least four echinoderm species, an asteroid, edrioasteroid, ophiocistioid and a crinoid (the last uninvestigated), at least three brachiopods (one an uninvestigated lingulid), an annelid, possibly two cnidarians (a coral and a possible hydrozoan, both uninvestigated), and two hemichordates (a graptoloid and a possible dendroid, both uninvestigated). The large number of unidentified specimens (1506; 41.0%) reflects poorly preserved examples and also the difficulty of identifying specimens on split concretions prior to reconstruction. Radiolarians are not included in the faunal composition assessment (Fig. 2a) because of the difficulty in estimating their specimen numbers (which are in the hundreds or possibly thousands). Additionally, a few thousand concretions remain unsplit.

The chelicerate *Offacolus kingi* is the most abundant at over 250 specimens. Many of the non-arthropods, however, such as the bivalve *Dinocysta philocricoides* (Fig. 2b), an order of magnitude more than the mandibulate *Tanaisos dokeron* and the malacostracan crustacean *Cinerocaris magnifica*. Most of the arthropods are known from just a few specimens (e.g. the megacheiran *Enalikter aphson*), or single individuals, such as the horseshoe crab *Dibasterium durgae*. Of non-arthropod taxa the polychaete annelid *Kenostrycus clementsi* is the most abundant at over 250 specimens. Many of the non-arthropods, however, such as the edrioasteroid *Heropyrgus distosus*, are based on a few tens of specimens and some, such as the bivalve *Praectenodonta ludensis*, on one specimen only.

### Table 1. Faunal composition of the Herefordshire Lagerstätte

<table>
<thead>
<tr>
<th>Sponges</th>
<th>Crustaceans</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Caricospumia pedicula</em> (Nadhi et al. 2019; Fig. 5y)</td>
<td><em>Cinerocaris magnifica</em> (Briggs et al. 2003; Fig. 5c and d)</td>
</tr>
<tr>
<td>Some 20 other species (uninvestigated)</td>
<td>Cascolas rastis (Siveter et al. 2017; Fig. 51 and m)</td>
</tr>
<tr>
<td>Cnidarians</td>
<td><em>Dibasterium durgae</em></td>
</tr>
<tr>
<td>? Hydroid (uninvestigated colonial organism)</td>
<td></td>
</tr>
<tr>
<td>Coral (uninvestigated)</td>
<td>Cephalopods</td>
</tr>
<tr>
<td>Brachiopods</td>
<td><em>Dinocysta philocricoides</em></td>
</tr>
<tr>
<td><em>Bethia serraticulma</em> (Sutton et al. 2005a; Fig. 4k)</td>
<td><em>Dibasterium durgae</em></td>
</tr>
<tr>
<td>At least two other brachiopod species (both uninvestigated), one of them a lingulid</td>
<td></td>
</tr>
<tr>
<td>Lophophorater indet.</td>
<td><em>Drakozoon kalumon</em> (Sutton et al. 2010; Fig. 4j)</td>
</tr>
<tr>
<td>Annelids</td>
<td><em>Enalikter aphson</em> (Siveter et al. 2014a, 2015a; Fig. 5e)</td>
</tr>
<tr>
<td><em>Kenostrycus clementsi</em> (Sutton et al. 2001c; Fig. 5a)</td>
<td><em>Myodocopes</em></td>
</tr>
<tr>
<td>Molluscs</td>
<td>Colymbosathon eclecticos</td>
</tr>
<tr>
<td><em>Acaenoplax hayae</em> (Sutton et al. 2001a; Fig. 4s and t)</td>
<td><em>Nymphatella gravida</em> (Siveter et al. 2007c; Fig. 4b, q and t)</td>
</tr>
<tr>
<td><em>Kalindroplex perissokomos</em> (Sutton et al. 2012a; Fig. 4f and m)</td>
<td><em>Nassarius fluta</em> (Siveter et al. 2010b; Fig. 5a)</td>
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<tr>
<td><em>Bivalvia</em></td>
<td><em>Pauline avibella</em> (Siveter et al. 2013; Fig. 5zz)</td>
</tr>
<tr>
<td><em>Praectenodonta ludensis</em> Reed, 1931 (Fu 2016)</td>
<td><em>Spiricopia aurita</em> (Siveter et al. 2011a; Fig. 5u)</td>
</tr>
<tr>
<td><em>Gastropods</em></td>
<td>- Podocopa and palaeocopods</td>
</tr>
<tr>
<td><em>Platecras</em>? sp. (of Sutton et al. 2006; Fig. 5v)</td>
<td>Fragments of unidentified</td>
</tr>
<tr>
<td>A high spired species (uninvestigated)</td>
<td>species belonging to these ostracod groups have been</td>
</tr>
<tr>
<td><em>Cephalopods</em></td>
<td>recovered from acid residues</td>
</tr>
<tr>
<td><em>Nautoloids</em> (uninvestigated)</td>
<td><em>Pentastomids</em></td>
</tr>
<tr>
<td><em>Panarthropods</em></td>
<td><em>Invatita piratica</em> (Siveter et al. 2015b, Fig. 4p, q and r)</td>
</tr>
<tr>
<td><em>Lobopodians</em></td>
<td>Echinoderms</td>
</tr>
<tr>
<td><em>Thanhithia distos</em> (Siveter et al. 2018a; Fig. 5a and b)</td>
<td>Asteroids</td>
</tr>
<tr>
<td><em>Megaechinans</em></td>
<td><em>Bidellacoma sp.</em> (of Sutton et al. 2005b; Fig. 5f-i)</td>
</tr>
<tr>
<td><em>Enalikter aphson</em> (Siveter et al. 2014a, 2015a; Fig. 5e)</td>
<td>Edrioasteroids</td>
</tr>
<tr>
<td><em>Pycnozonoids</em></td>
<td><em>Heropyrgus distosus</em> (Briggs et al. 2017; Fig. 5j and k)</td>
</tr>
<tr>
<td><em>Haliestes daios</em> (Siveter et al. 2004; Fig. 5n and o)</td>
<td>Crinoids (uninvestigated sp.)</td>
</tr>
<tr>
<td><em>Chelicerae</em></td>
<td>Ophiocistiods</td>
</tr>
<tr>
<td><em>Offacolus kingi</em> (Orr et al. 2000; Fig. 4c and f)</td>
<td><em>Sollasina cihilhu</em> (Rahman et al. 2019; Fig. 5q)</td>
</tr>
<tr>
<td><em>Dibasterium durgae</em> (Briggs et al. 2012; Fig. 4d, e, g and i)</td>
<td><em>Hemichordates</em></td>
</tr>
<tr>
<td><em>Trilobites</em></td>
<td>Pterobranchs</td>
</tr>
<tr>
<td><em>Dalmanites sp.</em> (uninvestigated)</td>
<td>Graptoloids (uninvestigated)</td>
</tr>
<tr>
<td><em>Tapinocaymene</em> sp. (uninvestigated)</td>
<td><em>Dendroids?</em> (uninvestigated)</td>
</tr>
<tr>
<td><em>Marrellomorphs</em></td>
<td><em>Radiolarians</em></td>
</tr>
<tr>
<td><em>Xylokorys chiledophila</em> (Siveter et al. 2007b; Fig. 5r and w)</td>
<td><em>Inanihella sugena</em> (Siveter et al. 2007a; Fig. 5x)</td>
</tr>
<tr>
<td><em>Mandibulata</em></td>
<td><em>Inanihella sp.</em> (of Siveter et al. 2007a)</td>
</tr>
<tr>
<td><em>Aquillonifer spinosus</em> (Briggs et al. 2016; Fig. 4h)</td>
<td><em>Haploentactinia armista</em> (Siveter et al. 2007a)</td>
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</tbody>
</table>

*The relevant primary reference is given after the species name. Other relevant references are given throughout the text.*
essential to extract maximum morphological information. Data are ‘marked up’ to identify separate structures for visualization, e.g. a particular arthropod appendage. Prepared datasets are reconstructed to triangle-mesh isosurfaces using the Marching Cubes algorithm (Lorensen & Cline 1987). These are visualized and studied using the SPIERSview component of the software suite, which can combine multi-part models (e.g. part and counterpart) and enables stereoscopic viewing, arbitrary rotation, scaling, dissection and sectioning. Models are exported into VAXML/STL format (Sutton et al. 2012) for publication, or to the open-source rendering package Blender (Blender Foundation 2019) to produce maximal-quality ray-traced images and animations (see Sutton et al. 2014, pp. 27–31, 155–158 for details of the process). The quality of preservation is such that a single specimen can provide abundant data for detailed analysis.

**Unexpected character combinations and a possible role for evolutionary development**

The reconstruction of phylogenies and the ordering and timing of character-acquisition has been an overarching project in evolutionary biology and palaeontology for over 150 years. Reconstructing the history of life based on the living biota alone is attractive as vast quantities of data are obtainable, including the genetic sequences that have revolutionized phylogenetic practice in recent years. However, such data are restricted to crown-groups; no amount of avian sequences would reveal the origin of birds within Dinosauria, for example. Fossils document otherwise unknown character combinations that did not survive to the present. These combinations can illuminate relationships and evolutionary history (e.g. in arthropods: Legg et al. 2013), a reminder that the significance of fossils may be out of proportion to their morphological information content. It is no surprise therefore that the high-fidelity soft-tissue fossils provide important new data for determining the course of evolution in many groups, as illustrated by molluscs.

Deep molluscan phylogeny hinges on the position of the Aplacophora which comprise two worm-like groups, Chaetodermomorpha and Neomeniomorpha, united in lacking a shell and fully developed molluscan foot. Aplacophorans were traditionally interpreted (e.g. by Salvini-Plawen 1991) as the earliest branch of the mollusc lineage (Fig. 4a), but an alternative model places them as sister to the multivalved Polyplacophora (chitons) in a clade termed Aculifera, which is in turn the sister group to all other molluscs (Conchifera). This ‘Aculifera hypothesis’ is supported by both molecular and morphological data (Sigwart & Sutton 2007; Wanninger & Wollesen 2018; but see Salvini-Plawen & Steiner 2014). Resolution of the debate is critical for reconstructing molluscan evolution (did the ancestor of crown-group molluscs have a shell and/or foot?) and for determining their position in the tree of life.

Aplacophorans were unknown as fossils before they were discovered in the Herefordshire biota. Multivalved molluscs had been described from the Paleozoic (e.g. Cherns 1998a, b), but were treated as early polypelacophorans (chitons). The discovery of *Acaenoplax hayae* from Herefordshire (Sutton et al. 2001a, 2004; Dean et al. 2015) revealed an aplacophoran-like form bearing spicules, lacking a true foot and possessing a posterior respiratory cavity (Fig. 4s and i). Nonetheless *Acaenoplax* shows serialization and multiple dorsal valves reminiscent of Polyplacophora. The subsequent discovery of *Kulindroplax perissokomos* (Sutton et al. 2012a) documented an even more aplacophoran-like body with no trace of a foot but bearing a set of typical Paleozoic ‘polyplacophoran’ valves (Fig. 4i and m). This association appeared chimaeric but only because it represents an extinct character combination. *Acaenoplax* and *Kulindroplax* provide support for Aculifera (e.g. Vinther 2015), indicating that the ‘simple’ morphology of aplacophorans is derived rather than primitive for the Mollusca. Furthermore, these Herefordshire fossils reveal a sequence of evolutionary events that cannot be deduced from extant forms: a vermiform body predated the loss of valves, and a diversity of ‘plated aplacophorans’, previously misinterpreted as polyplacophorans, was present during the early Paleozoic. Modern
aplanoplacophorans evolved through a secondary loss of valves and are a remnant of a once larger group (Fig. 4v).

Research on evolutionary development has demonstrated how control genes can initiate major changes in morphology. Modern polyplacophorans (chitons) have a series of eight dorsal valves associated with the expression of the engrailed gene (Jacobs et al. 2000), whereas Acaenoplax and Kulindroplax (Fig. 4l, m, s and t) have only seven. Such seven-fold seriality is expressed during the ontogeny of living aculiferans (Scherholz et al. 2013) and may reflect an ancestral morphology evident in Kulindroplax (Wanninger & Wollesen 2018). The addition of an eighth shell, which occurs after metamorphosis in Polyplacophora, appears to be an advanced condition (Wanninger & Wollesen 2018). Acaenoplax is unusual in having an obvious gap between valves 6 and 7 where an additional valve might have been placed (Sutton et al. 2001a, 2004). The ‘missing’ valve may reflect the ancestral 7-valve morphology or, given that the space for an additional valve is present, may have been lost secondarily from an 8-valved form.

The remarkable details preserved in some of the Herefordshire arthropods provide evidence of ancestral morphologies and prompt questions as to how they might have been transformed into modern forms. Martin et al. (2016) used CRISPR/Cas9 mutagenesis and RNAi knockdown to show how shifting Hox gene domains in a larval stage can be interpreted as a stage in the loss of the exopod to segment: they insert in different places on the body wall. This arrangement can be interpreted as a stage in the loss of the exopod to yield a limb with a single ramus, as in Limulus. The expression of Distal-less (Dll) in larval Limulus (Mittmann & Scholtz 2001) suggests that the loss of the exopod may be developmental. Limulus shows a strong expression of Dll associated with the origin of the endopod and a weaker expression, in the early embryo, in an adjacent position corresponding to the insertion of the exopods in Dibasterium. This weaker expression disappears in later embryonic stages echoing the loss of the outer rami during the evolution of the group (Briggs et al. 2012). The chelicera of Dibasterium (limb 1) is also unusual in being an elongate flexible antenna-like appendage, in contrast to the familiar claw of Limulus. Here, too, knockdown of genes such as Dll and dachsund may have led to the loss of distal podomers and the evolution of the shorter chelicera in modern horseshoe crabs, echoing experimental results on the harvestman Phalangium (Sharma et al. 2013).

Extended stratigraphic ranges and the calibration of molecular clocks

The Herefordshire Lagerstätte is one of very few windows on soft-bodied organisms during the Silurian. It is not surprising, therefore, that the fossils provide important examples of stratigraphic range extensions. Thanahita (Fig. 5a and b), for example, falls in a clade with the three known species of the iconic lower to mid-Cambrian lobopod Halletucigenia (Siveter et al. 2018b). The long slender trunk appendages of Thanahita contrast with those of short-legged lobopodians, such as the Cambrian Antennacanthopodia (Ou et al. 2011). Long-legged lobopodians are also represented by Carbotubulus from the late Carboniferous Mazon Creek Lagerstätte of Illinois (Haug et al. 2012) which is some 135 Ma younger than Thanahita.

The discovery of the arthropod Endalikter (Siveter et al. 2014a, 2015a; Fig. 5e) revealed that megacheirans (short-great-appendage arthropods) were present in the Silurian. Phylogenetic analysis showed that Bundenbachiellus from the Devonian Hunsrück Slate, not previously interpreted as a megacheirian, is sister to Endalikter, extending the range of megacheirans nearly 100 Ma beyond the previously youngest known short-great-appendage arthropod, Leachooilla? sp. from the mid-Cambrian of Utah (Briggs et al. 2008). Xylokorys is the only known Silurian marrellomorph euarthropod (Siveter et al. 2007b; Fig. 5r and w). It belongs to the Acoelomorpha (see Legg 2016) which, in contrast to the familiar Cambrian Marrella, is characterized by a large shield-like carapace which covers the head and trunk. Xylokorys extends the Cambrian (Primiticaris and Skania) and Ordovician (Enosisaspis) acerostracan record and heralds the youngest known example, Vachonisia, in the Devonian Hunsrück Slate.
Fig. 4. Herefordshire Lagerstätte species. (a) Colymbosathon ecplecticos, valves removed, lateral view. (b) Nymphatella gravida, left valve removed, posterolateral view. (c, f) Officulus kingi, dorsal, ventrolateral views (see Fig. 3a). (d, e, g, i) Dibasterium durgae, ventrolateral stereo-pair, dorsal view; chelicerae (first appendages), lateral view; prosomal area and anterior part of opisthosoma, ventral view. (h) Aquilonifer spinosus, dorsal view. (j) Drakozoon kalamon, ventral view. (k) Bethia serraticulma, with attached Drakozoon kalamon and 'atrypide brachiopod, lateral view. (l, m) Kailinodroplax perissokomos, lateral, dorsal views. (n, o) Rhumphoverraptor reduncus, attached juvenile, free swimming stage, lateral views. (p) Invavita piratica, lateral view. (q, r) Nymphatella gravida, with valves, and valves removed, with an attached and an internal specimen of Invavita piratica, lateral views. (s, t) Acaenoplax hayae, anterior part of body, dorsolateral view; main and posterior parts of body, dorsolateral view (see Fig. 3d). (u, v) Cladograms depicting competing molluscan phylogenies (simplified from Wanninger & Wollesen 2018): (u) ‘Testaria’ hypothesis, one of several phylogenetic models in which aplacophorans are primitive with respect to all other molluscs; (v) ‘Aculifera’ hypothesis, in which aplacophorans and polyplacophorans form a sister clade (Aculifera) to all other molluscs (Conchifera). Scale bars are all 500 µm.
Haliestes (Siveter et al. 2004; Fig. 5n and o) is arguably the best preserved and most complete of just 13 known species (Sabroux et al. 2019) of fossil pycnogonid. These include a putative larval pycnogonid, *Cambropycnogon klausmuelleri*, from the upper Cambrian Orsten of Scandinavia (Waloszek & Dunlop 2002), and a basal stem group pycnogonid, *Palaeomarachne granulata*, from...
the Ordovician William Lake Lagerstätte of Canada (Rudkin et al. 2013). The Herefordshire pycnogonid Haliestes shows reduction of the body to a small trunk projection beyond the posteriormost limbs. This is a feature of Pantopoda, indicating that crown-group pycnogonids extended back to the Silurian (Siveter et al. 2004; Arango & Wheeler 2007; Dunlop 2010, but see Charbonier et al. 2007). Five pycnogonid species are known from the Devonian Hunsrück Slate, of which Palaeopontopus maucher and Palaeothea devonica show trunk end reduction. Three species from the Jurassic of La Voult-sur-Rhône, France, may also belong to extant pantopod families (Charbonier et al. 2007).

Where Herefordshire taxa extend the range of particular clades back in time, they provide fossil calibrations for the tree of life, notably in the case of arthropods. Haliestes provides one example (Wolfe et al. 2016), the barnacle Trilobite Bed of New York State (Siveter et al. 2018), the International Commission on Stratigraphy (ICS) Chronostratigraphic Chart.

the early Ordovician Fezouata biota of Morocco (Van Roy et al. 2015) is the most diverse open-marine Lagerstätte in the interval between the late Cambrian Weeks Formation of Utah (Lemsey-Abriel et al. 2018) and the mid-Silurian Herefordshire Lagerstätte (other Ordovician Lagerstätten are briefly reviewed in Van Roy et al. 2015). The Fezouata biota is much more diverse than Herefordshire, comprising over 160 genera, of which shelly taxa account for about 50%. As in Herefordshire, sponges are diverse and panarthropods dominate (over 60 taxa). Fezouata yields a greater diversity of shelly taxa including conulariids, bryozoans, machaeridian annelids, rostroconch and helcionellid bivalves, hyolithoids and echinoderms.

Apart from Herefordshire, open-marine Lagerstätten of Silurian age are rare (Fig. 6). Other exceptionally preserved faunas are almost exclusively preserved via Burgess Shale-type pathways as degraded organic (carbonaceous) compression fossils and almost all represent marginal-marine or ‘stressed’ environments (Orr 2014). The Ludlow age Eramosa of the Herefordshire Lagerstätte includes three biotas representing different environments. Soft-bodied fossils are characteristic of Biota 3, which contains a diverse marine fauna of conulariids, a lobopodian, trilobites, eurypterids, xiphosurans, diverse crustaceans, brachiopods, polychaete annelids, echinoderms, conodonts and possible fish. The fauna of the late Llandovery Waukesha Lagerstätte from Wisconsin (Mikulic et al. 1985a, b) shows some similarity to Eramosa but is peri-tidal. It is dominated by arthropods, especially trilobites (13 genera), and includes a xiphosuran and phyllocarcid crustaceans. Conulariids and graptolites are common, but brachiopods, bryozoans, corals, molluscs and echinoderms are rare or absent. The Pfidilod Bertie Group of Ontario and New York State is dominated by eurypterids, xiphosurans, scorpions and phyllocarcids preserved in fine carbonate muds (Clarke & Ruedemann 1912; Copeland & Bolton 1985). The presence of salt loppers was long regarded as evidence of hypersaline conditions, but it is likely that they were precipitated in the sediment after deposition and the Bertie Group represents a shallow subtidal setting (Vrazo et al. 2016). The deeper-marine Herefordshire fauna includes numerous sponges, two trilobite genera, and a greater representation of major arthropod groups, as well as four major (fully stenohaline) echinoderm taxa (Box 1, Table 1).

The other major Silurian Lagerstätten show a greater terrestrial influence. Late Llandovery to early Wenlock Lagerstätten in the Midland Valley of Scotland from the Priesthill and Waterhead groups of Lesmahagow, and correlatives in the Hagshaw and Pentland Hills, represent restricted quasi-marine to lacustrine settings and are typically dominated by eurypterids, phyllocarcids and fish (Ritchie 1968, 1985; Rolfe 1973; Allison & Briggs 1991; Siveter 2010a). The Stonehaven Lagerstätte (Siveter & Palmer 2010) in Scotland, which yields millipedes (Wilson & Anderson 2004), was considered to be of late Wenlock/Ludlow age on the basis of palynomorphs (Marshall 1991; Wellman 1993) but has recently been radiometrically dated as lowermost Devonian, Lochkovian (Suarez et al. 2017; see also Shillito & Davies 2017 for ichnological evidence). The basal Pfidilod Ludlow Bone Bed Lagerstätte at Ludlow Lane and Corner in the Welsh Borderland yields – in addition to fish bone fragments and thelodonts – centipedes, arthropleurid and kampecarid myriapods, eurypterids and scorpions (Jeram et al. 1990; Siveter 2000; Siveter 2010b).

The described Herefordshire biota includes five species of ostracods with preserved appendages, all of which are myodocopes:

- Nymphatelina gravida
- Nasunaris
- Pauline avibella
- Pauline aviformis
- Pauline aviformis (Siveter et al. 2003; Siveter et al. 2018c, 2010, 2013, 2015b, 2018a). All of these, except N. gravida, represent the earliest representatives of crown-group cylindroleberids, which are characterized by the presence of gills. The only other fossil myodocopes with possible gill preservation are Triacyclops from the lower Triassic of Spitzbergen (Weisschat 1983) and Juraleberis from the upper Jurassic of Russia (Vannier & Siveter 1996).

The Herefordshire molluscs Acaenoplax and Kalindroplax (Sutton et al. 2001a, 2004, 2012a; Sigwart & Sutton 2007;
amphinomid (Parry et al. 2016). Such data suggest that complexity of brooding strategies probably evolved early in the history of the Arthropoda. Specimens representing a free-living ‘cyprid’ larval stage and an attached juvenile of the barnacle *Rhampoverritor reduncus* demonstrate that the lifecycle of cirripedes has remained essentially the same over 430 myr (Briggs et al. 2005; Fig. 4n and o). A boring through a valve of *Rhampoverritor* (Fig. 4n) also provides evidence of predation in the biota. The discovery of a pentastomid pancrustacean, *Invivita piratica*, parasitic on the oxcocid *Nymphatelina gravida* is the only known fossil pentastomid preserved with its host and suggests that the group may have originated as ectoparasites on marine invertebrates (Siveter et al. 2015b; Fig. 4p–r). *Bethia serraticula* is the only described fossil rhynchonelliformean brachiopod with preserved soft parts (Fig. 4k). Evidence of its mode of life, shell size and lophophore configuration indicates that the only known specimen is an immature example. Its unusual pedicle morphology differs from that in living species, urgent caution in inferring stem-group anatomy based on crown-group species (Sutton et al. 2005a). The specimen of *B. serraticula* bears an *in vivo* epifauna including a tiny unmineralized lophophorate, *Drakozoon kalumon* (Fig. 4j), which may allude to a widespread occurrence of similar but unknown lophophorates in the Paleozoic (Sutton et al. 2010).

The majority of the 63 known Herefordshire species lived on the seafloor (Table 1; Fig. 7), either as sessile or vagile epibenthos. Unless the Herefordshire animals were transported from significantly shallower waters, it appears that the benthic components of the biota lived in dim light conditions at best. Several of the benthic animals lack eyes and there is an absence of photic-zone indicators such as algae. Given the evidence for rapid burial it is likely that the water column biota is under-represented. Sponges are the dominant sessile element, with brachiopods, echinoderms (the edrioasteroid *Heropyrgus* and a crinoid), a cirripede, coral, and a possible dendroid graptolite and gastropod (*Platycearis?*) as minor components. Most of the vagile epibenthos are arthropods, but this group also includes two echinoderms (the asteroid *Kulindroplax* and the annelid *Drakozoon*), the aplacophoran mollusc *Acaenoplax*, a gastropod and a bivalve mollusc. The nektobenthos is made up entirely of arthropods, with ostracods the most species abundant. A nanolid is the only nektic element. A graptolite and radiolarians comprise the pelagic plankton. A possible infaunal/semi-infaunal mode of life is interpreted for just three taxa, a lingulid brachiopod, the aplacophoran *Rhampoverritor reduncus* attached juvenile of the barnacle and the annelid *Kenotrychus*. The numerical dominance of *Olleculus* within the biota is probably real rather than representing an artefact of sampling, as concretions are selected and split randomly and, as one of the smaller taxa, its high yield is unlikely to result from being selectively preserved. The biota includes representatives of many major invertebrate groups but there is no obvious reason why some groups known from the Silurian of

Fig. 7. Ecological types and percentage abundance based on number of species (*n*= 63). It includes the four radiolarian species, and some species belonging to other major groups that are as yet undescribed and unassigned at species level.

**Box 3. Outstanding questions**

(1) Precisely when and how were the Herefordshire concretions formed?

(2) Will more sensitive scanning techniques become available in the future which can facilitate imaging the fossils, even if only for initial identifications?

(3) What will be revealed when additional fossils are reconstructed? A diversity of sponges, as well as cnidarians, brachiopods, molluscs, trilobites and other arthropods, crinoids and other echinoderms, graptolites and various microfossils remain to be investigated.

(4) How does the Lagerstätte fauna compare with that of the interbedded Coalbrookdale Formation mudstones?

(5) What further insights on the palaeoecology will emerge when more taxa have been described?

(6) Lagerstätten rarely prove unique. Where are there other examples in the stratigraphic record preserved in a similar fashion to the Herefordshire example? No other Silurian locality has yet been identified, even within the Welsh Basin.
the Welsh Basin elsewhere, such as vertebrates and bryozoans, have not been found in the concretions.

Why is the Herefordshire Lagerstätte apparently unique?
The Herefordshire biota is one of a number of examples of soft tissue preservation in concretions. Concretion formation requires carbonate (or more rarely silica) supersaturation and the presence of a nucleus. In some cases, a buried carcass can provide both. Soft tissues can be preserved within concretions in a number of ways (McCoy et al. 2015): as carbonaceous remains, as a result of replication in a variety of authicogenic minerals, or by void fill, as in the case of the Herefordshire biota. Exceptional preservation is promoted where concretion growth is rapid, and void fills are more likely to occur where cementation occurs from the inside out, slowing diffusion at an early stage and isolating the organism from its environment (McCoy et al. 2015). An analysis of factors associated with exceptional preservation in concretions (based on 88 concretion sites, of which 20% preserve soft-tissues) showed that concretion formation enhances the chances of exceptional preservation only where other conditions are favourable, such as burial in fine-grained sediment (McCoy et al. 2015). The volcanic ash that buried the Herefordshire organisms may have played a role in their exceptional preservation. Fine grain size may have promoted anoxia within the sediment and inhibited scavengers.

Predictably, perhaps, most examples of exceptional preservation associated with volcanic ash are in terrestrial settings (Briggs et al. 1996), in lacustrine and fluvial environments. Preservation of plant materials in volcanic ash may be enhanced by rapid burial and anoxic conditions, as in the Cretaceous of Argentina (Lafuente Diaz et al. 2018) and the Miocene Clarkia Beds of Idaho, USA (Ladderd et al. 2015). The Triassic Chañares Formation of Argentina yields a diversity of tetrapods in carbonate concretions in volcanic ash that likely formed where microbial decay promoted carbonate precipitation (Rogers et al. 2001) but concretion biotas are rare in terrestrial environments. Giant radiodonts are preserved in silica-chlorite concretions in the lower Fezouata Formation of Morocco, including silica, iron and aluminium thought to be sourced from volcanic ash (Gaines et al. 2012). A volcanic influence has also been reported impacting fossil preservation in other marine settings, including some from the Silurian of the UK and Ireland. Coral communities in the Llandovery Kilbride Formation of Co. Mayo, Ireland are buried by volcanic ash (Harper et al. 1995), as are shelly fossils in the Wenlock Ballynamme Formation of the Dingle Peninsula, Co. Kerry, Ireland (Ferretti & Holland 1994), but soft tissue preservation is unknown and associated concretions have not been reported. The cuticle of decapod moults and the ligament of bivalves are preserved in concretions in the Cretaceous Bearpaw Formation of Alberta (Bentonite number 5) following rapid burial in volcanic ash (Heikoop et al. 1996), but carbonate concretions associated with volcanics in marine settings are rare.

Preservation of the Herefordshire fossils involved an unusual combination of circumstances: rapid burial of small living animals in thick, fine-grained volcanic ash in a marine setting, and very rapid formation of near-spherical carbonate-cemented concretions. Other biotas preserved in a similar fashion to the Herefordshire example have yet to be discovered. The tiny crystalline infauna are unlikely to attract the interest of a casual collector and the fossils are often off-centre and may not be intersected by the plane of splitting. Silurian bentonites are widespread in the UK, but they are generally only a few centimetres thick (Cave & Loydell 1998). Examples of concretions within ashes of any age merit serious scrutiny but early formed concretions in fine-grained marine mudstones may also yield exceptionally preserved fossils depending, perhaps, on the clay minerals present.

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