Review focus

JGS
Journal of the Geological Society

https://doi.org/10.1144/jgs2018-042 | Vol. 175 | 2018 | pp. 705–715

The Weeks Formation Konservat-Lagerstätte and the evolutionary transition of Cambrian marine life

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Abstract: The Weeks Formation in Utah is the youngest (*c.* 499 Ma) and least studied Cambrian Lagerstätte of the western USA. It preserves a diverse, exceptionally preserved fauna that inhabited a relatively deep water environment at the offshore margin of a carbonate platform, resembling the setting of the underlying Wheeler and Marjum formations. However, the Weeks fauna differs significantly in composition from the other remarkable biotas of the Cambrian Series 3 of Utah, suggesting a significant Guzhangian faunal restructuring. This bioevent is regarded as the onset of a transitional episode in the history of life, separating the two primary diversifications of the Early Paleozoic. The Weeks fossils have been strongly affected by late diagenetic processes, but some specimens still preserve exquisite anatomical details.

Supplementary material: a supplementary text (material and methods), four supplementary tables (compositions of the lower and upper Weeks faunas, structure of the upper Weeks fauna, and results of the similarity analyses), and a supplementary data file (generic presence/absence matrix) are available at https://doi.org/10.6084/m9.figshare.c.4109588

Received 18 February 2018; **revised** 23 May 2018; **accepted** 23 May 2018

Walcott (1908*a*) described the middle Cambrian Stephen Formation, which includes what has become the most celebrated Cambrian Konservat-Lagerstätte: the Burgess Shale (Aitken 1997; Caron *et al.* 2010). This brief contribution formally defined 27 other Cambrian formations in North America. Unbeknown to Walcott, whose career would become increasingly devoted to the Burgess Shale biota he discovered in 1909, five of the other units he defined were subsequently found to contain soft-bodied fossils: the Langston (Spence Shale Member), Wheeler, Marjum and Weeks formations of Utah and the Pioche Formation of Nevada (e.g. Lieberman 2003; Robison *et al.* 2015). This paper is dedicated to the youngest and least well-known of these macroscopic, exceptionally preserved faunas from the American Great Basin: the Guzhangian upper Weeks Formation fauna (referred to hereafter, unless otherwise stated, as the 'Weeks fauna').

The Cambrian System is extraordinarily rich in deposits yielding remarkable macroscopic fossil assemblages (Allison & Briggs 1993; Muscente *et al.* 2017), the study of which has profoundly modified our understanding of how metazoan-dominated marine ecosystems first evolved. However, these Konservat-Lagerstätten are largely restricted to a 20-myr interval between the beginning of the Cambrian Age 3 (first appearance of trilobites) and the end of the Drumian, a pattern that has been linked to changes in the distribution of marine sedimentary environments on the continents (Gaines 2014). In fact, the Terreneuvian is almost barren of macroscopic body fossils (Zhang *et al.* 2017) and the Guzhangian–Age 10 interval, occurring well after the Cambrian explosion and prior to the Great Ordovician Biodiversification, has attracted relatively little attention. However, this 15-myr interval holds an increasing allure for palaeobiologists as a period associated with remarkable evolutionary and ecological changes: (1) the onset of the replacement of the Cambrian Evolutionary Fauna by the Paleozoic Evolutionary Fauna (Sepkoski 1990); (2) a major diversification of phytoplankton (Servais *et al.* 2016); (3) the first exploration of terrestrial habitats by animals (e.g. MacNaughton *et al.* 2002; Collette & Hagadorn 2010); and (4) the evolution of groups that have played prominent parts in marine or even terrestrial ecosystems ever since, such as malacostracan crustaceans (Collette & Hagadorn 2010), cephalopod molluscs (Kröger *et al.* 2011), crown-group annelids (Parry *et al.* 2014; Eriksson & von Bitter 2015) and crown-group euchelicerates (Dunlop *et al.* 2004; Van Roy *et al.* 2010). For the sake of simplicity, this time interval, extending from the beginning of the Guzhangian Age (500.5 Ma) to the end of the Furongian Epoch (485.4 Ma), is informally referred to as the 'late Cambrian' hereafter, without reference to any past stratigraphic scheme.

Although macroscopic remains of non- or weakly biomineralizing animals have been recovered from at least 17 deposits of that age around the world, most of them have been only cursorily explored and therefore have yielded few remarkable fossils thus far (Lerosey-Aubril 2017). However, there is an untapped potential in these localities because late Cambrian exceptionally preserved faunas

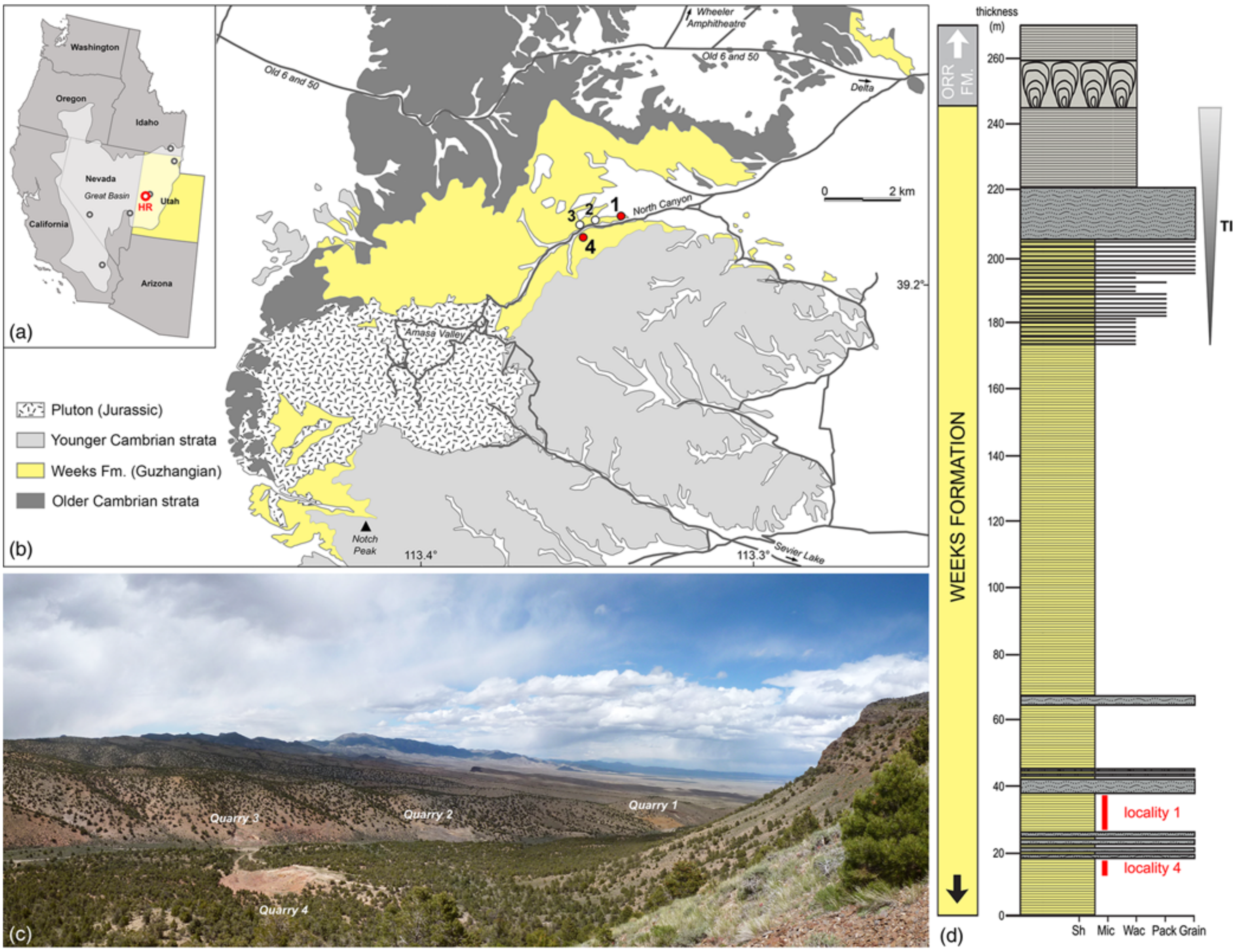

Fig. 1. Location and stratigraphy of the Weeks Konservat-Lagerstätte. (**a**) Map of the western USA showing the locations of the main Cambrian Konservat-Lagerstätten (circles) of the Great Basin (light shading), including the three occurring in the House Range (HR) of western Utah. (**b**) Simplified geological map of the Notch Peak area, House Range, showing the geographical extent of the Weeks Formation and the locations of the four quarries in the North Canyon (in red, quarries yielding remarkable fossils). (**c**) Photograph of the four quarries taken facing north from the south flank of the North Canyon. (**d**) Generalized stratigraphic column of the upper Weeks Formation showing the positions of the intervals with exceptional preservation; note that they are located *c.* 130 m below the transitional interval (TI), evidencing a shallowing of the depositional environment.

could significantly illuminate this cryptic phase of metazoan evolution. In this context, the Weeks fauna is of particular interest because it appears to capture a typical animal community living in an open marine, distal shelf environment at the beginning of this lesser known time period. This paper provides the first detailed description of its composition and preservation and shows that it significantly differs from faunas that previously inhabited similar environments.

Location, stratigraphy and age

The Weeks Formation is one of 12 Cambrian Konservat-Lagerstätten of the American Great Basin (Muscente *et al.* 2017) and one of three located in the House Range of Utah (Fig. 1a, b). These three remarkable deposits – the Wheeler, Marjum and Weeks formations (in stratigraphically ascending order) – constitute a continuous succession of fine-grained sediments that filled a fault-controlled basin, the House Range Embayment, which is interpreted as a half-graben (Rees 1986; Miller *et al.* 2012). During Cambrian Age 5, faulting formed a prominent re-entrant into the seaward margin of the carbonate platform that rimmed Laurentia, resulting in the deposition of fine-grained clastic sediments typical of the outer detrital belt lithofacies across a portion of western Utah. The Weeks Formation represents the final stage of basin filling and, consequently, its geographical extent is considerably more reduced (*c.* 120 km^2) than that of the underlying Wheeler and Marjum formations (Rees 1986; Foster & Gaines 2016); its exposures are confined to areas SW and NE of the Notch Peak Intrusive (Fig. 1b). The finest exposures occur in North Canyon, including two abandoned quarries that yield soft-bodied fossils (Fig. 1b, c). The relative stratigraphic positions of these two quarries allow us to constrain the occurrence of exceptional preservation in the Weeks Formation to an interval *c.* 230–205 m below the top of the unit (Fig. 1d), which belongs to what is traditionally known as the upper Weeks (e.g. Hintze & Davis 2003). The informal distinction between the basal-most Weeks (*c.* 30–50 m thick) and the rest of the unit (*c.* 270 m thick) is not defined by lithology, but by the palaeontological content. The lower Weeks Formation has yielded an exclusively shelly, agnostoid-rich fauna belonging to the *Lejopyge laevigata* agnostoid Zone (part of the *Bolaspidella* trilobite Zone), common to the uppermost part of the underlying Marjum Formation (Robison & Babcock 2011, their fig. 1). This fauna differs markedly from the fossil association found in the rest of the unit, which belongs to the overlying *Proagnostus bulbus* agnostoid Zone (part of the *Cedaria* trilobite Zone; Robison & Babcock 2011). This biozone corresponds to the middle part

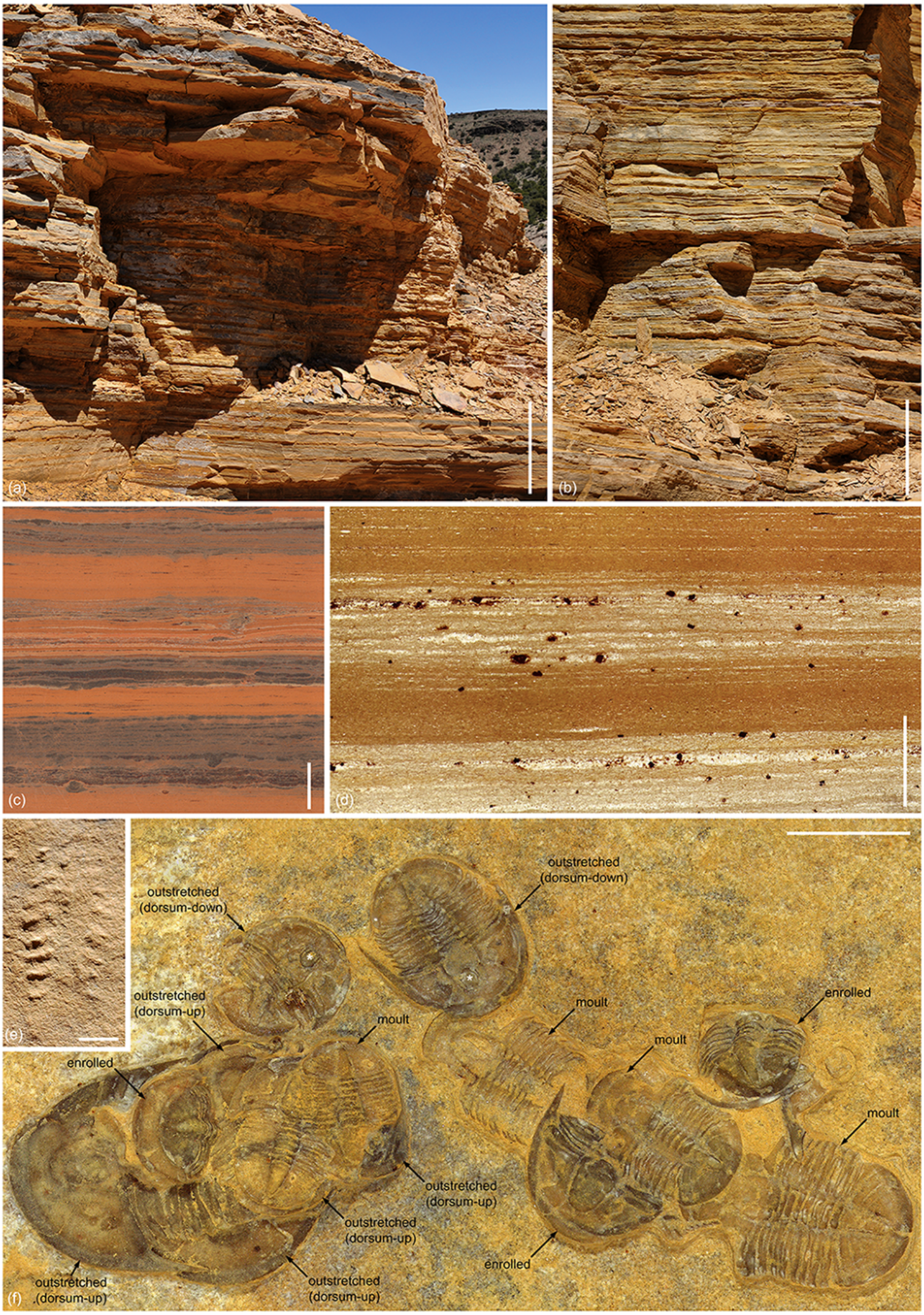

Fig. 2. Lithofacies and biostratinomy of the Weeks Konservat-Lagerstätte. (**a**, **b**) Exceptional fossil-bearing interval of the Weeks Formation, *c.* 210 m below the top of the unit. Thin to medium planar-bedded micritic limestones form resistant layers separating thin packages of calcareous claystones containing soft-bodied fossils. (**c**) Polished slab from *c.* 213 m below the top of the Weeks Formation showing centimetre-scale alternation between carbonate-dominated (grey) and clay-dominated (yellow–red) intervals, each consisting of millimetre-scale laminae with carbonate and clay components.

Fig. 2. *Continued*. (**d**) Transmitted light micrograph of thin section of fossil-bearing lithology from *c.* 210 m below the top of the Weeks Formation. Clay-dominated intervals appear dark and carbonate-dominated intervals appear bright. Iron oxide euhedra after pyrite are abundant in the carbonate-dominated intervals and appear black in the transmitted light micrograph; several show rounded oxide rims that represent iron staining of the matrix during pyrite oxidation. (**e**) *Diplichnites* sp., one of the two arthropod trackways found in the Weeks Formation, UU07041.26. (**f**) Monospecific (*Cedaria minor*) cluster of trilobites composed of moult ensembles (lacking librigenae) and complete exoskeletons (carcasses?), UU17122.02. Note the diversity of sizes, orientations (dorsum-up/dorsum-down) and postures (outstretched/enrolled), and the presence of hypostomes *in situ* (asterisks). Scale bars: (**a**, **b**) 25 cm; (**c**) 1 cm; and (**d**–**f**) 5 mm.

(*c.* 499–498.5 Ma) of the Guzhangian Stage of the Cambrian Series 3 according to the developing global chronostratigraphy of the Cambrian (Peng *et al.* 2012).

The Weeks Formation has a complex post-Cambrian diagenetic history, which includes a granitic intrusion during the Jurassic that led to extensive metasomatism of the fossil-bearing localities (Nabelek 2002). Fieldwork has also shown that the Weeks Formation was uplifted during the early Paleogene Sevier Orogeny and exposed to intense oxidative weathering during the greenhouse climates of that time, followed by burial under Sevier-age alluvial conglomerates of the Skull Rock Pass Formation, as well as rhyolitic ignimbrites erupted during the Oligocene (Hintze & Davis 2003). Extensive hydrothermal fluid flow and subsequent subaerial weathering during the early Paleogene have greatly affected the Weeks Formation and its fossils, obscuring the primary taphonomic pathways that facilitated the preservation of organic structures in these strata.

Depositional environment and taphonomy

The Weeks biota was preserved on a gently sloping ramp that descended from carbonate platform environments, presently exposed within the House Range, into a muddy basin that lay at the axis of the House Range Embayment (Rees 1986). The Weeks Formation represents the final phase of basin filling and a transition from distal ramp settings below storm wave base to storm-dominated ramp and carbonate platform environments.

Previous interpretations have suggested a shallow, shelfal depositional setting for the Weeks Lagerstätte based on the presence of silt- and sand-sized quartz and its relative stratigraphic proximity to shallow water facies, including stromatolites. This view was reinforced by the presence of aglaspidids, found primarily in shallow shelf settings during the Furongian. Our comprehensive analysis of all exposures of the Weeks Formation in North Canyon and the vicinity, however, shows that the Weeks fauna occurs in a deep water facies identical to those of the Wheeler and Marjum biotas. This facies is characterized by a regular, centimetre-scale alternation of calcareous claystones and planar-bedded micritic limestones (Fig. 2a, b), each internally laminated at the millimetre scale (Fig. 2c, d). It is well documented from the House Range Embayment and interpreted to represent accumulation in distal ramp settings below storm wave base (Elrick & Snider 2002; Gaines & Droser 2010).

The expression of this facies in the Weeks Formation has been significantly affected by Jurassic metasomatism and subsequent weathering (Fig. 2; Box 1, Fig. 3). Scanning electron microscopy shows that quartz grains, previously interpreted as detrital, are a product of the late-stage replacement of calcite, as evidenced by the occurrence of aggregated masses of quartz pseudomorphs rather than discrete detrital grains. Stratigraphic study further indicates that the distal ramp strata yielding the soft-bodied fossils are separated from massive stromatolites by a transitional interval that represents the final phase of basin filling in the House Range Embayment in the study area (Fig. 1d). This transition is characterized by a loss of mud, an increase in grain content and bed thickness, and by the first appearance of evidence for a storm wave influence over the substrate.

The palaeoenvironmental context inferred herein for the preservation of the Weeks biota is similar to those of many lower–middle Cambrian Burgess Shale-type deposits, including the Wheeler and Marjum formations: muddy outer detrital belt settings at the offshore margin of extensive carbonate platforms (Gaines 2014). Similar to these deposits, exceptional preservation in the Weeks Formation occurs in mixed siliciclastic–carbonate facies characterized by an exclusively fine grain size, the absence of silt and sand, and organization into fine laminae that lack grading, cross-bedding and other sedimentary structures (Fig. 2c, d; Gaines *et al.* 2012). The episodic deposition of claystone occurred from distal sediment gravity flows initiated by storm wave disturbance of the platform and proximal ramp environments (Elrick & Snider 2002), represented in the transitional interval (Fig. 1d), and served to promote the rapid burial of benthos, possibly following brief entrainment (Gaines & Droser 2010; Gaines 2014).

The low-energy deep water environment appears to have been subject to repeated episodes of oxygen stress that also characterize the distal ramp facies of the Wheeler and Marjum formations (Gaines & Droser 2010). The abundance of fine (5–500 µm)

Box 1. Preservation

During its diagenetic history, the Weeks Formation and its fossils underwent intense physical and chemical alteration, which have profoundly affected the expression and composition of soft-bodied fossils. Their overall morphologies are characteristically preserved as greenish–bluish films of chlorite (Fig. 3a), as confirmed by their richness in oxygen, magnesium, aluminium, silicon and iron. This mineral usually surrounds an inner layer consisting of crystals of iron oxide pseudomorphs after pyrite, which are often well-formed, euhedral and striated (Fig. 3a, b). The putative chlorite phase sometimes shows pyrite crystal moulds, attesting to its emplacement after pyrite (Fig. 3c). The distribution, mode and habit of pyrite within the fossils indicates that it, too, is a late diagenetic phase. Early diagenetic pyritization affects specific organic structures (e.g. Gabbott *et al.* 2004) and begins prior to their collapse, allowing some three-dimensional aspects to be retained (e.g. Farrell 2014). The occurrence of pyrite as continuous, two-dimensional sheets across entire body fossils, with individual crystals cutting across tissue types, is atypical of a Konservat-Lagerstätte and is interpreted as a post-Cambrian alteration of previously formed compression fossils.

The only surviving aspect of soft-tissue fossilization definitively Cambrian in origin is the replacement of anatomical structures by authigenic apatite. This early diagenetic phosphatization was histologically and taxonomically controlled – it always occurs in the vicinity of phosphorus-rich tissues, such as the cuticle in aglaspidids, the scleritome in palaeoscolecids (Fig. 3d–g) or the mid-gut epithelium in arthropods (Lerosey-Aubril *et al.* 2012; Lerosey-Aubril 2015; Figs 3h–m, 5j, q). This pattern suggests a spatially restricted process: the dissolution/degradation of the phosphorus-rich tissues led to a local enrichment in phosphorus ions, which eventually triggered their re-precipitation in neighbouring tissues. Although rare, partial pyritization of arthropod guts may also be observed (Fig. 3n, o).

It is possible that, as in the identical facies of the Wheeler and Marjum formations (Gaines *et al.* 2008), the Weeks soft-bodied organisms were originally conserved via carbonaceous films (Burgess Shale-type preservation), later lost during Jurassic metasomatism. The oxidation of these organic remains may have created reducing microenvironments allowing the precipitation of iron sulphides, derived in part from the leaching of pyrite in the host rocks. Subsequently, chlorite may have precipitated from metasomatic fluids, or may have grown around the pyrite sheets by metamorphic transformation of the host rock clays (Butterfield *et al.* 2007). Pyrite in the fossils and host rocks was oxidized by fluid flow during later metasomatism, weathering, or both.

authigenic euhedral pyrite in claystones of the Weeks Formation (Fig. 2d) and the near-total absence of bioturbation (see Fig. 2e for an exception) from these finely laminated strata suggest oxygen-limited conditions. The preponderance of articulated specimens and moult ensembles of trilobites (Fig. 2f), however, indicates only limited to no transport of the essentially epibenthic fauna. Together, these attributes indicate a setting near the margin of a fluctuating oxycline and suggest that oxygen-limited conditions, typical of the underlying strata, persisted across a large portion of the Weeks Formation and throughout much of the history of the House Range Embayment.

Although the physical and chemical depositional environments of the Weeks Formation afforded biostratinomic conditions that are common to many other Cambrian Lagerstätten, the early diagenetic taphonomic pathways by which its remarkable fauna was preserved have been fundamentally obscured by post-Cambrian geological processes (Box 1).

Overview of the upper Weeks fauna

The Weeks fauna consists of more than 70 species belonging to at least eight phyla (Box 2; Fig. 4). Twelve taxa are illustrated for the

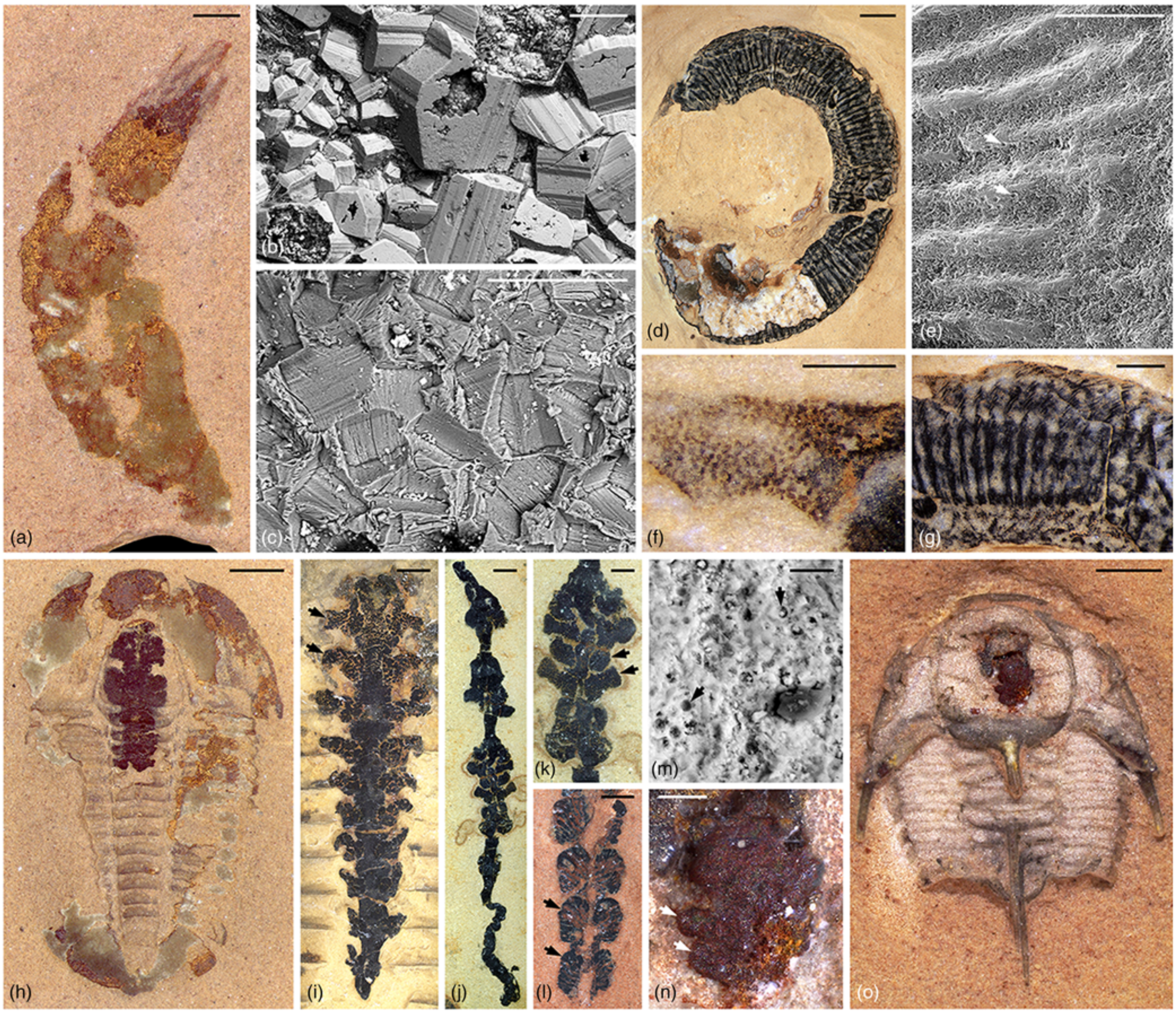

Fig. 3. Preservation in the Weeks Konservat-Lagerstätte. (**a**–**c**) Enigmatic organism showing the two materials typically composing soft-bodied fossils: iron oxides (orange–red) and chlorite (green), UU17122.03. (**a**) General view. (**b**) Euhedral crystals of iron oxide pseudomorphs after pyrite. (**c**) Detail of the putative chlorite showing how it moulded iron oxide crystals. (**d**–**g**) Palaeoscolecid worm with secondarily phosphatized integument, UU17122.04. (**d**) General view. (**e**) Surface of the integument showing impressions of skeletal plates (arrows). (**f**) Area where the phosphatic plates are not dissolved. (**g**) Area where the phosphatic plates have been dissolved and the subjacent soft tissues secondarily phosphatized. (**h**–**m**) Phosphatized digestive structures of arthropods. (**h**) Trilobite *Modocia* cf. *M. whiteleyi*, incomplete dorsal exoskeleton, UU17122.05; note the phosphatized gut (dark blue structure under axis), the iron oxides predominantly occurring within cephalic and pygidial doublures, and the chlorite moulding the entire visceral surface of the dorsal exoskeleton. (**i**) Trilobite *Meniscopsia beebi*, detail of the gut, BPM1017; note the metamerically disposed, club-shaped digestive glands (arrows). (**j**, **k**, **m**) Undetermined arthropod showing a unique organization of its gut, BPM1013. (**j**) General view of the gut and its clustered, simple digestive glands and posterior circumvolutions. (**k**) Detail of a cluster of digestive glands (arrows). (**m**) Spongy texture of the phosphatic material replacing the gut. Note the size of the spherical cavities (*c.* 2–4 µm; arrows), compatible with them being external moulds of decaying bacteria. (**l**) Undetermined arthropod, detail of the large, lamellar-type digestive glands (arrows), BPM1019. (**n**, **o**) Trilobite *Lonchocephalus pholus*, BPM1034a, documenting a rare case of three-dimensional preservation of the anterior gut as oxidized pyrite. (**n**) Digestive tract with at least two digestive glands (arrows). (**o**) General view. Scale bars: (**d**) 2 mm; (**a**, **g**–**j**, **l**, **o**) 1 mm; (**e**, **f**, **k**) 500 µm; (**n**) 200 µm; (**b**, **c**) 50 µm; and (**m**) 10 µm.

Box 2. Structure and distinctiveness of the fauna

The upper Weeks fauna is dominated by arthropods (66%) and, to a lesser extent, sponges and brachiopods (Fig. 4a). Thirty-one per cent of these taxa are exclusively composed of non-biomineralized tissues and 29% have a lightly biomineralized skeleton (Fig. 4b). About 78% of these animals are epibenthic (Fig. 4c), whereas pelagic forms account for *c.* 18% of the fauna. Endobenthic taxa represent only 4% of the assemblage, possibly due to an underestimated diversity of typically poorly preserved groups (e.g. scalidophorans). Conversely, bioturbation is particularly rare in these strata, suggesting that endobenthic life might have truly been limited in this environment (Fig. 4c).

Comparisons with the other remarkable Cambrian faunas of Utah – the Drumian Wheeler-HR and Marjum faunas from the House Range, the Drumian Wheeler-DM fauna from the nearby Drum Mountains and the Cambrian Stage 5 Spence fauna from northern Utah – show why the Weeks fauna may provide unique insights into the evolution of Cambrian marine ecosystems. In term of species richness, it is comparable ($n = 73$) with the Wheeler-HR ($n = 68$) and Wheeler-DM ($n = 74$) faunas and, to a lesser extent, the Spence ($n = 87$) and Marjum faunas ($n = 113$). The relative contribution of each phylum to species richness is also similar among these Cambrian faunas, but analysis of intra-phylum compositions shows a more complicated picture. Cnidarians, hyoliths, priapulimorphs and sponges from the Weeks Formation are essentially represented by taxa described from older deposits. Likewise, some arthropods (e.g. megacheirans, radiodonts), although represented by different taxa, are typical of early–middle Cambrian biotas. However, the Weeks fauna also includes taxa better known from younger strata (e.g. aglaspidids) and a substantial diversity of forms with uncertain affinities.

Perhaps the best way to illustrate this taxonomic distinctiveness is through a quantitative assessment of taxonomic similarity. Whether entire assemblages or subsets of them are considered, the Weeks fauna always appears as the most dissimilar (Fig. 4d). This result cannot be explained by bathymetry, palaeogeography or stratigraphy. Instead, it yields evidence for a major biotic turnover during the Guzhangian, a time interval formerly spanning the middle–late Cambrian boundary in some countries (e.g. Babcock *et al.* 2014). We hypothesize that this taxonomic restructuring marks the onset of a transitional episode within the Early Paleozoic evolution of marine ecosystems.

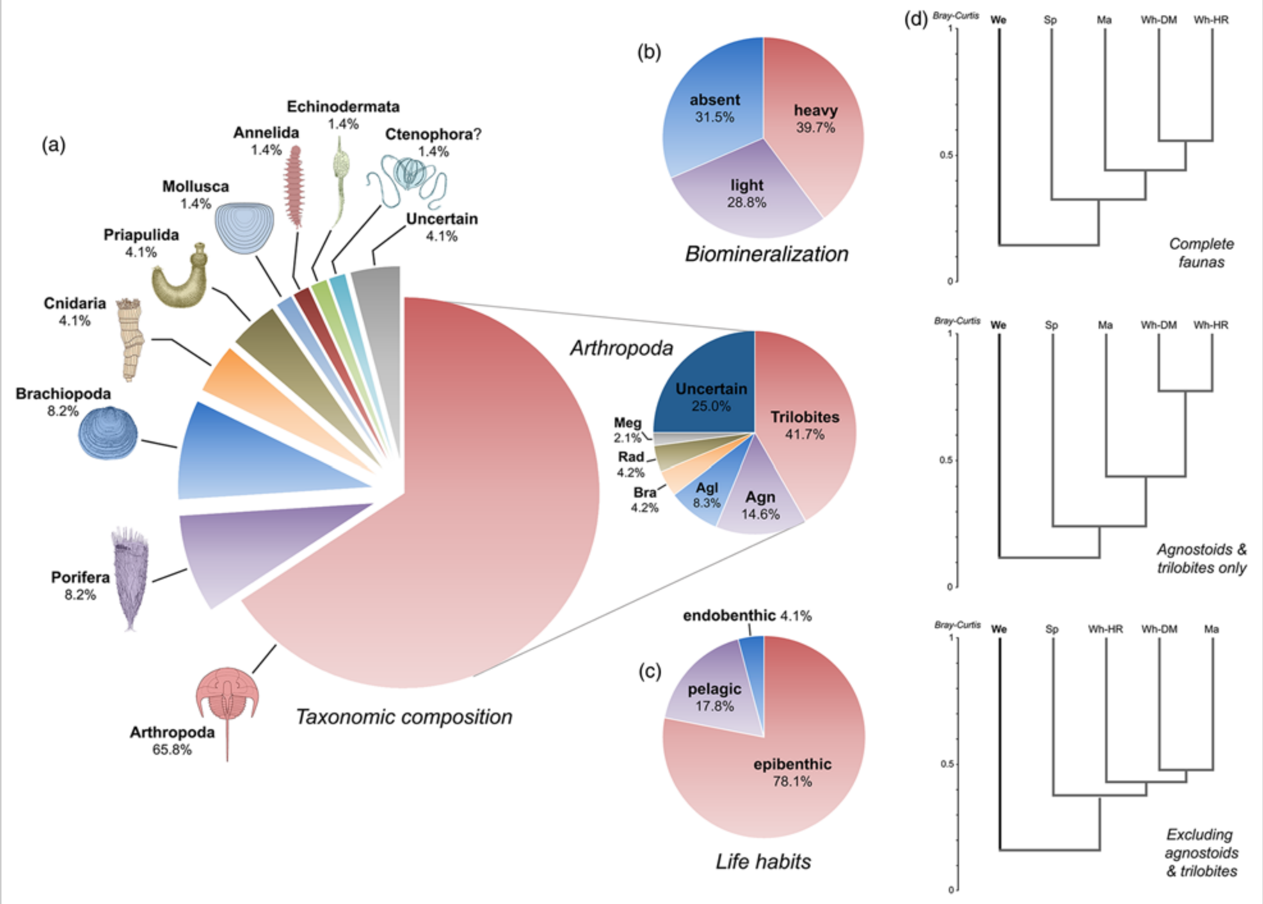

Fig. 4. Structure and distinctiveness of the upper Weeks fauna. (**a**–**c**) Structure of the entire assemblage with regard to (**a**) taxonomy, (**b**) biomineralization and (**c**) life habits; percentages express the contributions of each category to the total species richness ($N = 73$). (**d**) Similarity analyses of the taxonomic compositions (genera) of the five exceptionally preserved faunas of Utah or subsets of them (paired group-UPGMA, Bray–Curtis index). Agl, Aglaspidida; Agn, Agnostida; Bra, Bradorida; Ma, Marjum fauna; Rad, Radiodonta; Sp, Spence Shale fauna; We, Weeks fauna; Wh-DM, Wheeler fauna from the Drum Mountains; Wh-HR, Wheeler fauna from the House Range.

first time in Figure 5 and the main components of the fauna are briefly discussed in the following sections.

Arthropods

Trilobites and agnostoids

With 20 species, trilobites are the most diverse arthropods of the upper Weeks fauna, followed by agnostoids (seven species). Of these 27 species, only one also occurs in the lower Weeks and two in the Marjum Formation, agnostoids in both cases. Agnostoid diversity decreases (13 to seven species), whereas that of trilobites increases (eight to 20 species) between the lower and upper Weeks, which may suggest increasingly proximal settings. Small forms (<2 cm) dominate, especially *Cedaria* and *Modocia* (Peters 2003), but larger taxa (>5 cm) are not rare. Most specimens represent carcasses or moult ensembles, sometimes forming clusters (e.g.

Robison & Babcock 2011; Fig. 2f) or preserving delicate gut structures (e.g. Lerosey-Aubril *et al.* 2012; Fig. 2h–o), which suggests little post-mortem disturbance. Conversely, some horizons are rich in silicified disarticulated sclerites, allowing the reconstruction of ontogenetic sequences.

Aglaspidids, bradoriids, megacheirans and radiodonts

The Weeks fauna consists of at least four aglaspidids, a diversity only reached or surpassed in the Furongian St Lawrence (USA) and Sandu (China) formations (Zhu *et al.* in press). They include the oldest members of the two families composing the Aglaspidida (Aglaspididae, Fig. 5l, m; Tremaglaspididae, Lerosey-Aubril *et al.* 2013 and Fig. 5k) and *Beckwithia typa*, a large (up to 20 cm) atypical representative (Resser 1931; Hesselbo 1989; Fig. 5j). Some specimens exhibit appendages or guts (Fig. 5j, m), rarely preserved structures of phylogenetic significance. *Anabarochilina australis* was the only known bradoriid (Siveter & Williams 1997; Robison *et al.* 2015), but recent fieldwork has shown that it co-occurs with *A. primordialis* in the upper Weeks strata. These mostly Guzhangian taxa display wide palaeogeographical distributions, previously thought to be mutually exclusive. These transcontinental distributions have been used to hypothesize the evolution of a planktic lifestyle in late representatives of the Bradoriida (Collette *et al.* 2011; Williams *et al.* 2015). A 3 cm long megacheiran is particularly common at locality 1 (Fig. 1b), which has yielded dozens of specimens. It displays leanchoiliid characters (Fig. 5i), such as triflagellate first appendages, 11 trunk tergites and lamellar digestive glands, but the telson is spiniform rather than lanceolate to triangular. Poorly preserved specimens are difficult to differentiate from a similar arthropod of undetermined affinities (Fig. 5p) occurring in the same beds. Lerosey-Aubril *et al.* (2014) assigned isolated frontal appendages to two separate anomalocaridids, a view confirmed by later findings. Although not formally defined, *Anomalocaris* aff. *canadensis* is a distinct species of *Anomalocaris* and the youngest representative of this renowned genus. It is only known from appendages three to seven times smaller than those of congeneric species, possibly indicating that it is a dwarf species or, alternatively, that only juveniles lived in the House Range Embayment.

Arthropods of uncertain affinities

More than a dozen taxa are at present difficult to confidently assign to any well-established clades (Fig. 5p, q). Two of them have been the subject of formal descriptions. *Falcatamacaris bellua* is a 12 cm long artiopod characterized by a bipartite trunk and hook-shaped pleural spines (Ortega-Hernández *et al.* 2015). A new specimen displays dorsal eyes flanking a glabellar region antero-medially, suggesting possible affinities with aglaspidids (Lerosey-Aubril *et al.* 2017). With its inverted drop-shaped body terminated by a rectangular, spine-bearing telson, *Notchia weugi* is easily distinguished from any other Weeks arthropods (Fig. 5q). It was regarded as vaguely similar, but unrelated, to older taxa (e.g. *Palaeomerus*, *Sidneyia*; Lerosey-Aubril 2015). Additionally, a problematic taxon with four antenniform appendages was discussed in Lerosey-Aubril *et al.* (2014). Non-trilobite arthropods from the Weeks fauna confirm its great distinctiveness compared with older remarkable biotas from Laurentia (Fig. 4d) and yield evidence for an unexpected morphological disparity of arthropods in the late Cambrian.

Scalidophorans

The Weeks Formation has yielded a new palaeoscolecid species – the second largest (up to 13 mm in width) after the Australian *Wronascolex antiquus* (García-Bellido *et al.* 2013) – with a scleritome made of numerous, uniformly small (20 µm), smooth plates. Only fragments are known, progressively fading out towards the body extremities. Other priapulid-like worms are common in the Weeks limestone, but their preservation only allows tentative assignments to *Ottoia*, a slender undetermined taxon, and possibly *Selkirkia*.

Lophophorates

Brachiopods have remained virtually unstudied since Walcott (1908*b*, 1912), which is surprising considering their ubiquity, commonly paving large areas of bedding surfaces. Five species were reported in the upper Weeks (Beebe 1990; Peters 2003), but only *Canthylotreta marjumensis* and *Fordinia perfecta* have been suitably studied (Rowell 1966; Holmer & Popov 2000; Streng & Holmer 2006). Extreme abundance, coupled with low diversity, are typical of aquatic organisms adapted to life in stressed environments – thus the characteristics of this brachiopod fauna might be regarded as evidence for episodes of environmental perturbation (e.g. oxygen-depletion). The repeated observation of brachiopods attached to carcasses of arthropods (Fig. 5j) might also suggest that ectosymbiosis between Cambrian brachiopods and mobile animals was relatively common (Topper *et al.* 2014). As already noticed by Walcott (1908*b*, 1912), hyoliths occur in the upper Weeks strata, but their preservation is insufficient for generic assignment.

Annelids and molluscs

The upper Weeks has yielded a dozen specimens of an annelid bearing *c.* 15 pairs of parapodia with short chaetae (Fig. 5g, h) and resembling *Ophryotrocha*, an extant eunicid known to thrive in organic-rich, stressed environments (Thornhill *et al.* 2009). However, *Ophryotrocha* species are about ten times smaller than the Weeks fossils and they have large resistant jaws (Paxton 2004) or scolecodonts, as yet never observed in any Weeks specimen. Scolecodonts first appeared in the latest Cambrian and became conspicuous components of marine faunas during the Middle–Late Ordovician (Eriksson & von Bitter 2015). A univalved shell, probably of a tergomyan monoplacophoran, is the only mollusc fossil found in these deposits to date. This 6 cm long fossil shows that the drastic increase in maximum shell size (from 2 to 10 cm) characterizing mollusc evolution during the Furongian (Runnegar & Pojeta 1985) had already started by the Guzhangian.

Sponges, cnidarians and ctenophores

According to Robison *et al.* (2015), sponges are diverse in the Wheeler and Marjum deposits, but none occur in the Weeks Formation. Actually, they are not rare in the upper strata, where at least six species occur that are tentatively assigned to *Crumillospongia*, *Diagonella* (Fig. 5d), *Halichondrites* (Fig. 5c), *Hintzespongia* and an undetermined leptomitiid. Cnidarians are represented by *Cambrorhytium major* (Fig. 5a), also reported in the Marjum Formation (Conway Morris & Robison 1988), *C. fragilis* and a probably new taxon (Fig. 5b). Two poorly preserved fossils might represent ctenophores.

Deuterostomes and problematica

Deuterostomes are represented by a single species of echinoderm. Together with a couple of taxa from the Wheeler and Marjum formations, *Pahvanticystis utahensis* is one of the oldest representatives of the class Soluta (Lefebvre & Lerosey-Aubril 2018). These three species remarkably illustrate the evolution of an entirely free-living lifestyle in the early history of the group and yield evidence of its Laurentian origin.

Numerous fossils cannot be assigned to modern phyla, usually due to incomplete or poor preservation. More rarely, the affinities of

Fig. 5. Representatives of the upper Weeks fauna. (**a**) Cnidarian *Cambrorhytium major*, UU17122.06. (**b**) Cnidarian undetermined species, UU17122.07. (**c**) Sponge *Halichondrites*?, UU17122.08.01. (**d**) Sponge *Diagonella*?, UU17122.09. (**e**, **f**) Palaeoscolecid gen. et sp. nov., BPM1056: (**e**) fragment of posterior trunk and (**f**) electron micrograph (back-scattered) of plates. (**g**, **h**) Annelid gen. et sp. nov.: (**g**) detail showing the short chaetae (arrows), UU17122.10 and (**h**) complete body with material extruded from the anus, BPM1024.

Fig. 5. *Continued.* (**i**) Megacheiran arthropod gen. et sp. nov., PE57196; note the three axes (black arrows) of the first appendage, and the eye (white arrow). (**j**) Aglaspidid arthropod *Beckwithia typa*, BPM1037; note the phosphatized gut (black arrow) and the brachiopod shells attached to the dorsal surface of the trunk region (white arrows). (**k**) Aglaspidid arthropod *Tremaglaspis vanroyi*, BPM1035. (**l**) Arthropod *Aglaspis*? sp., BPM1032. (**m**) Arthropod *Glypharthrus*? sp. with preserved appendages (arrow), BPM1039-01. (**n**) Aglaspidid(?) arthropod, UU17122.11. (**o**) Arthropod *Aglaspis*? sp., UU17122.12. (**p**) Arthropod gen. et sp. nov. G with preserved antenna (arrow), BPM1023a-02. (**q**) Arthropod *Notchia weugi*, UU14022.01a; note the phosphatized gut (arrow). (**r**) Lophotrochozoan(?) undescribed species, UU17122.13. Specimens were photographed: (**a**, **b**, **e**, **g**–**i**, **m**–**p**, **r**) immersed under dilute ethanol using normal light; (**c**, **d**, **j**–**l**, **q**) dry using cross-polarized light; (**f**) uncoated using a scanning electron microscope (back-scattered). Scale bars: (**j**) 1 cm; (**a**, **c**–**e**, **h**, **i**, **k**, **l**, **p**–**r**) 5 mm; (**b**, **g**, **m**–**o**) 2 mm; and (**f**) 50 µm.

a taxon remain unclear, despite a correct understanding of its morphology. This is the case for *Kinzeria,* represented in the Weeks Formation by a new, more slender species. Another Weeks taxon (Fig. 5r) displays a body enclosed in a lightly phosphatic sheath and anchored by a thick stalk(?), both with complex sculptural features. Neither these features nor the general anatomy of the animal are evocative of a particular phylum.

Summary and prospects

The Weeks Formation stands as the youngest and least studied of the Cambrian Konservat-Lagerstätten in the American Great Basin. It forms, with the Wheeler and Marjum formations, a continuous succession of predominantly fine-grained clastic deposits typical of the outer detrital belt. However, its remarkable fauna markedly differs from that of the other Cambrian Series 3 Lagerstätten of Utah and thus hints towards a significant biotic turnover during the Guzhangian. Interestingly, Muscente *et al.* (2018), using palaeocommunity analysis, showed that the last 15 myr of the Cambrian stand as an interval of particularly low diversity bounded by major ecological reorganizations. These researchers mentioned an insufficient rock record, stratigraphic gaps, endemic faunas and/or a time-limited taphonomic window as possibly having partly influenced the significance of the older of these two ecological changes. However, none of these potential biases can explain the distinctiveness of the upper Weeks fauna compared with the Marjum and Wheeler biotas, the three formations forming a continuous succession of sediments in western Utah. Thus the upper Weeks Formation might well record the onset of a distinct period in the evolution of Early Paleozoic marine life, as supported by the occurrence of fossils characteristic of Furongian or younger strata (e.g. aglaspidids; Lerosey-Aubril 2017). This phase is associated with the appearance of taxa of intermediate taxonomic levels (e.g. orders, families; Lerosey-Aubril *et al.* 2017) and an overall low generic diversity (Muscente *et al.* 2018). These new taxa are early members of groups assigned to the Paleozoic Evolutionary Fauna (Sepkoski 1990), as well as new representatives of components of the Cambrian Evolutionary Fauna, such as trilobites (Fortey & Owens 1990, their fig. 7.6). Interestingly, 70% of the trilobite families present at the base of the Ordovician originated in the Cambrian (Adrain 2013), but none of these Cambrian–Ordovician families significantly contributed to the Ordovician diversification of the class (i.e. belong to Ibex faunas; Adrain *et al.* 2004). The case of trilobites calls for caution in interpreting this late Cambrian phase of metazoan history as the onset of the Ordovician radiation, especially because it is punctuated by extinction events and rapid environmental changes (Saltzman *et al.* 2015) and is not accompanied by a major increase in generic diversity. Muscente *et al.* (2018) depicted a formidable ecological change in the Early Ordovician, which indicates that the late Cambrian is best regarded as transitional to, but distinct from, the Great Ordovician Biodiversification.

A way to test this assumption is to quantitatively assess the degree of similarity between the Weeks, Guole (Furongian; Zhu *et al.* 2016) and Fezouata (distinct Tremadocian and Floian associations; Van Roy *et al.* 2015) faunas, but these four remarkable assemblages remain largely undescribed. This point stresses the need for formal taxonomic treatment of the numerous undescribed taxa of the Weeks fauna (Box 3). Another avenue for the development of research on this biota will concern anatomical structures of phylogenetic (e.g. aglaspidid appendages) or palaeoecological (e.g. arthropod guts) significance. For instance, we have successfully applied computer-aided microtomography to reconstruct three-dimensionally preserved guts of Weeks arthropods; these early results offer great promise for studying how digestive structures may inform us about feeding habits and the reconstruction of past trophic webs. Investigations of the Weeks shelly fossils provide complementary information on the structure of the fauna or the biostratinomic context of its preservation. In particular, the study of the silicified sclerites of immature trilobites will help to differentiate the taxa that became part of the community at an adult stage from those that spent most of their life in this environment – for the latter, larvae/juveniles should be considered in palaeoecological reconstructions.

Box 3. Outstanding questions

(1) What made the late Cambrian a distinct, transitional phase between the Cambrian Explosion and the Ordovician Radiation?

(2) What was the structure of the trophic web in the Weeks community?

(3) Which factors controlled diagenetic phosphatization in the Weeks fossils, and its anatomical and taphonomic selectivity?

Acknowledgements This contribution is dedicated to R.A. Robison for his foundational works on the Cambrian fossils of Utah, including the Spence Shale, Wheeler, Marjum and Weeks remarkable biotas. He is also thanked for providing taxonomic lists of fossils occurring in the lower and upper parts of the Weeks Formation. We are grateful to the following colleagues for helpful discussions on various components of the Weeks fauna: L. Babcock (arthropods), J. Botting (sponges), H. Paxton and L. Parry (annelids), and M. Williams (bradoriids). J. Christensen, N. Liming, C. Peters-Kaffenberger, H. Starr and A. Turner are thanked for their assistance in the field. We also warmly thank the people who contributed to this research by making specimens available for study through loans or donations: M. Donovan (Salt Lake City), R. Harris (Delta), M.A., M.J. and M.S. Pankowski (Rockville), S.E. Peters (Madison), A. Weug (Greifenstein) and especially Q. Sahratian (University of Utah). This paper benefited from the constructive comments of the handling editor, P. Donoghue, and three referees (D. Harper, J. Paterson and an anonymous colleague). This is a contribution to the IGCP Project 653, 'The onset of the Great Ordovician Biodiversification Event'.

Funding This work was funded by the National Geographic Society (9567-14) and Agence Nationale de la Recherche (ANR-11-BS56-0025).

Scientific editing by Philip Donoghue

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