The Winneshiek biota: exceptionally well-preserved fossils in a Middle Ordovician impact crater

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Abstract: The Winneshiek Shale (Middle Ordovician, Darriwilian) was deposited in a meteorite crater, the Decorah impact structure, in NE Iowa. This crater is 5.6 km in diameter and penetrates Cambrian and Ordovician cratonic strata. It was probably situated close to land in an embayment connected to the epicontinental sea; typical shelly marine taxa are absent. The Konservat-Lagerstätte within the Winneshiek Shale is important because it represents an interval when exceptional preservation is rare. The biota includes the earliest eurypterid, a giant form, as well as a new basal chelicerate and the earliest ceratocarid phyllocarid. Conodonts, some of giant size, occur as bedding plane assemblages. Bormolites and rarer elements, including a linguloid brachiopod and a probable jawless fish, are also present. Similar fossils occur in the coeval Ames impact structure in Oklahoma, demonstrating that meteorite craters represent a novel and under-recognized setting for Konservat-Lagerstätten.

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The Winneshiek Konservat-Lagerstätte was discovered in 2005 in the Winneshiek Shale, which directly underlies the Ordovician St Peter Sandstone, during mapping by the Iowa Geological Survey (Liu et al. 2005) (Fig. 1). The only exposure, which represents the top of the Winneshiek Shale, is in the valley of the Upper Iowa River near Decorah in Iowa. Collections from this locality yielded conodonts, linguloid brachiopods, large fragments of eurypterid cuticles and phyllocarid crustaceans (Liu et al. 2005). A coal-like layer had been reported in local newspapers in the 1920s, which could only have been a concentration of eurypterid cuticles, perhaps to encourage speculators. H. Paul Liu recognized the exceptional nature of these fossils and he and colleagues published a preliminary account of the discovery in 2006 (Liu et al. 2006). A collaborative grant to the authors funded the construction of a temporary dam in 2010, which isolated the exposure of the Winneshiek Shale on the north bank of the Upper Iowa River near Decorah (Fig. 2a–c). This allowed access to the shale and a sequence of large samples, representing c. 4 m of the section, was extracted by hand with the aid of earth-moving equipment (Fig. 2b, c). The shale was split at the Iowa Geological Survey sample repository over the next three years and yielded >5000 macrofossil specimens.

The biota of the Winneshiek Shale is characterized by exceptional preservation combined with a restricted diversity, both of which reflect the unusual depositional setting. The dominant macrofossils are arthropods: the giant Pentecopterus decorahensis (Fig. 3) is the earliest described eurypterid (Lamsdell et al. 2015b) and a diversity of bivalved arthropods includes a phyllocarid, Ceratioarcis winnesiekiensis, and ostracods (Fig. 4). Conodont elements are the most abundant fossils, many occurring as bedding plane assemblages (Fig. 5), and extrapolation indicates that some are from individual animals of very large size (Liu et al. 2017). Recent specimens interpreted as the head shield of an early armoured vertebrate (Liu et al. 2006) are also present (Fig. 5d). Dissolution of the organic-rich shale has yielded a variety of microscopic carbonaceous fossils, including arthropod appendages (Fig. 3h, i) (Nowak et al. 2018) and filamentous algae (Nowak et al. 2017).

The meteorite crater and the age of the Winneshiek Shale

The Winneshiek Shale, an unusual greenish brown to dark grey organic-rich shale up to 26 m thick, was noted in cores and well cuttings some years prior to the discovery of the exposure near Decorah (Young et al. 2005). It overlies an unnamed unit dominated by breccia (Fig. 1c), the two reaching a combined thickness of c. 200 m. Occurrences of the shale in drill core and in outcrop delimit a circle with a diameter of c. 5.6 km (Liu et al. 2009) (Fig. 1b). This outline was also detected in electromagnetic and gravity data from airborne geophysical surveys. The circular structure and its sedimentary fill are concealed by the overlying St Peter Sandstone and Quaternary alluvium, except at one small locality in the Upper Iowa River Valley near Decorah, where the top of the shale is at the land surface. The circular depositional basin is characterized by evidence of local deformation near the perimeter (Fig. 2e) and its unusual stratigraphy. The Winneshiek Shale and underlying breccia are found only within the circular structure, where the units are completely different from the regional stratigraphic sequence (Liu et al. 2009; French et al. 2018). All these attributes are consistent with deposition within a meteorite crater. This inference was elegantly confirmed by the demonstration that quartz grains observed in drill samples from the breccia show shock-induced phenomena (Liu et al. 2009; McKay et al. 2011), particularly the fractures and deformation features characteristic of an impact (French et al. 2018).

The stratigraphic context and fossils indicate that the Winneshiek Shale is Darriwilian (Middle Ordovician) in age, i.e. from 458.4 to 467.3 Ma (Gradstein et al. 2013). None of the conodonts associated with the exceptionally preserved fossils are zonal index fossils, but they include Multiostodus subdentatus,
which is known from Darriwilian strata around Laurentia from Alberta to New York State (Witzke et al. 2011; Liu et al. 2017). The presence of the unusual conodont Archeognathus primus (Fig. 5a, b) is consistent with this age. The St Peter Sandstone overlies the Winneshiek Shale (Fig. 1c) and drill cores through this formation in Iowa, Minnesota and Indiana have yielded a diversity of conodonts indicating a late Darriwilian age. Characteristic early Darriwilian conodonts (the Histiodella–Paraprioniodus–Pteracontiodus–Fahraeusodus fauna) are absent in the Winneshiek Shale. Thus the conodont data constrain the age of the exceptionally preserved fossils, which were collected near the top of the Winneshiek Shale, to middle–late Darriwilian (Liu et al. 2017). Chemostratigraphic data, based on δ¹³Corg data from 36 drill core samples, narrow the age of the Winneshiek Shale to c. 464–467 Ma (Bergstrøm et al. 2018), i.e. early–middle Darriwilian. Thus the exceptionally preserved fossils are likely to be middle Darriwilian. The meteorite impact clearly predates deposition of the Winneshiek Shale and the underlying breccia. The Winneshiek Shale provides a minimum age for the impact of c. 464–467 Ma (Bergstrøm et al. 2018). A maximum age is provided by the Shakopee Formation, the youngest unit penetrated by the crater, which is separated from the overlying St Peter Sandstone by a major unconformity (Fig. 1c). The Shakopee Formation yields conodonts of Middle Tremadocian age, indicating that the impact occurred no earlier than c. 482 Ma. The impact penetrated a marine embayment or estuary in the southern part of the palaeocontinent Laurentia (Witzke 1990; Liu et al. 2009, 2017; Witzke et al. 2011). The complexity of the crater-fill and the lithological variability of the breccia suggest that the meteorite entered a significant depth of water (French et al. 2018). Cratering models indicate that a substantial thickness of younger sediments was present at the time of the impact, possibly 300–500 m, which was subsequently removed by erosion. This period of erosion may have lasted for 10–20 myr, after which the St Peters Sandstone was deposited, burying the crater and the surrounding area (French et al. 2018).

The age of the Decorah impact structure is not well constrained, but it coincides with the break-up of an L-chondrite meteorite parent body, which resulted in a series of Middle Ordovician impacts (Bergstrøm et al. 2018) at c. 470 Ma (Korochantseva et al. 2007) or 468 Ma (Lindskog et al. 2017). A possible link between the asteroid...
break-up and the Great Ordovician Biodiversification Event (Schmitz et al. 2008) is uncertain because major diversification began before the meteorite bombardment (Lindskog et al. 2017). The discovery of the Winneshiek Shale biota is notable in identifying a novel context for exceptional preservation and it prompts a consideration of whether other impact craters could be important in revealing new information about soft-bodied taxa and their evolutionary and stratigraphic importance (Box 1).

Faunal composition

The most striking member of the Winneshiek fauna is the eurypterid Pentecopterus decorahensis (Fig. 3a–g); the size of some of the tergites indicates that it reached lengths of 1.7 m. P. decorahensis is represented by >150 specimens, including some juveniles, preserved as carbonaceous cuticular remains. Although eurypterid remains make up <7% of the Winneshiek specimens, they account for the bulk of the fossil material. The fossils are mostly partially disarticulated elements of the exoskeleton (Fig. 3a, c–e). The way in which different parts are preserved in association suggests that the specimens are a product of moulting (Tetlie et al. 2008); numerous individuals may have congregated to moult together (Braddy 2001). The specimens found at this site allowed a full reconstruction of the adult eurypterid (Fig. 3b). The distribution of spines on the appendages and the characteristic morphology of the scales, including those forming a narrow median band down the axis of the trunk tergites (Fig. 3d), indicate that Pentecopterus is related to Megalograptus, which is known from the Upper Ordovician of Ohio. Rare specimens of juvenile P. decorahensis (Fig. 3g) show that the spiny appendages became more differentiated during transition to the adult, revealing a change during ontogeny, which is unusual among chelicerates (Lamsdell et al. 2015b). P. decorahensis is c. 9 myr older than the previously oldest known eurypterid, Brachyopterus stubblefieldi from the Sandbian of Wales (Stormer 1951). Ordovician eurypterids are very rare; <5% of all eurypterid species are Ordovician in age (Tetlie 2007). Phylogenetic analysis placed P. decorahensis at the base of the Megalograptidae, which occupy a relatively derived position among the eurypterids. This indicates that most eurypterid clades had originated by the Middle Ordovician (Lamsdell et al. 2015b). Eurypterids must have radiated rapidly soon after they evolved, or significantly older examples may remain to be discovered, perhaps in rocks of Cambrian age.

Pentecopterus is not the only chelicerate in the Winneshiek fauna. A much rarer and less well preserved form reveals a semi-circular carapace and 13 tergites, but provides no information on the appendages. This basal euchelicerate, Winneshiekiya youngae, shares features with both xiphosurans and with eurypterids and chasmataspisids (Lamsdell et al. 2015a). Winneshiekiya helps to resolve the relationships of early euchelicerates and confirms that xiphosurans (‘horse-shoe crabs’) are a paraphyletic group. Small carbonaceous fossils extracted from acid-treated samples of Winneshiek Shale include gnathobasic structures (Fig. 3i), which
may represent the coxae of Winneshiekia or some similar xiphosuran (Nowak et al. 2018).

There are at least seven different taxa of bivalved arthropods in the Winneshiek Shale, which represent nearly 10% of the fossils by specimen (Briggs et al. 2016). The small crustacean *C. winneshiekensis* (Fig. 4a) is the most abundant and preserves evidence of features other than the valves; the trunk segments are often evident, the appendages very rarely. *C. winneshiekensis* is the oldest representative of one of the most species-rich phyllocarid families, the Ceratiocarididae; the next oldest ceratiocarid is from the Sandbian of Virginia (Collette & Hagadorn 2010). Another crustacean group, the notostracan branchiopods, may be represented by a single incomplete abdomen with a telson bearing furcal rami. The largest bivalved taxon is *Decoracaris hildebrandi* with a carapace reaching lengths of 9 cm (Fig. 4b). The valves extend anteriorly into a bulbous projection overlying a shallow notch reminiscent of the outline in thylacocephalans, an extinct group of probable crustaceans. If future discoveries confirm that *D. hildebrandi* is a thylacocephalan, it is the oldest known representative of the group (Haug et al. 2014), although a thylacocephalan identity for even older bivalved forms has been suggested (Vannier et al. 2006; see Haug et al. 2014 for discussion). A smaller form,
Iosuperstes collisionis (Fig. 4c), is represented by sub-oval valves up to 25 mm long, which are sometimes articulated; the absence of preserved limbs prevents its affinities from being resolved. A smaller bivalved arthropod, commonly preserved in a butterflied configuration (Fig. 4d), has a rim on the valves characteristic of leperditicopes, a group previously considered to be giant ostracods. Leperditicopes are probably crustaceans, but their place within the group is uncertain. The Winneshiek fauna also includes at least three different ostracods (Briggs et al. 2016). Filtering appendages preserved as small carbonaceous fossils (Fig. 3h) may belong to some of these taxa (Nowak et al. 2018).

Conodonts are the most abundant fossils in the Winneshiek fauna (Liu et al. 2017), which is dominated by these vertebrates (Aldridge et al. 1986; Briggs 1992). Isolated elements and bedding plane assemblages account for just over 50% of the fossil specimens recovered (Liu et al. 2017) and isolated elements are also known from bromalites (Hawkins et al. 2018), indicating that the conodonts fell victim to some unknown predator, perhaps eurypterids or larger conodonts. More than a dozen taxa are present, most of them awaiting description, including coniform and prioniodinid apparatuses. Two of the more common apparatuses represent giant forms. The unusual apparatus of Archaeognathus primus (Fig. 5a, b), previously described from the Ordovician of Missouri, consists of just six elements: two pairs of archeognathi-form (P) and one pair of coleoidiform (S) elements. The elements in this highly modified apparatus have robust basal bodies and appear to be well equipped for grasping and cutting prey. The apparatus architecture of Iowagnathus grandis (Fig. 5c) is more familiar, being reminiscent of the prioniodinid type, and consists of two pairs of P elements, four pairs and one unpaired S element, and a pair of M elements, all of which also preserve robust basal bodies. The preservation of basal bodies in the Winneshiek Shale is unique among Ordovician conodont faunas. Although these larger conodont elements tend to be intact, the preservation of other Winneshiek conodont taxa is variable. The individual elements of A. primus and I. grandis in these two Winneshiek conodonts are some of the largest conodont elements known; the unpaired S element in I. grandis reaches dimensions >16 mm. Inferences of total body size based on element or apparatus dimensions are problematic, but comparison of the apparatus size in the Winneshiek specimens with the Carboniferous conodont animal with preserved soft parts from Scotland (Briggs et al. 1983; Aldridge et al. 1993) suggests that the Iowa animals may have reached lengths of 0.5–1.0 m. Conodonts are not the only vertebrates in the fauna. Rare bilaterally symmetrical, possible dermal, plates ornamented with tubercles have also been found (Fig. 5d). These isolated plates are unlike any such structures reported from elsewhere and may represent a new early armoured jawless fish (Liu et al. 2006, 2009, 2011).

Bromalites account for just over 25% of the Winneshiek Shale fossils (Hawkins et al. 2018). The term includes both coprolites and cololites, the latter representing gut contents which have become mineralized within a carcase that has decayed. The morphology of the Winneshiek bromalites is variable. Rod-like forms (Fig. 5e, f), near-circular in cross-section, commonly show a wrinkled surface (Fig. 5e), which suggests moulding by the gut wall. Some rod-like forms are partly flattened, suggesting a partial gut-fill or more fluid content, or collapse prior to complete mineralization. The density of wrinkles (from closely spaced to absent) and the degree of flattening vary, sometimes even along the length of an individual bromalite (Fig. 5g), resulting in a morphological spectrum that presumably reflects the nature of the...

Fig. 4. Bivalved arthropods from the Winneshiek biota. (a) The phyllocarid Ceratiocaris winneshiekensis in right lateral view, showing the trunk and telson extending beyond the valves (SUI 138435). (b) A right valve of Iosuperstes collisionis, which cannot be assigned to a group in the absence of evidence other than the valves (SUI 138464). (c) A right valve of Decoracaris hildebrandi showing a pronounced notch, which may indicate an affinity with Thylacocephala; the rest of the arthropod is unknown (SUI 138453). (d) An undetermined probable leperditid with the two valves flattened in the butterflied position (SUI 138486). All figures from Briggs et al. (2016), reproduced with permission.
faecal material and its taphonomic history. The bromalites are phosphatized, although areas of carbonaceous material occur in association with some of them, and they contain phosphate microspherules, which may have been features of the gut of the living animal. In the absence of associated soft tissues, it is often difficult to determine whether specimens originated as coprolites or cololites, and both may be represented in the Winneshiek Shale.

Rare examples of a very different type of bromalite, more variable in shape and consisting of aggregates of quartz sand, are also present (Fig. 5h). These structures are likely to be coprolites, but the source of the sand, and why it was ingested, are uncertain.

Taphonomy

The source of the laminations in the Winneshiek Shale is unknown. The possibility of a tidal influence in the vicinity of the crater has been suggested (Liu et al. 2009), but there has been no analysis to test for tidal rhythmicity. The light colour of the organic-walled algal fossils indicates a low degree of thermal maturation (Nowak et al. 2017), consistent with the conodont alteration index values, which range from 1.5 to 2.0 (Liu et al. 2017). Some fossils, including conodont elements (Liu et al. 2017), linguloid brachiopods and the valves of Decoracaris, Iosuperstes and the probable leperditid (Briggs et al. 2016), were biomineralized and therefore more readily preserved. A number of taxa, however, are preserved as organic remains, including organic-walled algae (Nowak et al. 2017), small carbonaceous arthropod remains (Nowak et al. 2017) and the eurypterid Pentecopterus (Lamsdell et al. 2015b). The phyllocarid C. winneshiekensis is likewise commonly represented by organic cuticles, but some specimens also preserve phosphatized gut contents and even traces of musculature (Briggs et al. 2016). The bromalites, which are a product of larger animals, are also preserved as three-dimensional structures mineralized in apatite. Such a rapid formation of authigenic apatite (Martill 1988, as discussed in Briggs 2003) requires high concentrations of phosphate and locally reduced pH, which can occur within a decaying carcase (Briggs & Wilby 1996). It emphasizes the potential for the preservation of other soft tissues in the Winneshiek Shale,
associated with cuticular remains in other Lagerstätten, including sourced from the gut contents. Phosphatized soft tissues are also may have been the phosphate source, while the cuticle provided a sediment (Fig. 2d), the presence of pyrite and the nature of the fauna palaeogeographical setting, the undisturbed organic-rich laminated deposits in the absence of familiar shelly taxa and graptolites. The Winneshiek Shale is unusual among Middle Ordovician marine Palaeoecology of the epicontinental sea (Witzke suggest a restricted basin associated with a large-scale embayment evidenced by a diversity of acritarchs and coenobial green algae inimical to life. In spite of the remarkable preservation, it is not clear of life in the water column (Liu specimens are conodonts, which were probably a major component in the case of conodonts, it is difficult to determine ukranian Shield preserves Paleogene molluscs, ostracods and fish (Gruver et al. 2006). The Darwin Crater in Tasmania (Howard & Haines 2007) provides one of the longest continuous pollen records in Australia in c. 60 m of late Pleistocene and Holocene lacustrine sediments (Colhoun & van de Geer 1998; Cook et al. 2012). Fossils may also occur in impact breccia and associated sediments, as in the concentration of lignite fragments in the nearshore marine Late Cretaceous Wetumpka Crater in Alabama (King et al. 2006). Volcanic craters show some similarity to impact craters in their circular outline and relatively steep sides. Some of the best known examples of exceptional preservation in volcanic crater lakes are those in the Tertiary Central European volcanic belt in Germany, which include important Lagerstätten of Eocene and Oligocene age at Messel, Eckfeld and Enspel (Pirung et al. 2001). Most lake sediments that yield Lagerstätten, however, occur in orogenic belts or fault-bounded basins (Allison & Briggs 1991). perhaps even of conodonts. In the case of Ceratiocaris, the body may have been the phosphate source, while the cuticle provided a barrier to diffusion. The phosphate in the bivaliates may have been sourced from the gut contents. Phosphatized soft tissues are also associated with cuticular remains in other Lagerstätten, including Cerin and Solnhofen (Briggs & Wilby 1996).

Box 1. Fossils in impact structures

The discovery of exceptionally preserved fossils in the Decorah impact structure highlights the potential importance of such settings as a source of Konservat-Lagerstätten. Impacts create deep craters, which may favour low-energy sedimentation in a stratified water column with anoxic conditions at depth. However, they are often small in area with a relatively thin infill overlying a crater-fill breccia, and they may not be exposed at the surface. It is not surprising therefore that records of fossils preserved in impact craters are rare. The occurrence of significant fossiliferous deposits reflects the circumstances associated with each crater – its size and depth, marine or non-marine setting, and the nature of infill lithologies – rather than generic features associated with impact cratering. Perhaps the best-known fossil structure in an impact crater was discovered in the c. 3.5 km diameter Miocene Steinheim Basin in SW Germany, which includes 30–40 m of lacustrine sediments preserving multiple speciation events over time in the gastropod genus Gyraulus (Planorbidae) (Gerritsen 1992). The Steinheim snails were investigated by Franz Hilgendorf in the 1860s, who documented a now classic example of endemoe speciation and generated the first phylogenetic tree (Hilgendorf 1867; Rasser 2014). Other Neogene lake sequences in central and southeastern Europe also preserve abundant shelly fossils, but only the Steinheim crater and the simultaneously formed larger c. 25 km Nördlinger Ries structure originated as the result of an impact (Harzhauser & Mandic 2008).

Non-shelly and soft-bodied taxa such as those in the Decorah impact structure are rarely found in impact crater-fill sediments. The Bolysh crater (c. 65 Ma) on the Ukrainian Shield preserves Paleogene molluscs, ostracods and fish (Guver et al. 2006). The Darwin Crater in Tasmania (Howard & Haines 2007) provides one of the longest continuous pollen records in Australia in c. 60 m of late Pleistocene and Holocene lacustrine sediments (Colhoun & van de Geer 1998; Cook et al. 2012). Fossils may also occur in impact breccia and associated sediments, as in the concentration of lignite fragments in the nearshore marine Late Cretaceous Wetumpka Crater in Alabama (King et al. 2006). Volcanic craters show some similarity to impact craters in their circular outline and relatively steep sides. Some of the best known examples of exceptional preservation in volcanic crater lakes are those in the Tertiary Central European volcanic belt in Germany, which include important Lagerstätten of Eocene and Oligocene age at Messel, Eckfeld and Enspel (Pirung et al. 2001). Most lake sediments that yield Lagerstätten, however, occur in orogenic belts or fault-bounded basins (Allison & Briggs 1991).

The large size of the conodonts and eurypterids suggest a nutrient-rich environment, but it is not clear how much time they spent in this setting and evidence for food web interactions is incomplete. The large, rare bivalved arthropod D. hildebrandi may also have been a predator if its affinities lie with thylacocephalans (Briggs et al. 2016), which have an anterior raptorial appendage. The phyllocarid C. winnesiheikensis may have been nektobenthic, adapted to low oxygen conditions, allowing it to feed on organic matter in the sediment (Briggs et al. 2016). One example of multiple Ceratiocaris individuals in a coprolite shows that it was preyed upon. Other bivalved arthropods, including ostracods, are rarer and are only represented by carapaces; presumably the thinner cuticle that made up the rest of the exoskeleton decayed. Benthic animals are rare, confined to a small linguloid brachiopod (Liu et al. 2006) and a single gastropod specimen (Briggs et al. 2016). Filamentous algae similar to chlorophytes were probably also benthic, perhaps living in adjacent shallow water (Nowak et al. 2017).

Palaeoecology

The Winneshiek Shale is unusual among Middle Ordovician marine deposits in the absence of familiar shelly taxa and graptolites. The palaeogeographical setting, the undisturbed organic-rich laminated sediment (Fig. 2d), the presence of pyrite and the nature of the fauna suggest a restricted basin associated with a large-scale embayment of the epicontinental sea (Witzke et al. 2011) where bottom conditions, or at least the sediment itself, were anoxic and largely inimical to life. In spite of the remarkable preservation, it is not clear how representative the assemblage is of the original community ecology. Soft-bodied organisms without biomineralized skeletal elements or decay-resistant cuticles are unrepresented, except perhaps by bivaliates. Primary productivity in the plankton is evidenced by a diversity of acritarchs and coenobial green algae (Zippi 2011; Nowak et al. 2017). More than half the Winneshiek specimens are conodonts, which were probably a major component of life in the water column (Liu et al. 2017). The complex apparatuses, robust elements and large size of Archeognathus and Iowagnathus (Liu et al. 2017) suggest that they may have been high-level predators. The presence of small elements in coprolites shows that conodonts were also prey, perhaps for larger conodonts or other animals. Only a small proportion of the conodont specimens are complete apparatuses, so it is difficult to estimate the number of individuals represented.

The appendage morphology of the giant eurypterid P. decora-hensis indicates that it was also a predator (Lamsdell et al. 2015b). The apparent dominance of predators in the assemblage is anomalous, but the eurypterid is represented by the remains of exuviae so, in the case of conodonts, it is difficult to determine the number of individuals. Eurypterids congregated in shallow water to mate and moul to where salinity or other factors inhibited predators (Braddy 2001; Vraza & Braddy 2011), in which case they may have been seasonal visitors to the depositional basin. Only one example of a genital appendage of Pentecopterus is known and it is incomplete (Lamsdell et al. 2015b), so it is not possible to determine whether the skewed sex ratio characteristic of mass moulting is present (Tettie et al. 2008; Vraza & Braddy 2011). The
(including a xenopod and marrellomorph), a phyllocarid, vermiliform taxa, palaeoscolecids and graptolites. All these Konservat-Lagerstätten, however, like the more remarkable older Ordovician (Tremadocian-Floian) Fezouta Formation of Morocco (Van Roy et al. 2015, Lefebvre et al. 2018), preserve a diversity of shelly taxa, indicating an environmental setting representative of more normal marine conditions than the Winneshiek Shale.

Closer comparisons with the Winneshiek Shale are offered by Late Ordovician Lagerstätten situated around the margins of Laurentian land masses. The Katian William Lake and Airport Cove biotas of Manitoba, Canada include linguloids, conodonts, eurypterids and xiphosurids, although the proportions differ between them (Young et al. 2007, Fig. 2). The Big Hill biota of Michigan yields a similar suite of taxa (Lamsdell et al. 2017). These lithologies are predominantly carbonate, however, in contrast with Winneshiek, but the shared faunal components reflect a shallow marine marginal setting (Young et al. 2007). There are also similarities between the Winneshiek Shale and the Hirnantian Soom Shale of South Africa, even though it was deposited in a cold water shallow marine setting on Gondwana (Gabbott et al. 2016). The Soom Shale biota is preserved in a laminated mudstone and is dominated by conodonts, some giant, and includes a eurypterid, phyllocarid and ostracods, as well as linguloid brachiopods and bivalves (Aldridge et al. 2006), but a diversity of shelly taxa is also present. Thus the similarities between the Winneshiek Shale and these other Ordovician Konservat-Lagerstätten reflect exceptional preservation combined with atypical marine settings, but do not imply equivalent environments.

The Winneshiek Konservat-Lagerstätte occurs in a very unusual setting, but it is unlikely to be unique. Other examples of exceptional preservation originally thought to be one of a kind have been shown to occur in multiples following further exploration: examples include the Cambrian Burgess Shale (Collins et al. 1983) and Ordovician Beecher’s Trilobite Bed (Farrell et al. 2009). The Decorah impact structure is one of a number of meteorite craters of similar age in North America (Liu et al. 2009; Schmieder et al. 2015): could others also host exceptionally preserved fossils? The Middle Ordovician Rock Elm structure in Wisconsin is about the same size as the Decorah structure. The Rock Elm Shale, which is confined to the crater, has yielded brachiopods, gastropods, trilobites, crustaceans and polychaetes (as sclerocadonts) as well as conodonts (Peters et al. 2002; French et al. 2004). This fauna, which has received little attention, is apparently more diverse and includes more normal marine taxa (French et al. 2004) than the Winneshiek Shale; no evidence of exceptional preservation has been reported.

The Ames structure in NW Oklahoma (Johnson & Campbell 1997; Koeberl et al. 2001) is larger than the Decorah impact structure, up to 15 km in diameter, and is buried 2.75 km below the surface. Conodont elements found in core chips of black shale within the Ames crater included Erismodus and Phragmodus, indicating a mid-Middle Ordovician age (Repetski 1997). Most of the elements occur as clusters or bedding plane assemblages, like those from the Winneshiek Shale, and they include examples associated with carbonaceous films, indicating that they represent the remains of carcases (Repetski 1997). The black shale within the Ames structure has yielded two phyllocarids (Hannibal & Feldmann 1997), one similar to C. winneshiekensis, the other probably Carycaris (Briggs et al. 2016). Rare brachiopods and ‘small phosphatic masses’ (Hannibal & Feldmann 1997), which may represent bivalves, are also present. Thus the biota, although incompletely known, shows some similarities with the Winneshiek assemblage. We are unaware of detailed reports of fossils associated with other coeval Ordovician impact sites in North America (Schmieder et al. 2015), at East Clearwater Lake in Québec, Gladstone in Illinois and Glover Bluff in Wisconsin. However, it is clear that impact structures represent a potential source of other exceptionally preserved fossils (Box 1).

Conclusions

The large number of Burgess Shale-type Konservat-Lagerstätten in Cambrian rocks provides unparalleled evidence of the history of life during that period, which coincides with the Cambrian radiation. The discovery of the Fezouta formations of Morocco, with their similar preservation of soft-bodied organisms (Van Roy et al. 2015), extended this record into the Early Ordovician (Lefebvre et al. 2018). The nature of the animals represented in the Fezouta biota suggests that the Cambrian radiation and Great Ordovician Biodiversification Event are more of a continuum than previously thought. Thereafter the fossil record of soft-bodied taxa is much less rich, perhaps as a result of the closure of the taphonomic window that favoured Burgess Shale-type preservation (Gaines et al. 2012). It has been suggested that the Mid Ordovician asteroid break-up and meteor shower, which resulted in the Decorah impact structure, might have promoted the Great Ordovician Biodiversification Event by disrupting communities (Schmitz et al. 2008). There is no obvious mechanism to explain such a relationship on a global scale, however, and biodiversification during the Darrwilian is only part of a longer and more complex Great Ordovician Biodiversification Event (Servais & Harper 2018). The Winneshiek Konservat-Lagerstätte is important because it is Middle Ordovician in age, an interval when non-shelly fossils are poorly represented in the fossil record. Some of the Winneshiek Shale arthropods are of fundamental stratigraphic and phylogenetic importance, including the earliest eurypterid, a basal cheilicerate and the earliest ceratiocarid phyllocarid. The conodonts provide new evidence of apparatus architecture and giant size. The Winneshiek Lagerstätte also reveals

Box 2. Outstanding questions

(1) Some of the Winneshiek Shale fossils await further investigation. What is the nature of other algal material? What is the total conodont fauna?

(2) What new taxa would further excavation reveal?

(3) What is the detailed history of the depositional basin? This would require further drill core data.

(4) What are the details of the crater-fill sequence, including lithologies and thickness?

(5) What were the roles of impact and post-impact processes in generating an environment for exceptional preservation?

(6) How does the Decorah impact structure relate to any proposed ‘cluster’ of Mid Ordovician impact events?

(7) What is the potential of impact structures in general as hosts of Konservat-Lagerstätten and how could modelling determine which kinds of impact structures should be targeted?
the potential importance of impact craters as a novel context for exceptional preservation. Borehole samples from the coeval Amشاشة Oklahoma contain similar fossils, and sedimentary sequences in other depositional basins created by impacts await exploration with the insights provided by the Decorah discovery. Box 2 lists some of the questions yet to be answered about the Winneshiek biota and the nature, history, and significance of the Decorah impact structure.

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References


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