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Exceptionally preserved arthropodan microfossils from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA

HENDRIK NOWAK , THOMAS H. P. HARVEY, HUAIBAO P. LIU, ROBERT M. MCKAY AND THOMAS SERVAIS 

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The Middle Ordovician (Darriwilian) Winneshiek Shale from Winneshiek County, Iowa, USA, hosts a Konservat-Lagerstätte that has yielded a diverse fauna including soft-bodied fossils. The shale is rich in organic content; in particular, algal material and fragmentary cuticular remains. Palynological acid treatment alongside modified, low-manipulation processing enables the extraction of these ‘small carbonaceous fossils’ (SCFs) from the matrix, allowing a more detailed view of their morphology. Together these methods have yielded exceptionally well-preserved crustacean-type setae and a population of distinctive microfossils which we identify as the feeding appendages of a small-bodied arthropod. We present two hypotheses for their identity: as either pancrustacean mandibles, or euchelicerate coxae. Overall, the detailed topological similarities and implied functional equivalence to the coxae of xiphosurid chelicerates, in particular, outweigh the resemblance to certain branchiopodan and hexapodan mandibles. In turn, however, the restricted size range and lack of associated limb or carapace fragments pose a taphonomic conundrum, suggesting an extreme biostratigraphic bias. By comparison with previously described arthropodan SCFs from the Cambrian of Canada, the Winneshiek fossils extend the geographic, palaeoenvironmental and temporal range of this taphonomic window and provide a complementary tool for reconstructing the diversity and ecology of the Winneshiek biota. □ *Arthropods, Chelicerata, Crustacea, Konservat-Lagerstätte, Middle Ordovician, small carbonaceous fossils.*

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The Winneshiek Shale in Iowa, USA, is a Darriwilian (Middle Ordovician) Konservat-Lagerstätte (site with exceptionally well-preserved fossils; see Seilacher 1970) that is notable not least for its arthropod fossils. It has yielded the currently oldest described eurypterids (Lamsdell *et al.* 2015a), phyllocarids with soft-tissue preservation (Liu *et al.* 2006; Briggs *et al.* 2016), ostracods and other bivalved arthropods (Briggs *et al.* 2016), and a dekatriatan-like euchelicerate (Lamsdell *et al.* 2015b). Apart from this, unusually large conodonts (elements up to 16 mm in length) with complete apparatuses (Liu *et al.* 2017), possible jawless fishes, linguloid brachiopods, molluscs, algae and acritarchs have been found (Liu *et al.* 2006; P.A. Zippi 2011, unpublished report). This site is one of few Konservat-Lagerstätten in the Ordovician (Van Roy *et al.* 2015), the only other Konservat-Lagerstätte known so far from the Middle Ordovician (also Darriwilian) being the Llanfallteg Formation in south-west

Wales (Whittington 1993; Legg & Hearing 2015). The documented occurrence of diverse arthropods in the Winneshiek biota, combined with the exceptional preservation of eurypterid cuticle (Lamsdell *et al.* 2015a) and various algal palynomorphs (P.A. Zippi 2011, unpublished report), has prompted a search for ‘small carbonaceous fossils’ (SCFs) (*sensu* Butterfield & Harvey 2012). Previous SCFs reported from the Cambrian include crustacean remains including branchiopodan filter plates (Harvey & Butterfield 2008; Harvey *et al.* 2012b) and branchiopod, copepod and ostracod-type mandibles (Harvey & Butterfield 2008; Harvey *et al.* 2012a,b; Harvey & Pedder 2013), providing valuable insight into the evolution and ecology of early crustaceans. The attempt to search for organic microfossils in the Winneshiek Shale has now yielded numerous objects that we tentatively identify as crustacean filter plates and coxae of a diminutive euchelicerate, which are described herein.

Geological context

The Winneshiek Shale (Darriwilian, Middle Ordovician) is found around the city of Decorah, Winneshiek County, Iowa, USA. It is a well-laminated, greenish brown to medium or dark grey, sandy shale with a thickness of 18–27 m (Liu *et al.* 2006). Its distribution is limited to a circular area with a diameter of about 5.6 km (25 km²). Multiple geological evidences have indicated that this structure is an impact crater, the ‘Decorah impact structure’. The fossil component, as well as the results from palaeoenvironmental studies, indicates that the Winneshiek Shale was deposited in a restricted, brackish, shallow marine environment (Liu *et al.* 2006, 2009).

Only one small outcrop of the Winneshiek Shale is known, which is mostly submerged under the Upper Iowa River. At this site, the Iowa Geological Survey (IGS) excavated the upper four metres of the Winneshiek Shale in 2010 by damming the river temporarily. Otherwise, the shale succession is accessed by wells (Liu *et al.* 2009). The Winneshiek Shale overlies an unnamed impact depositional unit and is unconformably overlain by the widely distributed sandstones of the St Peter Formation (Liu *et al.* 2006).

Materials and methods

Several tons of the Winneshiek Shale were collected from the drained section of the Upper Iowa River during the excavation in 2010. This section was subdivided into 18 sampling intervals, which represent the uppermost about 4 m of the Winneshiek Shale and its discordant upper boundary with the St Peter Formation (Fig. 1). A borehole throughout the Winneshiek Shale was drilled and sampled in close proximity to the excavated section.

A few tens of grammes of rock from each sampling interval were treated with a standard palynological maceration technique, employing hydrofluoric and hydrochloric acid. The residue was filtered with mesh sizes of 51 and 15 µm. Extracts of the size fraction between 15 and 51 µm were then mounted in resin on permanent palynological slides. The same material and samples from the borehole were also treated with a low-manipulation approach for the extraction of SCFs (modified from Butterfield & Harvey 2012). Specimens were studied and photographed under a ZEISS Axio Imager.A2 transmitted light microscope with a mounted AxioCam ERc5s camera.

All samples are deposited at the University of Iowa Paleontology Repository, Department of Earth and Environmental Sciences (SUI).

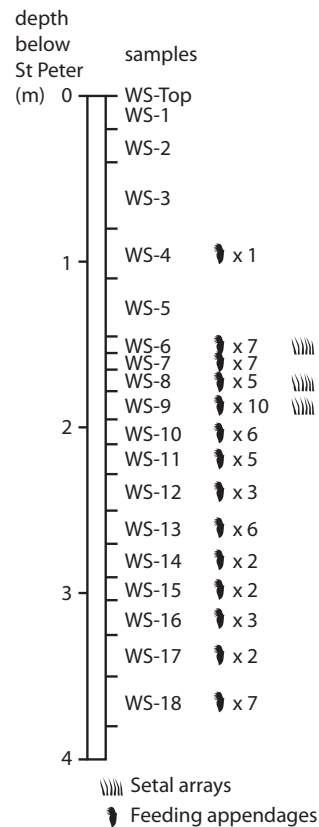


Fig. 1. Stratigraphical position relative to the St Peter Formation and yield of samples from the Winneshiek Shale.

Results

All samples, except for one from near the boundary with the overlying St Peter Formation, yielded a rich organic fossil content (Fig. 1). Aside from fragmentary eurypterid cuticle (Fig. 6A shows an example; compare Lamsdell *et al.* 2015a), and cyanobacterial sheaths, algae and acritarchs similar to those recovered during a separate earlier study (P.A. Zippi 2011, unpublished report), we recovered organic-walled microfossils with possible chelicerate and crustacean affinity that presently cannot be linked to macrofossil groups known from this section.

Setal arrays

Description. – Among the Winneshiek SCFs are rare specimens of arthropodan setae, occurring either as isolated units or in semi-articulated arrays (Fig. 2). A variety of setal morphologies are present in the assemblage, including ‘simple’ forms, that is tubular shafts lacking finer-scale elaboration (following the terminology of Garm & Watling 2013; see Fig. 2A, B), and those with well-preserved setules, that is

filamentous side branches much less than 1 μm in diameter. The setule-bearing setae have plumose forms, with precisely spaced straight setules in two longitudinal series (Fig. 2C, D). Standard palynological processing yielded disarticulated single setae ($n = 6$), but also rare semi-articulated arrays, including one which comprises ten narrow (1–1.5 μm) plumose setae with partly overlapping setules that define a ca. 0.6- μm mesh (Fig. 2D), and another array of five more robust plumose setae which may have formed a similar mesh of interlocking setules, originally (Fig. 2C). The most extensive setal arrays were recovered using a low-manipulation technique (Fig. 2A, B). One specimen consists of several tens of setae that are densely arranged and superimposed on a remnant cuticular sheet, to which they presumably were also attached in life (Fig. 2B). A more informative specimen preserves multiple arcuate fans of setae lacking setules, organised into four series with an extraneous (displaced?) fan superimposed on one series at ca. 90° (Fig. 2A).

Interpretation. – Setae resembling the simple and plumose types described here are widespread among aquatic arthropods, where they fulfil various mechanical and sensory functions dependent on their arrangement and position on the body. Planar arrays of plumose setae with closely spaced setules

(e.g. Fig. 2C, D) often have roles in filter feeding, whereas fans of simple setae (Fig. 2A) commonly function as barriers for controlling the flow of particles and/or water (e.g. Garm & Watling 2013). More precise phylogenetic and functional inferences require additional information, which is lacking in most Winneshiek specimens, although the arrangement of up to four arcuate series of setae in one specimen (Fig. 2A) is suggestive of the thoracic appendage series in branchiopod crustaceans. If this interpretation is correct, the lack of setules is unexpected, but may be a taphonomic artefact.

The arcuate arrays of setae in the Winneshiek assemblage are very similar to SCFs from marine sediments of the lower and middle Cambrian of western Canada (Mount Cap and Earlie/Deadwood formations), which have been identified as branchiopod filter plates based on the overall shape of the plumose arrays, the range of accessory setae and, in the better articulated specimens, the disposition of setal armatures on appendage lobes (Harvey & Butterfield 2008; Harvey *et al.* 2012a,b). The Winneshiek specimens, though more fragmentary, may likewise derive from branchiopods. Extant branchiopods inhabit mostly freshwater environments, with only a minor part of the order Cladocera ('water fleas') living secondarily (being descendants of freshwater dwellers) under marine or brackish

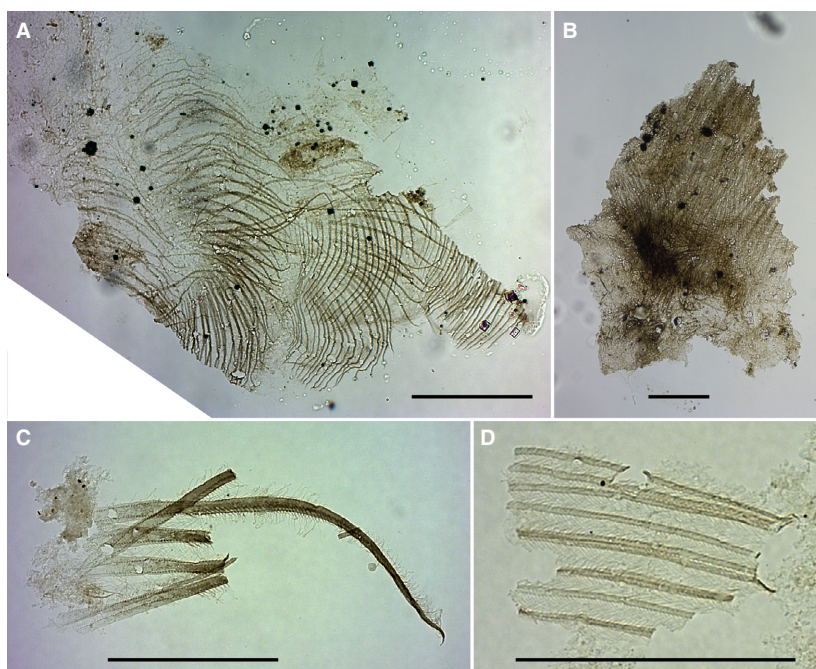


Fig. 2. Setal arrays from the Winneshiek Shale. Repository numbers are followed by sample numbers (with slide number in parentheses) and (where applicable) England Finder Graticule coordinates. Scale bars = 100 μm for A, B and 50 μm for C, D. A, B, membranes with arrays of unbranched setae (size fraction >51 μm). A, SUI 143641-1, WS-8(lm1). B, SUI 143641-2, WS-8(lm1). C, D, crustacean-type filter plates (size fraction 15–51 μm). C, SUI 143632-1, WS-9(1), O41/4. D, SUI 143647-1, WS-6(1), Y27/3. [Colour figure can be viewed at wileyonlinelibrary.com]

conditions (Bowman & Abele 1982). Our material raises the possibility that by the Middle Ordovician, small-bodied, filter-feeding branchiopods had spread to restricted, marginal marine environments, or even freshwater habitats (from which the remains may have been transported). However, more material is needed to rule out alternative affinities for the Winneshiek SCFs, especially because both ostracods and phyllocarids have been documented from the biota (Liu *et al.* 2006; Briggs *et al.* 2016). Ostracods can possess one or two pairs of sequential, arcuate filter-like structures (e.g. Fenchel 1988; Horne *et al.* 2011), so could conceivably account for the four-series array, if limbs are overlapping (Fig. 2A). Phyllocarids have longer series of filtering appendages but, based on modern leptostracans, could be expected to have more linear (less arcuate) filter arrays (Martin & Christiansen 1995). A combined examination of SCFs and exceptionally preserved whole-body fossils could help test these competing hypotheses.

Feeding appendages

Description. – Of nineteen samples representing the uppermost 3.8 m of the Winneshiek Shale, fourteen yielded a distinct type of carbonaceous microfossil that we identify as components of arthropod feeding appendages (Fig. 3). They were not recovered from the uppermost four (WS-Top through WS-3) and the sixth (WS-5) samples treated (see Fig. 1). The number of specimens recorded from each sample varies between one and ten. In total, 66 specimens were identified, including fragments. They were only found in the grain size fraction between 15 and 51 μm . Left and right specimens cannot be recognised nor distinguished on morphological grounds.

Discounting protrusions, the appendage elements occur as microfossils with an overall elongate D-shaped or skewed oval outline, sometimes curved into a hook-like or arm-like form. Their total length has a range of 55–130 μm (measured from 25 complete specimens). The fossils are characterised by an elongate boat-shaped part (assumed to be proximal; Fig. 4, b) with a large opening (Fig. 4, o) and a toothed distal extension (Fig. 4, t). The opening is outlined by a thickened rim, which also, together with a shorter rim on the opposite side, partly frames a more faint area near the proximal end. The elements taper towards their proximal end, which extends into two short, blunt projections which are often more or less folded and deformed, obscuring their original shape and orientation (Fig. 4, a). The elements show a pattern of longitudinal wrinkles, most strongly near the toothed edge, which is also darker or less translucent (presumably due to stronger sclerotisation). In

some specimens, the toothed edge is recurved so that it is oriented more or less parallel to the long axis of the proximal part. It is convexly curved, carrying 7–11 (commonly 8–10) backwards-arched, partially overlapping teeth. The teeth of each element are of unequal length, with those near the anterior end being longer and broader, except for a smaller, rudimentary tooth at the distal end of the row that is not always developed (Figs 3D–G, 4, r). The tips of the teeth are usually broken off, but lengths of up to 11 μm were measured. There is a strong and statistically significant linear correlation between the total length of the mouthparts and the length of the tooth row (t) ($r^2 = 0.91$; $P = 0.003$; $n = 25$; Fig. 5A), but no correlation between total length of elements and number of teeth ($r^2 = 0.14$; $P = 0.523$; $n = 22$; Fig. 5B). On the edge of the element opposite to the main opening, and close to the distal toothed extension, is a more or less prominent knob or protuberance (Fig. 4, p), which defines the proximal edge of a smoothly concave indentation contiguous with the leading edge of the toothed extension. The indentation defines the position of a second opening in the element, smaller than the main opening and positioned distally (Fig. 4, s).

Interpretation. – The toothed Winneshiek microfossils resemble various arthropodan feeding structures, particularly the mandibles (jaws) of certain pancrustaceans (crustaceans and hexapods), and the toothed leg bases (coxae) of some euchelicerates (eurypoterids and xiphosurans). They can be distinguished from other podomeres by the presence of a distinct toothed edge and a basal articulation. Gastric teeth in crustaceans can also appear superficially similar, but have no opening for musculature. Likewise, scolecodonts (polychaete jaws) have at most one basal opening per element. Distinguishing between the two remaining hypotheses of identity – crustacean mandibles or euchelicerate coxae – requires a detailed anatomical comparison and a consideration of functional morphology. Aside from biological affinity, the correlation between total length and the length of the toothed part (Fig. 5A), with independence of the number of teeth from size (Fig. 5B), indicates a stable morphology across growth stages concerning these features and provides no evidence for the presence of different species. Most likely, there was some variation in the number of teeth between individuals, but differences between appendages are also possible, if these objects represent coxae.

If the fossils are interpreted as mandibles, the proximal boat-shaped part would represent the coxal body, with the large opening (Fig. 4, o) as the

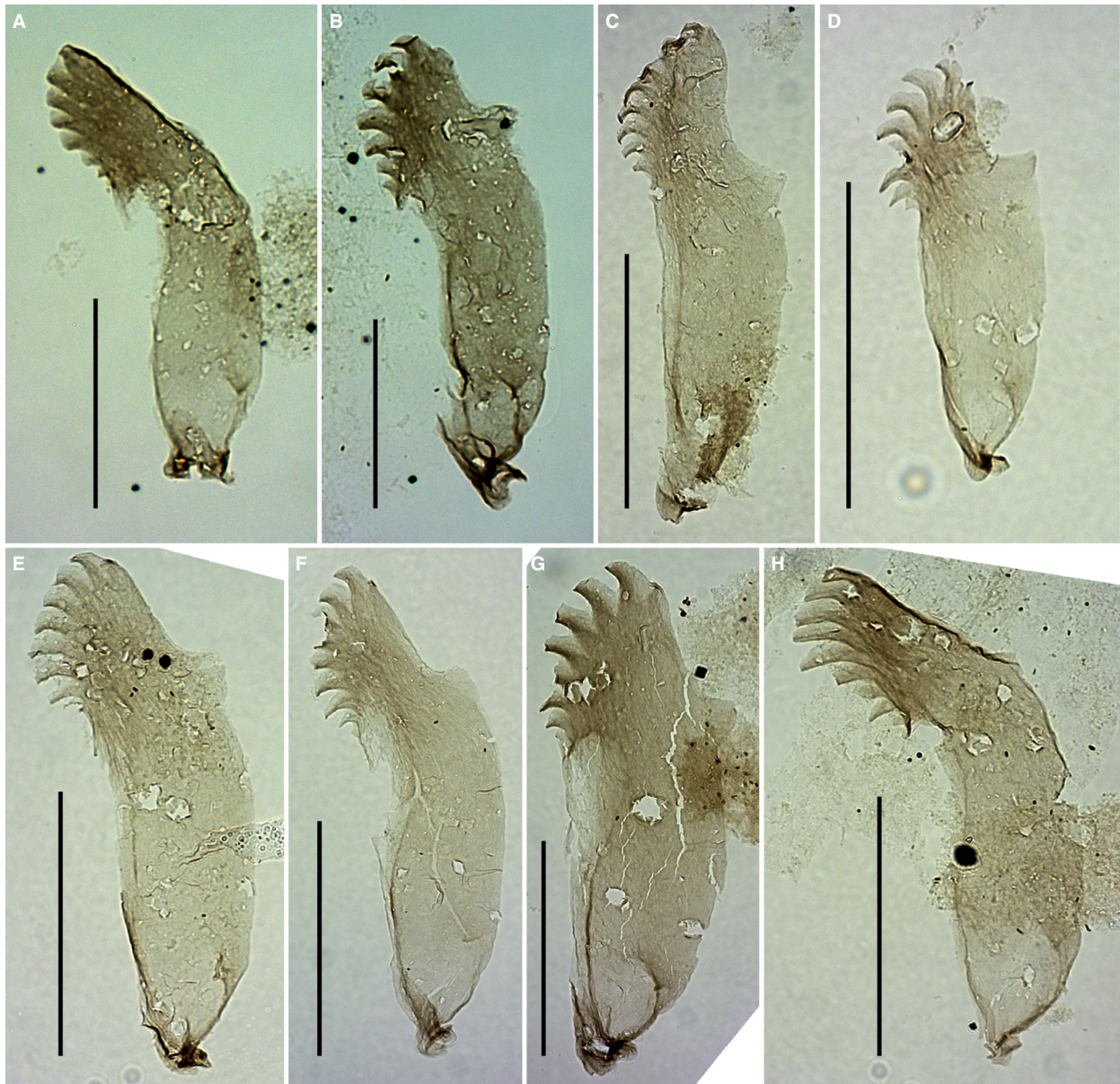


Fig. 3. Possible euechelicerate coxae from the Winneshiek Shale. Repository numbers are followed by sample numbers (with slide number in parentheses) and England Finder Graticule coordinates. Scale bars = 50 μm . A, SUI 143587-1, WS-18(1), E26. B, SUI 143587-2, WS-18(1), V29/1. C, SUI 143647-2, WS-6(1), P39. D, SUI 143627-1, WS-10(1), M45/4. E, SUI 143617-1, WS-12(2), W53/2. F, SUI 143607-1, WS-14(1), G49. G, SUI 143637-1, WS-15(1), O45/4. H, mirrored, SUI 143622-1, WS-11(1), G24. [Colour figure can be viewed at wileyonlinelibrary.com]

site of muscle insertion and the pointed tip (Fig. 4, a) as the principal articulation point. The toothed extension (Fig. 4, t) would represent the gnathal edge, which in life would be situated close to the mouth to process food and pass it towards the oesophagus. The second, smaller and more distal opening (Fig. 4, s) could be the attachment site for a mandibular palp. The protuberance adjoining this attachment site (Fig. 4, p) could conceivably represent a second articulation point reflecting a dicondylar structure.

However, several features call into doubt a mandibular identity. First, the gnathal edge is not obviously divided into a molar process (typically used for grinding) and an incisor process (for biting/cutting). This would be atypical, though not unknown: the mandibles of many copepods and some branchiopods (notably notostracans and laevicaudatans) have an undivided toothed or ridged gnathal edge (e.g. Edgecombe *et al.* 2003; Richter 2004). Intriguingly, the mandibles of dipluran hexapods can have a 'shovel-like' gnathal edge with

curved, faceted teeth not dissimilar to those in the fossils, and lack a differentiated molar region (cf. Koch 2001; their figs 15, 16). However, the pronounced curvature of the tooth row in the fossils is more problematic. Mandibular gnathal edges are almost always much straighter, presumably reflecting constraints imposed by having to fit closely with the gnathal edge of the opposing mandible, combined with the angle of swing. Furthermore, the position of the second opening would be unusually distal were it for insertion of a mandibular palp. And if the protuberance were interpreted as a second articulation point, it would seem too far removed from the proximal muscle attachment site to constrain the mandible during rolling motions (based on comparisons with dicondylar mandibles in basal hexapods; see Blanke *et al.* 2015).

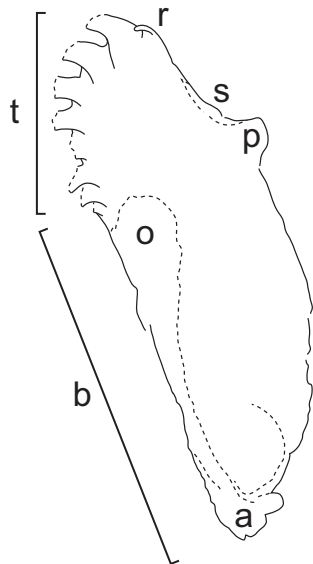


Fig. 4. Line drawing of the possible euchelicerate coxae in Figure 3G with main morphological features marked. a = proximal articulation; b = basal/proximal part; o = main opening; p = protrusion; s = secondary opening; t = toothed edge; r = rudimentary tooth.

A more compelling comparison is with the leg bases of certain euchelicerates, which like mandibular coxae have a proximal opening for muscle insertion and a toothed edge (= gnathobase) for food-processing, but have different topological relationships among the functional parts. This can be seen in xiphosurans and eurypterids. Xiphosurans are commonly divided into xiphosurids (the clade including modern horseshoe crabs) and synziphosurines. Lamsdell (2013) determined the latter to be a paraphyletic grouping of euchelicerates. The oldest xiphosurid and the oldest synziphosurine (both as yet undescribed; Fig. 7C, E) were both found in the Lower Ordovician Fezouata Formation of Morocco (Van Roy *et al.* 2010; Briggs *et al.* 2012). The next youngest xiphosuran on record is the xiphosurid *Lunataspis aurora* Rudkin *et al.* 2008 (Fig. 7F) from the Upper Ordovician William Lake and Airport Cove Lagerstätten in Manitoba, Canada. Eurypterids and synziphosurines are extinct, but the leg bases of the four extant species of xiphosurids (horseshoe crabs) still exhibit the characteristic features. The American horseshoe crab *Limulus polyphemus* Linnaeus, 1758 (Figs 6C, 7G) is particularly well studied. The coxa of each walking leg is extended into an elongate sub-triangular element with a long dorsal slit-like opening for muscle insertion, and a recurved spiny gnathobase is positioned near the mouth and used for food-processing, and a second, smaller opening ventrally for the insertion of the walking limb (trochanter attachment) (see Hayes & Barber 1967; their fig. 1, for detailed anatomy including musculature in *Limulus*; and Yamasaki *et al.* 1988; their fig. V-13, for shape variation among taxa). Importantly, the spiny margin of the gnathobase may be strongly curved, and the trochanter attachment is located adjacent to the gnathobase, associated with a concave depression and a marginal protuberance – just as in the Winneshiek fossils. Furthermore, the pinched proximal articulation

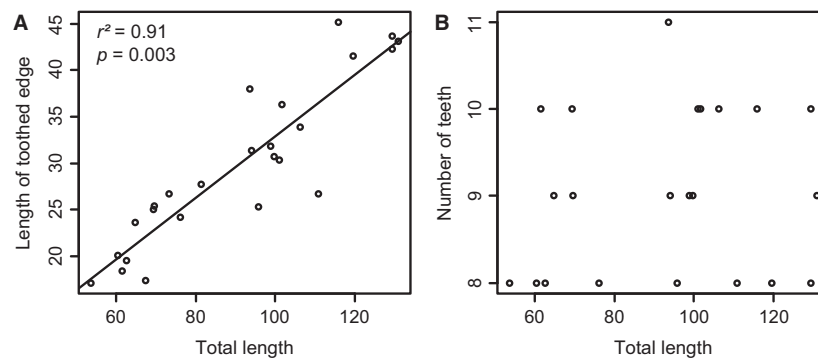


Fig. 5. Scatterplots of morphometric values of possible euchelicerate coxae. A, total length versus length of toothed edge ($n = 25$). B, total length versus number of teeth ($r^2 = 0.14$; $P = 0.523$; $n = 22$).

extends in *Limulus* in a short, angled projection of complex three-dimensional morphology (the pleuro-coxal articulation), potentially accounting for the variably deformed projections in the equivalent position in the fossils (Fig. 4, a). Overall, despite various differences in overall outline and gnathobase armature, the topological relationships between parts in the fossils are more closely comparable to xiphosurid coxae than pancrustacean mandibles.

Among extinct aquatic chelicerates, broadly comparable gnathobasic appendages are known to occur in synziphosurines and eurypterids. Details of the legs of the synziphosurine *Dibasterium durgae* Briggs *et al.* 2012 (Fig. 7D) from the Silurian Herefordshire Lagerstätte were preserved in high detail and three dimensions (Briggs *et al.* 2012). However, the biramous legs and specifically the leg bases of *D. durgae* were markedly different from our mouthparts and present-day horseshoe crabs. Eurypterid coxae differ from the mouthparts discussed herein in their overall shape, the position of the toothed edge on and its orientation perpendicular to the long axis, as well as the distance between the coxotrochanteral joint and the toothed edge (e.g. Selden 1981; Lamsdell *et al.* 2015a).

While the lack of comparable fossils of xiphosurids in particular makes a certain identification based solely on the leg bases impossible, the characteristics of the Winneshiek mouthparts are sufficiently distinct to argue for a euchelicerate affinity, with a closer relationship to xiphosurids than to eurypterids, based on similarities with the coxae of *Limulus polyphemus*.

Discussion. – The fossils are conspicuously small. The width of the smallest specimens is close to the

15 μm mesh size of the filter, and even smaller specimens might not have been retained. The extremely small size, limited size range and lack of other appendage components would fit well with a mandibular identity. For example, in Cambrian SCF assemblages, mandibles are often the most abundant arthropodan components and can be preserved in a similar manner, that is with the coxal body as well as the gnathal edge (see for example the ostracodan mandible described by Harvey *et al.* 2012b; their fig. 1P). The sizes are in the range of *Daphnia* (water flea; Fig. 7B) mandibles, relating to animals with a carapace length of a few millimetres (Edwards 1980).

A xiphosurid-like producer of the Winneshiek mouthparts would have been much smaller still. Assuming proportions similar to modern-day horseshoe crabs (with a coxal length to prosomal width ratio of about 3:10 as in *Limulus*), the largest specimen (Fig. 3B) would correspond to a prosoma of about 450 μm width (Fig. 7A). The whole animal might have had a total length of around 1 mm, smaller than newly hatched modern horseshoe crabs. The first instars of *Limulus polyphemus* are the smallest among the four extant species, with a prosomal width of 2.7–3.7 (mean 3.3) mm (Sekiguchi *et al.* 1988; Shuster & Sekiguchi 2003). Most Palaeozoic xiphosurans were significantly smaller than present-day horseshoe crabs (compare Fig. 7C–F, G). The oldest known synziphosurine (see Van Roy *et al.* 2010) was two orders of magnitude smaller than adult *Limulus* (Fig. 7C), comparable to a larger cladoceran (Fig. 7B). Considering the observed size range, it is prudent to assume that most, and probably all, of our specimens represent juvenile stages. With the available material, it is not possible to determine whether there was a growth limit in effect,

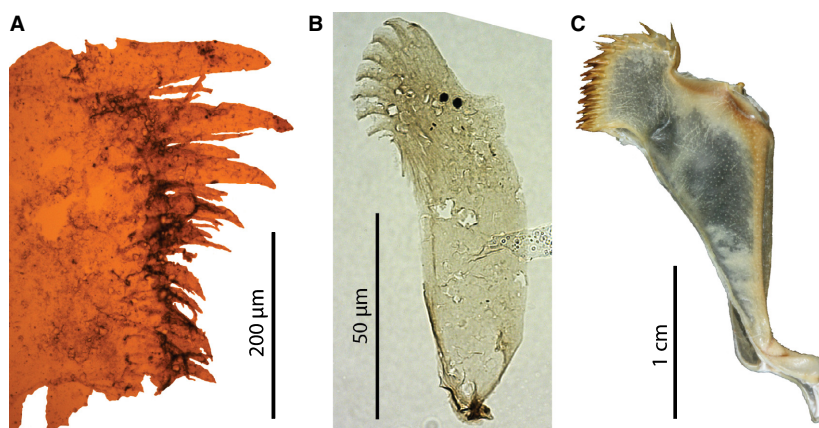


Fig. 6. Euchelicerate coxae. A, gnathobase of a eurypterid coxa from the Winneshiek Shale, SUI 143688-3, borehole H2, depth 15 ft (ca. 4.6 m). B, possible euchelicerate coxa from the Winneshiek Shale (same as Fig. 3E), SUI 143617-1, WS-12(2), W53/2. C, exuvial coxa of a juvenile *Limulus polyphemus* Linnaeus, 1758 (modern Atlantic horseshoe crab). [Colour figure can be viewed at wileyonlinelibrary.com]

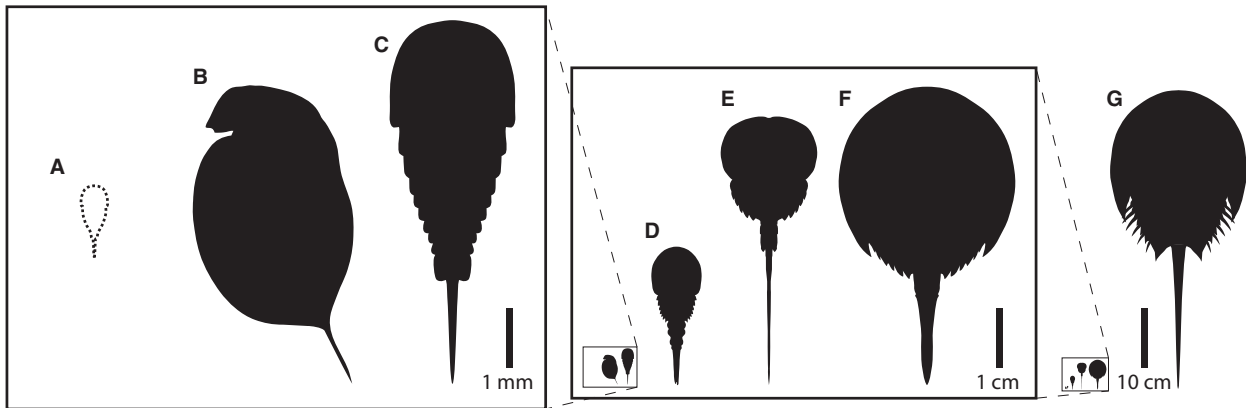


Fig. 7. Size comparison. A, the approximately reconstructed producer of the possible euchelicerate coxae from the Winneshiek Shale. B, *Daphnia magna* Straus, 1820 (large water flea), R recent. C, unnamed synziphosurine from the Fezouata Shale, Lower Ordovician, Morocco (after Van Roy *et al.* 2010). D, *Dibasterium durgae* Briggs *et al.* 2012, synziphosurine from the Herefordshire Lagerstätte, Silurian, UK. E, unnamed xiphosurid from the Fezouata Shale, Lower Ordovician, Morocco (after Van Roy *et al.* 2010). F, *Lunataspis aurora* Rudkin *et al.* 2008, Upper Ordovician, Manitoba, Canada. G, *Limulus polyphemus* Linnaeus, 1758 (Atlantic horseshoe crab), Recent.

or adult specimens were not observed because they are too rare or dwelled in a different habitat. It is also possible that all the specimens were transported and size-sorted, which would partly account for the lack of other body parts as well.

Chelicerates were found as macrofossils in the Winneshiek in the form of eurypterids (Lamsdell *et al.* 2015a) and the dekatratan *Winneshiekia youngeae* Lamsdell *et al.* 2015b. The coxae of the eurypterid *Pentecopterus decorahensis* Lamsdell *et al.* 2015a are known in detail and differ considerably from the microfossils and between appendage pairs. The identified specimens of *Winneshiekia* do not show preserved legs. Known specimens of both *Pentecopterus* and *Winneshiekia* are much larger than the bearer of the microscopic appendages would have been, but we do not know all the developmental stages of these animals.

Overall, we can say that the best anatomical correspondence is with euchelicerate coxae, but this requires a severe taphonomic filter to produce the observed size limit and size variation. Perhaps this is related to the original biology, if the spawning grounds or preferred environments of very young juveniles of these animals were closeby. Modern horseshoe crabs lay their eggs on specific shores (Brockmann 2003), and juveniles can be found most frequently in nearshore environments (Rudloe 1981). Eurypterids may have behaved similarly (mass-moult-mate hypothesis: Braddy 2001; Vrazo & Braddy 2011). Compared with other animal remains in the studied samples and considering the small sample sizes, the possible euchelicerate coxae are recurring with unusual regularity, if not (at this point) in high absolute numbers. However, until now, they were not found in articulation with other

body parts and no other microfossils in the assemblage matches them in colour, structure or frequency. They are most likely disarticulated moults, which possibly suffered a biostratinomic bias (current driven size-sorting; cf. Vrazo & Braddy 2011). They might also have been the most recalcitrant part of an otherwise hardly preservable organism. Harvey & Pedder (2013) made a similar observation about mandibles in Cambrian SCF assemblages.

Conclusions

The fossils presented herein cannot be assigned to any of the known macrofossils of the Winneshiek Shale. They appear to represent diminutive arthropods with a low preservation potential. Most likely, they include filter plates of a filter-feeding crustacean and coxae of a horseshoe crab-like chelicerate. The taphonomic history of the Winneshiek SCFs that allowed their preservation with finest details may have been similar to that of crustacean remains from the Cambrian of Canada reported from the Mount Cap Formation (lower Cambrian), the Deadwood Formation (middle-upper Cambrian), the Earlie Formation (middle Cambrian) and the Nolichucky Shale (middle-upper Cambrian) (Harvey & Butterfield 2008; Butterfield & Harvey 2012; Harvey *et al.* 2012a,b; Harvey & Pedder 2013). The fossil record of crustaceans in the Ordovician is largely represented by easily preserved ostracod shells and phyllocarid carapaces (Sepkoski 2000; Vannier *et al.* 2003; Racheboeuf *et al.* 2009; Perrier *et al.* 2015). Exceptionally preserved specimens from Konservat-Lagerstätten can contribute enormously to fill some gaps in the fossil record. Our findings demonstrate

how palynological studies can broaden our understanding of the diversity of ancient biota, even with a standard protocol, under favourable diagenetic conditions. The Winneshiek Shale in particular has proven to be an exceptional source of organic-walled microfossils, which is not exhausted by far, and of which we have presented only examples herein. But also regular palynological assemblages sometimes contain elements that are both hard to identify and rare, and are consequently often ignored in favour of the more readily useful classical palynomorph groups. However, these Microproblematica can hold information that we would otherwise miss. A major problem with the interpretation of such rare microfossils is the dearth of fossil material for comparison. Hopefully, this can be alleviated gradually, as similar findings are published. We advocate further SCF processing alongside standard palynological analysis with special attention to problematic findings, plus close examination of macrofossils to describe microscopic anatomy. Together, these complementary preservational modes promise to yield new insights into ontogeny, palaeoecology and diversity.

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