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Bivalved arthropods from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA

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Abstract.—The Middle Ordovician (Darriwilian) Winneshiek Lagerstätte of northeast Iowa is preserved in a meteorite crater. Besides conodonts, the fossils are dominated by arthropods, particularly eurypterids and phyllocarids. Here we describe the bivalved forms, which include at least seven different taxa. The small phyllocarid *Ceratiocaris winneshiekensis*, new species, is the most abundant; it is the oldest representative of the Ceratiocarididae. A single incomplete abdomen and telson bearing furcal rami is reminiscent of notostracan branchiopods but its affinities are unknown. *Decoracaris hildebrandi*, new genus and species, is a rare form with a shield that extends anteriorly into a swollen horn and reaches lengths of 9 cm: it may represent a thylacocephalan crustacean but this cannot be confirmed without soft parts. *Iosuperstes collisionis*, new genus and species, is represented by suboval valves 10–25 mm long: its affinities are unknown. A probable leperditicopid, which ranges in length from 8 to 18 mm, is commonly preserved in a 'butterflied' configuration. It does not preserve the scars and sinuses characteristic of three-dimensionally preserved leperditicopids from elsewhere. Finally the fauna includes at least three ostracods, including a palaeocope with a granular surface and relief similar to *Lomatopisthia*, and a smooth ?podocope. The Winneshiek fauna differs from those of other Ordovician Lagerstätten from restricted settings such as Airport Cove and William Lake in Manitoba (Katian) where, apart from ostracods, bivalved arthropods are absent, and Silurian examples such as Brandon Bridge (Telychian), which lacks eurypterids, and the Williamsville Member of the Bertie Formation (Pridoli) where conodont assemblages are absent.

Introduction

Exceptionally preserved fossil faunas (Konservat-Lagerstätten) are rare in the Ordovician (Allison and Briggs, 1993). Conditions during the Cambrian appear to have favored the preservation of soft-bodied fossils: at that time, the oceans were relatively low in sulfate and high in alkalinity that served to slow decay while promoting early cementation of the sediment (Gaines et al., 2012). Thus, some 50 Burgess Shale-type preservations (an approximate figure, which depends on how such biotas are enumerated) are known from Cambrian sequences. This taphonomic window appears to have persisted into the early Ordovician—a spectacular and diverse soft-bodied fauna is known from the Fezouata formations of Morocco, which are Tremadocian/Floian in age (Van Roy et al., 2010). Exceptional preservations are rare, however, through the rest of the Ordovician and any deposit that preserves lightly sclerotized or soft-bodied fossils provides an important window on biodiversity. The best known Lagerstätten are offshore marine and late Ordovician in age: Beecher's Bed near Rome, Upper New York State (Briggs et al., 1991b) is Katian and the Soom Shale in South Africa (Aldridge et al., 1994, 2001) is Hirnantian. The Winneshiek Lagerstätte of Iowa preserves an unusual fossil assemblage in finely laminated organic rich shales in a restricted nearshore setting (Liu et al., 2006) created by flooding of a meteorite impact crater.

Larger bivalved arthropods are relatively rare in Paleozoic shallow marine deposits because their cuticles are often thin or even exclusively organic. However, bivalved arthropods may be abundant where conditions for preservation are favorable. *Canadaspis perfecta*, for example, is the second most common arthropod in the Cambrian Burgess Shale at Walcott's Quarry (Conway Morris, 1986) and caryocaridids are widely distributed in Ordovician graptolitic shales (Vannier et al., 2003; Racheboeuf et al., 2009). Thus, the prevalence of phyllocarids in fine grained laminated lithologies such as in the Winneshiek Lagerstätte may reflect a taphonomic bias. The diversity of bivalved arthropods in the Winneshiek Lagerstätte is unusual, although specimens preserving appendages are very rare.

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Locality and geologic setting

The Winneshiek Lagerstätte was discovered in 2005 during geological mapping of the Upper Iowa River basin as part of multifacetted research by the Iowa Geological Survey. The fauna is preserved in the Winneshiek Shale (Wolter et al., 2011), a newly named formation 18 to 27 m thick (McKay et al., 2011). The lithology is a greenish brown to dark grey laminated sandy shale, of Middle Ordovician (Whiterockian, Darriwilian) age. The Winneshiek Shale is overlain disconformably by the St. Peter Sandstone, and overlies an unnamed thick massive breccia (Liu et al., 2009). The Winneshiek Shale crops out only in the channel of the Upper Iowa River near Decorah, where it is mostly submerged. Detailed field investigation and systematic sampling were carried out in the summer of 2010 by damming part of the channel and systematically excavating the exposed section with the aid of heavy machinery.

The extent of the Winneshiek Shale sequence was documented mainly in cores from two bore holes as well as a gamma log from an additional hole located close to the exposure. More than 20 other wells in the area also penetrate sections of Winneshiek Shale, where evidence from rock chips retrieved revealed details of the local stratigraphy (Liu et al., 2009, fig. 7). Although bore hole data indicate that the total thickness of the Winneshiek Shale is about 18 m at the collecting locality, most of the specimens described here are from the lower portion of the topmost 4 m, which was extracted in blocks from the river bed immediately below the overlying St. Peter Sandstone (labeled WS). Other samples were collected from blocks eroded during flooding, which are assumed to have been sourced from the uppermost 2–3 m (labeled WL).

The Winneshiek Shale and the breccia underlying it are confined to a circular basin approximately 5.6 km in diameter in the Decorah area. Multiple lines of evidence indicate that the basin originated as a meteorite impact crater (Liu et al., 2009; McKay et al., 2011). This structure, called the Decorah Impact Structure, has been confirmed by geophysical surveys (Koontz and McKay, 2013). Considerations based on the fossil content and paleogeography indicate that the crater environment was one of marginal to nearshore marine conditions with low-oxygen possibly brackish water, within tropical southern Laurentia (Liu et al., 2007, 2009; Witzke et al., 2011). Where rhythmic sandy-silty laminations occur within the shale they may indicate a local tidal influence (Liu et al., 2007, 2009; Witzke et al., 2011). The Winneshiek fauna is characterized by an assemblage of well-preserved fossils that is dramatically different from a normal marine fossil fauna in lacking shelly taxa such as trilobites and cephalopods (Liu et al., 2006, 2009). Arthropods make up the dominant and most diverse invertebrate group.

Materials and methods

The site on the Upper Iowa River near Decorah was dammed in 2010 and approximately 5,000 pounds (2,270 kg) of Winneshiek Shale were collected and transported to the Iowa Geological Survey storage and research facility at Oakdale, Iowa. The bulk rock was kept in water prior to splitting to prevent it drying out and fragmenting. The rock was split and carefully examined with binocular microscopes over the next three years by teams of trained students under the direction of H. Liu. The material yielded over 5,000 fossil specimens (n = 5,354) of which about 51% are conodonts (including assemblages), 26% are various bromalites, 6.6% are eurypterid parts (Lamsdell et al. 2015a), and 7.9% are phyllocarids. The rest of the collection comprises other bivalved arthropods (1.6%), a basal euchelicerate (Lamsdell et al. 2015b), linguloid brachiopods, fish material, a single gastropod, and some unknown forms. The type, figured, and other identified specimens are held by the University of Iowa Paleontology Repository, Department of Earth and Environmental Sciences, University of Iowa (SUI), 115 Trowbridge Hall, Iowa City, Iowa 52242.

Systematic paleontology

Crustacea Brünnich, 1772
Phyllocarida Packard, 1879
Family Ceratiocarididae Salter, 1860
Genus *Ceratiocaris* M'Coy, 1849

Type species.—*Ceratiocaris solenoides* M'Coy, 1849

Ceratiocaris winneshiekensis new species
Figures 1.1–1.15, 2.1–2.11, 3
2006 Phyllocarid Liu et al., fig. 2G.
2009 Phyllocarid Liu et al., pl. 1, figs. 1,2.

Holotype.—SUI 102858 (WL).

Other material.—SUI 138433-138442 (WL); SUI 138443-138451 (WS). SUI 138446 is a coprolite containing the remains of phyllocarids.

Diagnosis.—Small *Ceratiocaris* with smooth shield, ventral ridge, and telson approximately three times the length of the furca.

Description.—Most specimens of this small phyllocarid preserve the shield and trunk somites, but evidence of the appendages has only been observed on a few specimens (e.g., Fig. 1.1–1.4).

The majority of specimens are flattened in lateral or near lateral aspect (Fig. 1.1–1.4); dorso-ventral flattening is rare (Fig. 1.5–1.7) and a butterflied configuration (i.e., valves symmetrical about the hinge line and preserved with the outline more or less entire) has not been observed. The cuticle of the exoskeleton displays crumpling and folding, implying some flexibility. Adjacent specimens are preserved in different orientations to bedding indicating that the light delicate carcasses settled on the sediment surface in different attitudes. SUI 138433 (Fig. 1.5, 1.6) is a dorso-ventrally flattened specimen (see also Fig. 1.7): the gut trace runs along the mid line and the telson is flanked symmetrically by the furcal rami (Fig. 1.5, 1.6). It is clear that the valves were not wide (i.e., inflated laterally) when viewed in dorsal or ventral aspect. The pleon is usually inclined to the hinge line at an angle of

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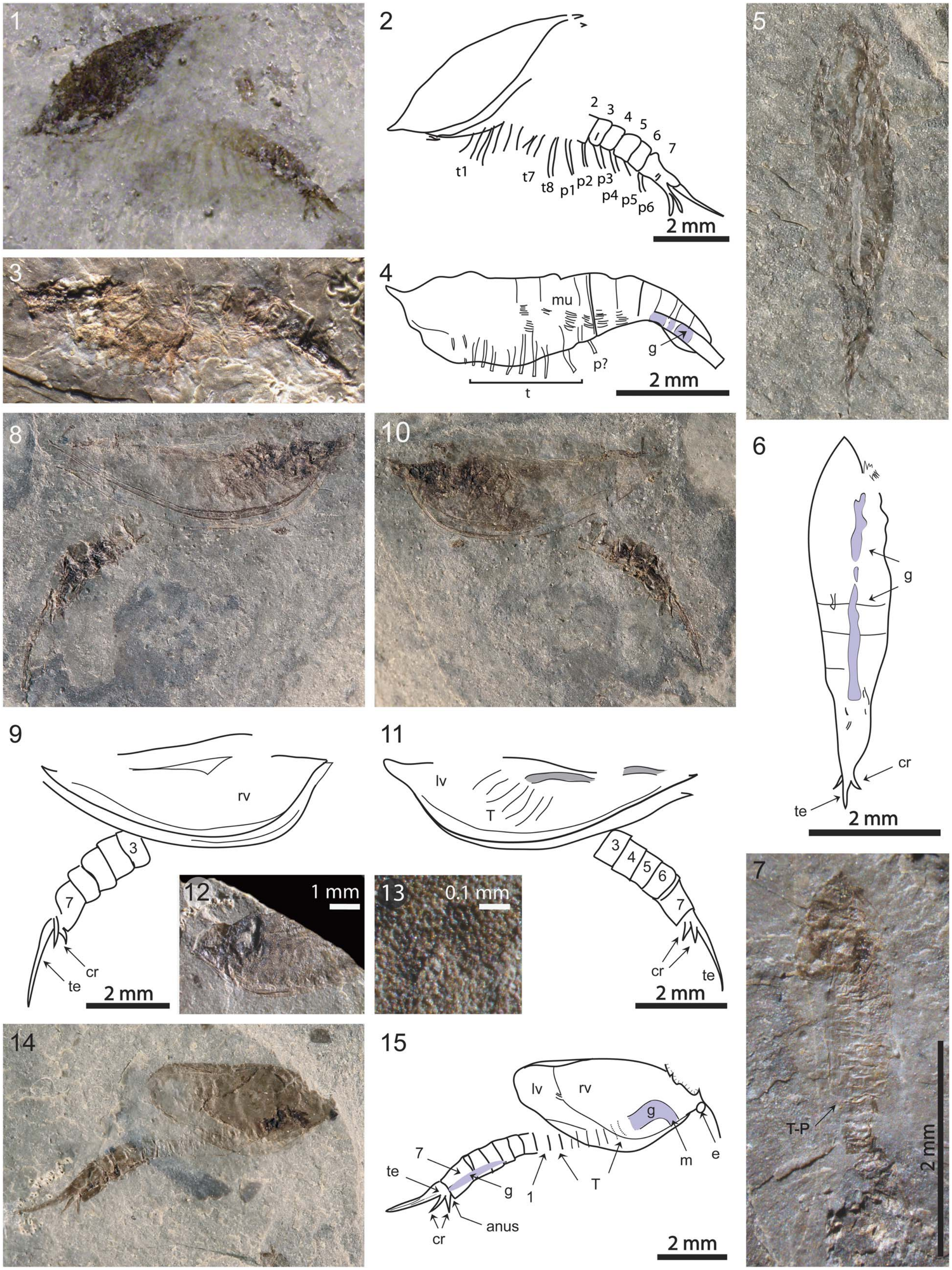

Figure 1. *Ceratiocaris winneshiekensis* n. sp.: (**1, 2**) holotype, SUI 102858, left lateral, preserving appendages; (**1**) part, and (**2**) explanatory drawing; (**3, 4**) SUI 138443, left lateral, preserving appendages; (**3**) part, and (**4**) explanatory drawing; (**5, 6**) SUI 138433, dorsoventrally flattened showing gut; (**5**) part, and (**6**) explanatory drawing; (**7**) SUI 138437b, oblique, shield foreshortened exposing thorax wider than pleon; (**8, 9**) SUI 138436, right lateral; (**8**) specimen, and (**9**) explanatory drawing; (**10, 11**) SUI 138442, left lateral; (**10**) specimen, and (**11**) explanatory drawing; (**12, 13**) SUI 138437a, left lateral; (**12**) incomplete left valve; (**13**) exfoliated surface showing internal polygonal structure; (**14, 15**) SUI 138435, right lateral oblique showing thorax; (**14**) specimen, and (**15**) explanatory drawing. cr, caudal rami; e, eye; g, gut trace, lv, left valve; m, mouth; mu, trunk muscles; p1 etc., limbs of pleon; rv, right valve; te, telson; t1 etc., thoracic limbs; T, thoracic somites; T-P, boundary between thorax and pleon; 1–7 somites of pleon.

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approximately 40° (Fig. 1.8–1.11) but some specimens preserve the valves flipped upward to varying degrees (e.g., Fig. 1.1, 1.2) in an attitude reminiscent of molt configurations. The prevalence of gut traces extending anteriorly well beyond the telson, however, indicates that the specimens are carcasses (Rolfe 1962b, p. 913), and the attitude may be a result of decay. Where the shield is exfoliated (Fig. 1.12, 1.13) it reveals a reticulate structure below the surface made up of polygons of the order of 30 to 50 μm across which may reflect a prismatic structure of the cuticle.

The valves are fusiform or lemon shaped in lateral view (Fig. 1.1, 1.2, 1.8–1.11). The hinge line is gently convex, the ventral margin more strongly so. The hinge-line projects anteriorly into a triangle or horn that tapers to a narrow rounded apex (Fig. 1.1, 1.2, 1.10, 1.11). There is no evidence of a separate rostrum, nor has it been identified in isolation. Posteriorly the hinge terminates in a sharp spine-like projection (Fig. 1.1, 1.8–1.11). The maximum height of the valves is anterior of the mid-length (preplete in ostracod terminology) (Fig. 1.8–1.11, 1.14, 1.15). The outline of the valves varies depending on the attitude of the specimen to bedding. This is illustrated by comparing the more usual outline with the maximum height anterior of the mid length (Figs. 1.8–1.11, 1.14, 1.15, 2.1, 2.2) with SUI 138448 (Fig. 2.3, 2.4) where the maximum height is behind the mid length. There is some evidence that the valves became more elongate as they increased in size (Fig. 2.5, 2.6) but in other specimens they are foreshortened by flattening (Fig. 2.7, 2.8). A narrow marginal ridge runs along the edge of the valves (Fig. 1.8, 1.9). A ventral ridge runs close to this margin converging with it anteriorly and posteriorly (Fig. 1.8–1.11). The ratio of length to height of the valves increases in larger specimens but this can only be measured in a small number of

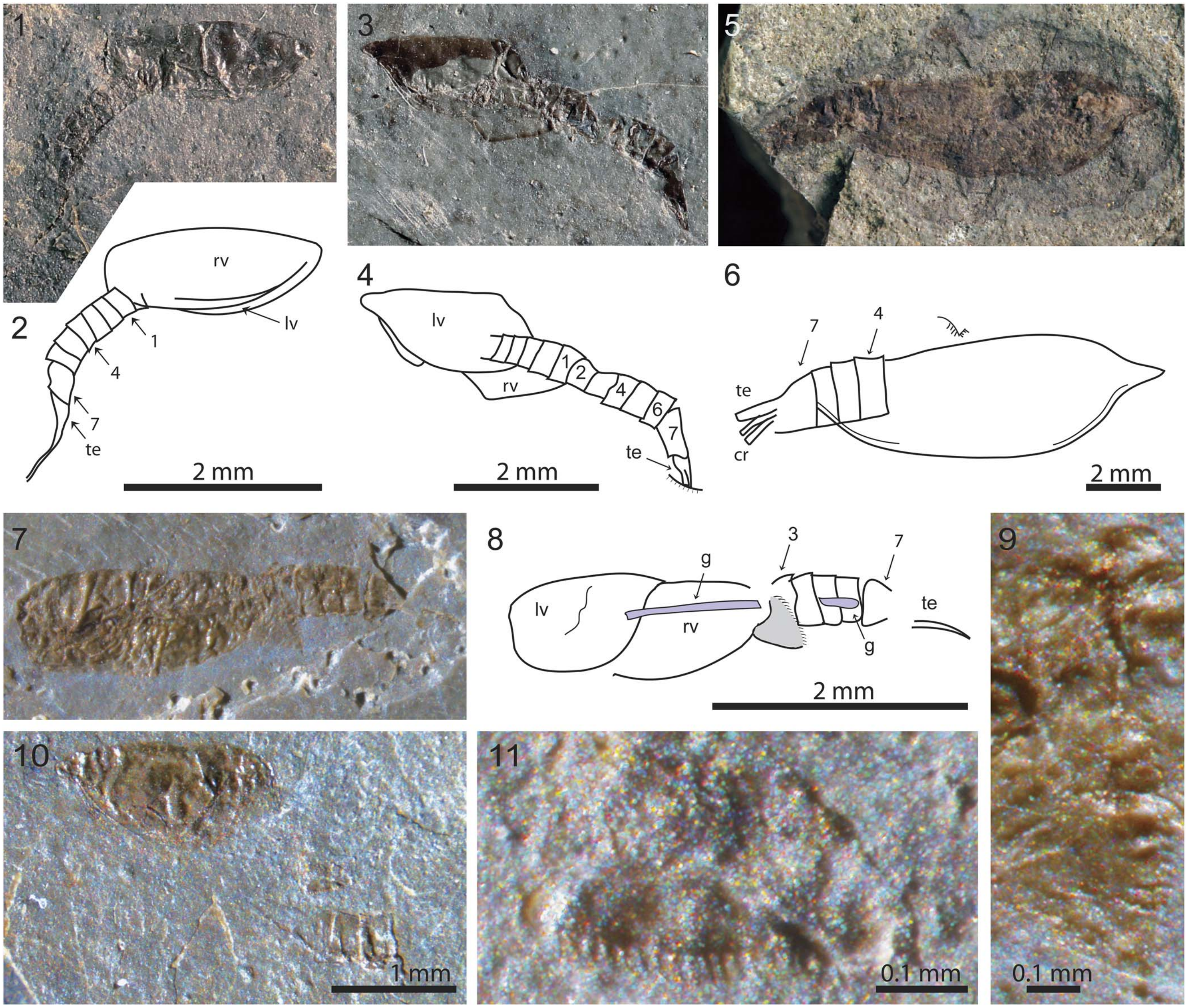

Figure 2. *Ceratiocaris winneshiekensis* n. sp.: (**1, 2**) SUI 138447, right lateral; (**1**) specimen, and (**2**) explanatory drawing; (**3, 4**) SUI 138448, left lateral; (**3**) specimen, and (**4**) explanatory drawing; (**5, 6**) SUI 138439, right lateral; (**5**) part, and (**6**) explanatory drawing; (**7–9**) SUI 138444, left lateral, valves offset; (**7**) specimen; (**8**) explanatory drawing; (**9**) isolated structure with denticles, shaded in Figure 2.8 where it overlies the rear of the right valve and somite 3 of the pleon; (**10, 11**) SUI 138437c; (**10**) disarticulated left valve, partial pleon and associated structure with denticles; (**11**) denticulated structure. cr, caudal rami; g, gut trace, lv, left valve; rv, right valve; te, telson; 1–7 somites of pleon.

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examples and is influenced by attitude to bedding: compare Figure 2.1, 2.2 at ~2.75 mm long with Figure 2.5, 2.6 at ~ 9.2 mm long, both with a height of ~1 mm (SUI 138442, not figured, is 6.7 mm long and 1.4 mm high).

Details of the head are rarely preserved, but extrapolation based on the distribution of appendages or segments (Fig. 1.1, 1.2, 1.14, 1.15) indicates that it was similar in length to the thorax; it appears to be shorter than the thorax in SUI 138443 (Fig. 1.3, 1.4) although the boundary is difficult to discern. The gut trace in SUI 138435 extends posterodorsally from the presumed position of the mouth and curves posteriorly to run the length of the trunk (Fig. 1.14, 1.15). A small dark circular structure overlapping the antero-ventral margin of the right valve in this specimen may represent the eye (Fig. 1.14, 1.15). The posterior appendages of the head may be preserved in outline in SUI 102858 and SUI 138443 (Fig. 1.1–1.4); the boundary between head and thorax in these specimens is not clear.

The thorax consists of eight somites that are normally largely concealed by the shield (Fig. 1.15). Where they are exposed they are not as well preserved as those of the pleon indicating that the cuticle was thinner, particularly in the more anterior part of the thorax, where they were protected by the shield (Fig. 1.7, 1.14, 1.15). Where traces of divisions are preserved (Figs. 1.14, 1.15, 2.3, 2.4) it is clear that the somites of the thorax are shorter than those of the pleon. Such traces rarely indicate the full height/width of the thorax but where the somites are exposed beneath the valves in SUI 138437b (Fig. 1.7) it appears that the thorax was more than two times wider than the pleon; likewise, the traces of intersomite divisions in SUI 138442 show that the thorax was higher than the pleon (Fig. 1.10, 1.11). Traces of the divisions between the 8 thoracic somites are evident in SUI 138435 (Fig. 1.14, 1.15).

Most specimens are preserved with the pleon, and sometimes part of the thorax (Fig. 1.1, 1.2, 1.14, 1.15), extending beyond the valves. The somites of the pleon are cylindrical in cross-section and similar in length to each other, apart from the seventh, which is approximately twice as long as the rest (Figs. 1.14, 1.15, 2.3, 2.4). SUI 138443 is unusual in preserving traces of ventral longitudinal muscles, arranged in segmental bundles, in the posterior somites of the thorax and anterior somites of the pleon (Fig. 1.3, 1.4). This segmental arrangement is reminiscent of that in living *Nebalia* (see Hessler, 1964, fig. 46). Investigation of these structures with the environmental scanning electron microscope revealed them to be 3–6 μm wide with the appearance of myofibrils and arranged in open bundles. Neither ultrastructural details nor microbes were observed. EDAX revealed significant calcium and phosphate (presumably apatite) in these muscles within a signature dominated by clay components. Higher peaks of calcium and phosphorus were obtained from the gut contents whereas the adjacent matrix, in contrast, contains negligible calcium or phosphorus.

An isolated incomplete subtriangular structure bearing rows of closely spaced denticles was found in association with two specimens. The larger example (Fig. 2.7–2.9), which overlies the anterior part of the pleon in SUI 138444, shows a row of larger denticles overlying a series of smaller ones (Fig. 2.9); the structure does not appear to belong to the specimen itself. The smaller example is associated with the disarticulated shield and pleon of SUI 138437c (Fig. 2.10, 2.11). These structures appear delicate compared to phyllocarid mandibles (Dzik, 1980). They might represent the furcal ramus of another taxon.

The gut trace runs through the ventral part of the pleon, terminating at the posterior extremity of the seventh somite, indicating the position of the anus (Fig. 1.14, 1.15). The telson extends beyond the posterior margin of the seventh somite a distance equivalent to more than the length of the preceding four somites of the pleon (Fig. 1.8–1.11, 1.14, 1.15). At least two ridges separated by a groove are evident running along the telson and there is a line of closely spaced setae at the proximal end (Fig. 1.14, 1.15). In some cases, the posterior part of the telson is flexed (Fig. 2.1, 2.2) or almost rope-like (Fig. 1.1, 1.2) presumably as a result of degradation. In specimens where the telson appears relatively short, the termination has been lost or is concealed in the matrix (e.g., Fig. 2.3, 2.4). Two short spine-like rami make up the caudal furca; a groove is evident running along the right one in SUI 138435 (Fig. 1.14, 1.15). The length of the caudal rami is approximately one-third that of the telson itself (Fig. 1.1, 1.2, 1.8–1.11, 1.14, 1.15).

Evidence of appendages has only been observed in a few specimens, including SUI 102858 (Fig. 1.1, 1.2) and SUI 138443 (Fig. 1.3, 1.4). The limbs of at least eight, maybe nine somites are evident in SUI 102858 in the thorax and posterior part of the head (Fig. 1.1, 1.2). Some of these appear paired or biramous. Elongate pleopods are present on the first six somites of the pleon, becoming smaller posteriorly. These are also paired or biramous. SUI 138443 preserves traces of limbs apparently corresponding to nine or ten somites in the head and thorax (Fig. 1.3, 1.4), most of them extending beyond the ventral margin of the valves; the pleopods are not preserved. Neither specimen preserves the antennae. No details of the limb morphology are evident.

The length of the shield of *Ceratiocaris winneshiekensis* varies from approximately 2.5 mm to approximately 10 mm.

SUI 138446 (Fig. 3) is a two-dimensional coprolite containing fragments of phyllocarid cuticle.

Etymology.—After the name of the formation in which the fossils occur.

Remarks.—*Ceratiocaris winneshiekensis* is the most abundant macrofossil (~16% if bromalites are included and individual

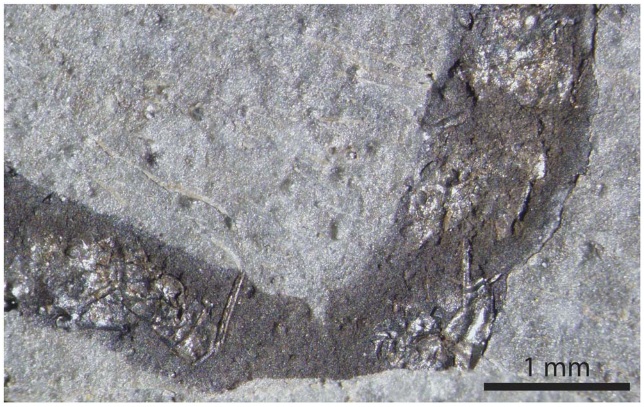

Figure 3. *Ceratiocaris winneshiekensis* n. sp.: SUI 138446. Portion of a coprolite (maker unknown) containing phyllocarid fragments.

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conodont elements are excluded) in the Winneshiek assemblage, and by far the most abundant bivalved arthropod in the fauna.

In the most recent review of Paleozoic phyllocarids Collette and Hagadorn (2010c, p. 802) diagnosed the genus *Ceratiocaris*, within Ceratiocaridina, by 'sinuous posterior carapace margin; carapace cuticle thin. Carapace ornamented with raised ridge ornamentation, roughly parallel to the ventral carapace margin.' The outline of *Ceratiocaris winneshiekensis* is consistent with this diagnosis, although it varies with attitude to the bedding as evidenced particularly by the height-length ratio. It differs from the bivalved shield of *Caryocaris* where the posterior margin is usually straight to oblique and typically fringed with spines (Collette and Hagadorn, 2010b). In contrast to other species of *Ceratiocaris*, however, some specimens of *C. winneshiekensis* show a ventral ridge, and the cuticle is smooth. The polygonal structure evident on some valves is an internal structure that emerges with exfoliation ('decortication' of Rolfe, 1962b, p. 916) and is similar in style and scale to that recorded in some specimens of the much larger *Ceratiocaris papilio* from the Silurian of Scotland (Rolfe, 1962c). The presence of a ventral ridge and absence of striae on *C. winneshiekensis* might be argued to provide a basis for erecting a new genus, but cuticle ornament varies with size even within species (Rolfe, 1962b).

The ratio of telson to furcal length is difficult to determine accurately in *C. winneshiekensis* but ranges from about 2.6 to 2.75, higher than that in other species of *Ceratiocaris* figured by Collette and Hagadorn (2010c, fig. 3) apart from *C. macroura* Collette and Rudkin, 2010a, and much higher than in *Caryocaris*, where the telson is equal to or shorter than the furcal rami (Collette and Hagadorn, 2010b). *C. winneshiekensis* and *C. macroura* also share the presence of lateral setae on the telson. *C. winneshiekensis* differs from *C. macroura*, however, not only in the presence of a ventral ridge and absence of cuticle ornament, but also in the more pronounced and pointed anterior projection of the valves and the greater width/height of the thoracic divisions relative to those of the pleon. We cannot discern any evidence of a rostral plate in *C. winneshiekensis* but this may be taphonomic. Collette and Hagadorn (2010c) regarded *Ceratiocaris silicula* from the Martinsburg Shale of Virginia (Caradoc-Ashgill – i.e., Sandbian and younger) as the oldest valid species of *Ceratiocaris*. Thus, the Winneshiek example is the earliest well documented representative of the Ceratiocarididae. Collette and Hagadorn (2010c) followed Rode and Lieberman (2002) in confining Ceratiocaridina to the family Ceratiocarididae.

Hannibal and Feldmann (1997) described two taxa of phyllocarids from core from the likely coeval Ames impact structure in Oklahoma. The first of these, which Hannibal and Feldmann (1997) referred to as 'resembling *Ceratiocaris*,' shares the valve outline, the presence of more robust cuticle on the pleon than the thorax, and the elongate telson, with the Winneshiek form. The telson of the Ames ?*Ceratiocaris* (Hannibal and Feldmann, 1997, figure 1), however, appears longer relative to the pleon than that of *C. winneshiekensis*. Racheboeuf et al. (2009, p. 402) regarded this Ames phyllocarid as a probable new archaeostracan (possible ceratiocarid). Phyllocarid taxonomy, at least at the species level, has been complicated by the erection of large numbers of species based on fragmentary material and inadequate criteria (Collette and Hagadorn, 2010c). Thus, pending a detailed description of the Ames ceratiocarid, we note that it is closely similar to the Winneshiek form. The second taxon from the Ames structure appears to be *Caryocaris*.

Only two other Paleozoic Lagerstätten preserve phyllocarids with traces of the limbs: the Silurian Herefordshire locality (*Cinerocaris magnifica*—Briggs et al., 2004) and the Devonian Hunsrück Slate (*Nahecaris stuertzi*—Bergström et al., 1987, and *Oryctocaris balssi*—Bergmann and Rust, 2014). In both cases, the taxa are larger and more details are available. In *C. magnifica*, the endopod of the last cephalic appendage is similar to those of the thorax, a condition that may also prevail in *Ceratiocaris winneshiekensis*. The Winneshiek phyllocarid does not preserve sufficient detail of the limbs to allow a comparison of their structure.

The phylogeny of phyllocarids has been subjected to a number of cladistic analyses, initially by Rode and Lieberman (2002), and subsequently by Briggs et al. (2004), Collette and Hagadorn (2010c), and Bergmann and Rust (2014). Rode and Lieberman (2002) demonstrated that traditional taxa were paraphyletic and redefined them to correspond to major clades: Ceratiocaridina, Pephricaridina, Rhinocaridina, and Echinocaridina. Briggs et al. (2004) obtained a similar result, but Pephricaridina fell out as a sister taxon to Echinocaridina. Collette and Hagadorn (2010c) extended these analyses with a comprehensive review of Ceratiocaridina and obtained a separate Caryocaridina. The phyllocarid phylogeny of Collette and Hagadorn (2010c) is similar to those obtained in the less comprehensive studies of Rode and Lieberman (2002) and Briggs et al. (2004) except that Pephricaridina fell out basal to Ceratiocaridina and Rhinocaridina rather than with Echinocaridina. Bergmann and Rust (2014) analysed a smaller number of taxa, including five genera not included in previous cladistic analyses, and used TNT rather than PAUP. They recovered Caryocaridina and Rhinocaridina but, in contrast to previous analyses, obtained paraphyletic Ceratiocaridina and Echinocaridina. The Winneshiek specimens do not provide sufficient new information to justify revisiting phyllocarid phylogeny.

The evidence of a coprolite containing fragments of *C. winneshiekensis* (Fig. 3) indicates that it was preyed upon, probably by larger arthropods or fishes.

Crustacea Brünnich, 1772
Family, genus and species indeterminate
Figure 4.1–4.3

Material.—SUI 138452 (WS).

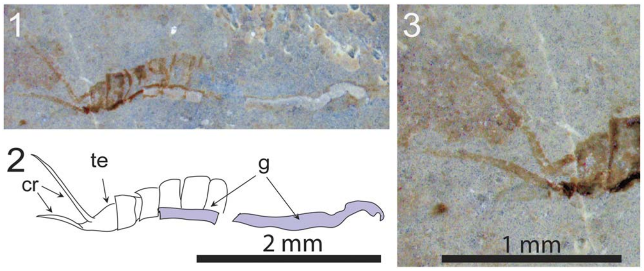

Figure 4. Undetermined trunk and telson: (**1–3**) SUI 1384552, right lateral; (**1**) specimen showing gut trace, rear abdominal somites and telson; (**2**) explanatory drawing; (**3**) telson showing multisegmented furcal rami. cr, caudal rami; g, gut trace, te, telson.

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Description.—A single tiny specimen preserves a gut trace, five abdominal somites, and a telson with caudal furca only (Fig. 4.1, 4.2). The telson does not project beyond the insertion of the furcal rami and the latter are long and multisegmented (Fig. 4.3).

Remarks.—The telson of this incomplete specimen reveals that it is not a phyllocarid. Multisegmented furcal rami are rare among living crustaceans where they tend to be diagnostic of notostracan branchiopods. Young et al. (2007, fig. 2) recorded a ?notostracan from the late Ordovician William Lake Lagerstätte in Manitoba but it has yet to be described. The oldest notostracan presently known is from the Upper Devonian Strud locality in Belgium (Lagebro et al., 2015) although molecular considerations indicate that notostracans could have originated by the Ordovician (e.g., Oakley et al., 2012). The telson of the unusual Early Ordovician arthropod *Douglasocaris collinsi* Caster and Brooks, 1956, from Tennessee is similar. Although Caster and Brooks (1956) assigned *Douglasocaris* to Phyllocarida, Rolfe (1969) thought it might belong with the notostracan branchiopods. Without evidence of the rest of the Winneshiek arthropod, it is not possible to determine its affinities.

?Crustacea Brünnich, 1772

?Thylacocephala Pinna, Arduini, Pesarini, and Teruzzi, 1982

Genus *Decoracaris* new genus

Type species.—*Decoracaris hildebrandi* new genus. new species

Diagnosis.—As for species.

Etymology.—From the locality Decorah combined with *caris* (L.), shrimp.

Decoracaris hildebrandi new genus, new species
Figure 5.1–5.5

Holotype.—SUI 138453 (WS).

Other material.—SUI 138454-138456 (WL); SUI 138457-138462 (WS) (SUI 138459 shows no obvious diagnostic ornament), and other fragmentary specimens.

Diagnosis.—Suboval valve more than two times longer than high, pronounced rounded anterior horn overlying shallow notch; fine anastomosing ridges around valve margin.

Description.—This large taxon is represented only by valves, which have a thick phosphatized cuticle. Flattening resulted in crushing and fragmentation, and the shale rarely split along the plane of the specimen. Usually only part of the valve outline is evident. For this reason, the description is based mostly on a single complete right valve (Fig. 5.1).

The valve of SUI 138453 is elongate suboval in outline, with an anterior horn (Fig. 5.1, 5.2). The maximum height of the valve, which occurs about the mid-length, is approximately 40% of the length. A straight hinge line runs about 75% the length of the valve. Beyond the hinge, the margin slopes down anteriorly to form a rounded anterior projection (horn) beneath which is a shallow notch (Fig. 5.1, 5.2). The ventral margin of the valve is gently convex, joining the short posterior margin, which makes an angle of approximately 115° with the hinge. The lack of distortion with flattening indicates that the relief on the valve was not very high; the vertical fold indicates that the maximum convexity was about the mid-length.

A marginal ridge, rounded on both outer and inner side, runs around the edge of the valve. Flanking this ridge, on the outer surface of the valve, is a rim about 1 mm wide which displays a sculpture of fine anastomosing ridges (Fig. 5.2). The remainder of the valve surface appears smooth.

The characteristic anastomosing sculpture allows other specimens to be identified with this taxon. SUI 138458 preserves part of the anterior of a right valve (Fig. 5.3, 5.4). It shows that the sculpted rim may be bounded on its inner margin by a shallow groove. This specimen also preserves a ventrolateral ridge running near-parallel to a short length of the margin (Fig. 5.3, 5.4), but this is not evident on all specimens (Fig. 5.1, SUI 138457, SUI 138461). SUI 138461 (not figured) preserves part of both right and left valves superimposed laterally, but partly offset, both showing marginal ornament and giving the impression of a ridge.

SUI 138453 (Fig. 5.1) is 88 mm long (maximum parallel to the hinge). The preserved portion of SUI 138456 (Fig. 5.5) is ~85 mm; the complete valve was slightly longer. None of the other specimens provides an indication of the complete length of the shield.

Etymology.—After Hildebrand, in honor of the landowner who kindly allowed us access to the site.

Remarks.—Only the bivalved shield of this taxon is known. Its morphology differs sufficiently from that of other shields to justify the erection of a new genus and species. In the absence of soft tissues, including appendages, the affinities of bivalved arthropods are difficult to establish (Briggs, 1983; Siveter et al., 2013). This is emphasized by the range of morphology in Cambrian bivalved arthropods (*Nereocaris*, *Jugatacaris*, *Pectocaris*, *Odaraia*, *Branchiocaris*, *Perspicaris*, *Canadaspis*) that fall on the arthropod stem (Legg et al., 2012); the bivalved shield alone provides little constraint on affinity. The diversity of bivalved stem arthropods in Cambrian Lagerstätten does not appear to persist into the Lower Ordovician—they are rare, for example, in the Fezouata Lagerstätten of Morocco (Van Roy and Briggs, 2011; Van Roy et al., 2015).

Anomalocaridids, however, persisted at least to the Lower Ordovician, where they occur in the Fezouata Lagerstätten. The outline of the valves of *Decoracaris hildebrandi* differs from known lateral elements from the Fezouata, but it is similar to that of some examples of the P-element of the Cambrian Burgess Shale anomalocaridid *Hurdia* (originally referred to *Proboscicaris*, see Rolfe, 1962a, fig. 1). The *Hurdia* shield, however, included a median triangular H-element (Daley et al., 2013) and no such structure has been found at Winneshiek. Furthermore the shield of *D. hildebrandi* lacks any posterior notch such as accommodates the eye in *Hurdia* (Daley et al., 2013) and a number of specimens of

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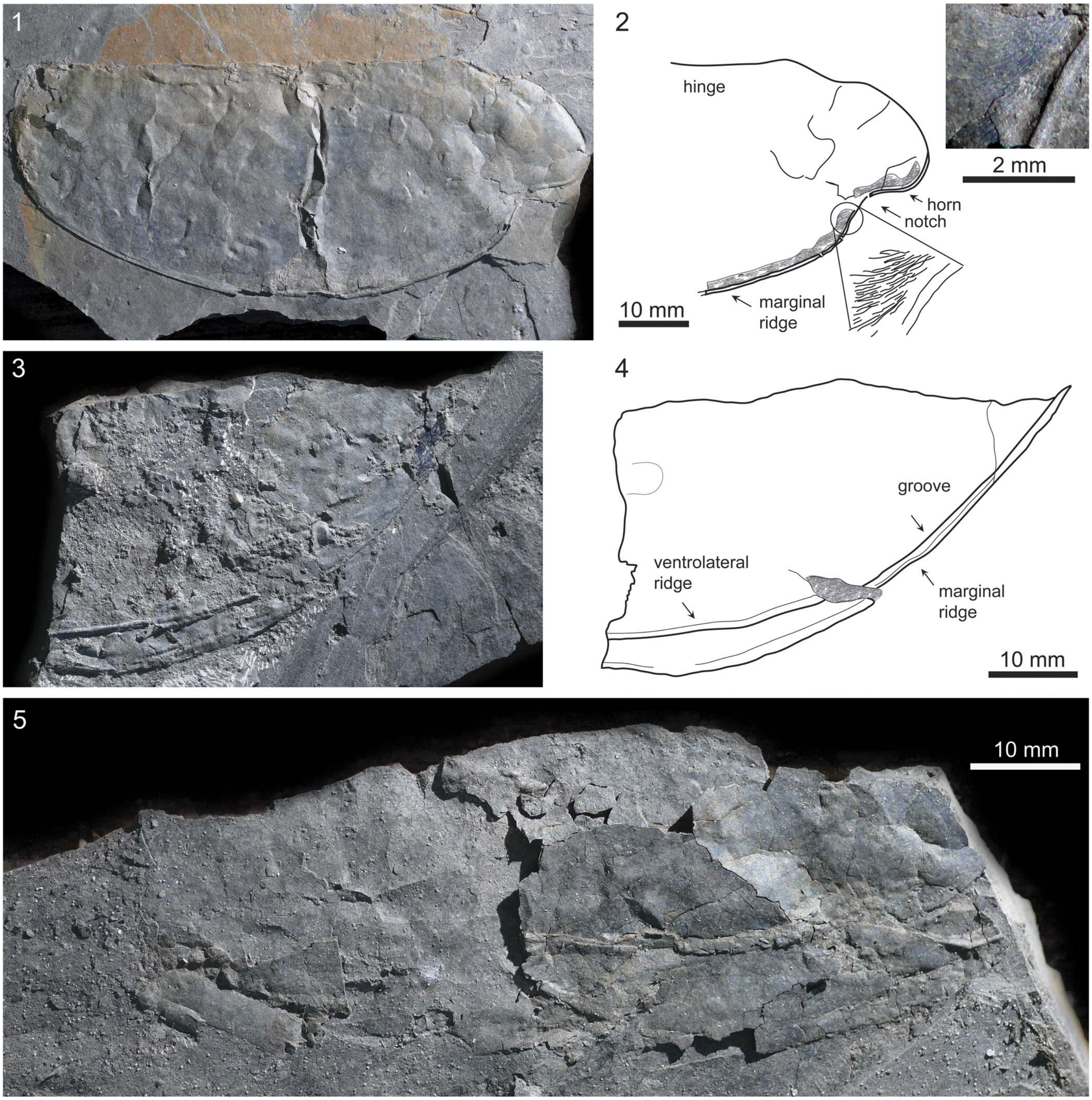

Figure 5. *Decoracaris hildebrandi* n. gen. n. sp.: (**1, 2**) holotype, SUI 138453, right lateral; (**1**) right valve; (**2**) explanatory drawing of anterior horn, with insert showing cuticle ornament; (**3, 4**) SUI 138458, right lateral; (**3**) portion of right valve; (**4**) explanatory drawing; (**5**) SUI 138456, right lateral, large incomplete specimen.

D. hildebrandi, albeit incomplete, show evidence of overlapping valves, favoring a bivalved nature.

The affinity of *Decoracaris hildebrandi* is likely to lie with forms characteristic of the post Cambrian. Its valve morphology is similar in general outline to that of phyllocarids assigned to *Ceratiocaris* or *Warneticaris* (Collette and Hagadorn, 2010c) but none of these shows the shallow anteroventral notch. *Aristozoe* also shows a rounded horn, but this phyllocarid has a much wider marginal rim, and pronounced anterodorsal nodes (Rolfe, 1969; Chlupáč, 1992). A phyllocarid of the size of *Decoracaris* would likely have robust mandibles, and although these would not necessarily be preserved in association with the valves, there is no sign of isolated examples in the Winneshiek assemblage in spite of detailed searching of bedding planes for conodont elements.

Bivalved thylacocephalans, like phyllocarids, are known from restricted environments, but the earliest known representatives of this group are Silurian (Mikulic et al., 1985; Haug et al., 2014), although Vannier et al. (2006) identified possible representatives in the Cambrian. The anterodorsal projection of

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the valve of *Decoracaris hildebrandi* is larger and more rounded, and the notch shallower and more ventral than that in most thylacocephalans, but the variation in the anterior morphology of the valves in the group as a whole is considerable (see e.g., Briggs and Rolfe, 1983, text-fig. 6; Schram, 2014, figs. 2, 3). Although the depth of the notch in *D. hildebrandi* is less pronounced than that accommodating the eye of most later thylacocephalans, it is comparable to that in the Silurian form *Thylacares brandonensis* (Haug et al., 2014). Thus, we tentatively assign *D. hildebrandi* to Thylacocephala, pending the discovery of more of its morphology. If this attribution were confirmed, it would make the Winneshiek taxon the earliest known example of the group (Haug et al., 2014).

?Crustacea Brünnich, 1772

Genus *Iosuperstes* new genus

Type species.—*Iosuperstes collisionis* new genus, new species

Diagnosis.—As for species.

Etymology.—Abbreviation of Iowa (Io was also a priestess in Greek mythology) combined with *superstes* (L.), witness, survivor.

Iosuperstes collisionis new genus, new species

Figure 6.1–6.9

Holotype.—SUI 138463 (WS).

Other material.—SUI 138464-138472 (WL); SUI 138473-138479 (WS).

Diagnosis.—Shield of two suboval valves with narrow defined margin and unevenly spaced pits <50 µm in diameter revealed when the outer surface of the cuticle is exfoliated.

Description.—*Iosuperstes collisionis* is represented only by valves, which have a mineralized cuticle. The valves are suboval in outline with a near-straight hingeline (Fig. 6.1–6.7). Most specimens are single isolated valves but examples articulated and splayed in a 'butterfly' fashion are also known (Fig. 6.3). The rounded posterior margin makes an angle of approximately 115° with the hinge; the anterior margin makes a shallower angle of approximately 150°. The maximum height lies to one side of the midlength (Fig. 6.1–6.7); the valves are assumed to be postplete, i.e., expanded posteriorly. The height:length ratio varies from ~50% to 67%, but this variation is, at least in part, a

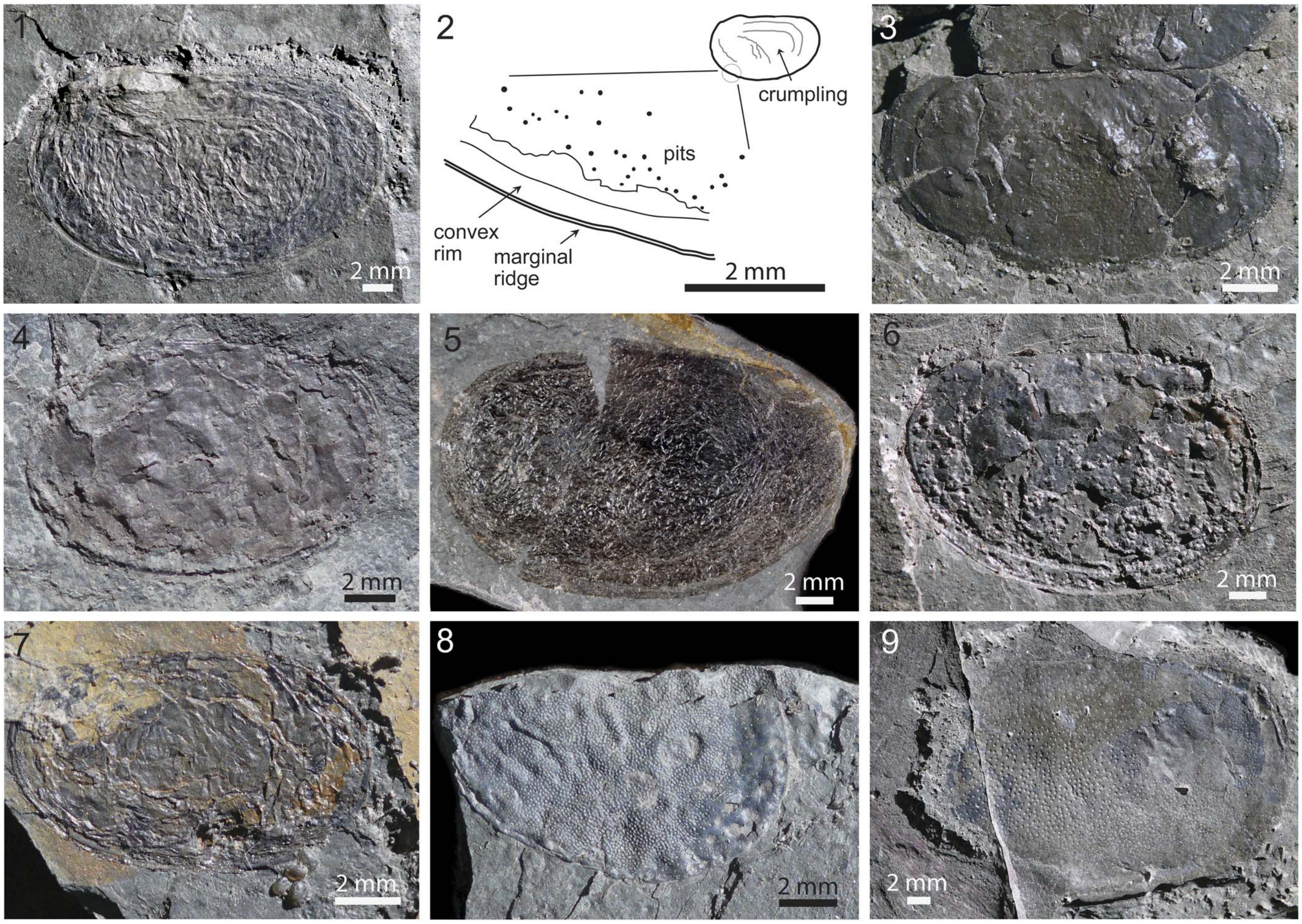

Figure 6. *Iosuperstes collisionis* n. gen. n. sp.: (**1, 2**) holotype, SUI 138463; (**1**) right valve; (**2**) explanatory drawing of marginal structures in posteroventral area with position circled in insert; (**3**) SUI 138471, left valve (specimen is 'butterflied', attached right valve dorsal of hinge line is incomplete); (**4**) SUI 138465, right valve; (**5**) SUI 138464, right valve; (**6**) SUI 138476, left valve; (**7**) SUI 138467, left valve; (**8**) SUI 138473, left lateral, left valve overlying and offset on right; (**9**) SUI 138479, incomplete left valve.

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function of orientation to bedding. Original relief is difficult to detect due to flattening of the valves. An indication of original convexity is provided by concentric and transverse crumpling (Fig. 6.1, 6.2, 6.4–6.7). There is no evidence that the pattern of flattening reflects structures within or between the valves; the trunk segments are not preserved. Variation in the degree of crumpling presumably reflects differences in diagenesis including, perhaps, demineralization of the cuticle (compare Fig. 6.1 and 6.7 with 6.3).

A narrow ridge flanked by a gently convex rim ~0.5–0.75 mm wide follows the margin of the valves (Fig. 6.1, 6.2). This convex rim is mirrored on the interior surface of the valve. In some specimens, an inner ridge is evident running near parallel to the anterior margin of the valve (Fig. 6.3) and in others there is an indication of raised structures in the postero-dorsal part of the valves (e.g., SUI 138463, Fig. 6.1). However, neither of these features is consistently preserved.

The surface of the valve is covered by unevenly spaced pits less than 50 μm in diameter (Fig. 6.1–6.3, 6.5, 6.8, 6.9). The pits are not always evident (e.g., on SUI 138465: Fig. 6.4). Their expression appears to be determined by the degree of exfoliation of the cuticle; i.e., they are evident when the outer surface of the cuticle is absent. The pits cover most of the central part of the valve of SUI 138471 (Fig. 6.3). They are evident on the marginal rim in SUI 138464 and SUI 138476 (Fig. 6.5, 6.6) and are also present, but less densely distributed, inside the rim in SUI 138464 (Fig. 6.5). In SUI 138463, they are not evident on the rim, but only inside it where the outermost layer of cuticle has been lost (Fig. 6.1, 6.2). In other specimens, they are only evident on part of the valve (e.g., Fig. 6.7).

The valves range in length from ~10 mm (SUI 138469: not figured) to 23 mm (Fig. 6.1, 6.2). SUI 138473, preserved in lateral aspect, is more heavily pitted (Fig. 6.8). The hinge and part of the anterior outline were lost when the shale was split. The left valve is offset anteriorly and overlies the right. Flattening of the valves obscures any larger scale structures (nodes, tubercles) that might be present on the surface. The major part of the left valve is covered with small pits. Where these are closely spaced, as in the center, they create the appearance of fine scale reticulation on the surface. Toward the margin of the valve, the pits are more widely spaced and discrete, and in places, particularly along the antero-ventral margin and at the posterior, the valve surface is largely smooth. The pits are evident as tubercles on the interior surface of the underlying right valve where it is exposed on the edge of the shale fragment.

Larger fragmentary specimens are thought to belong to this taxon, although this cannot be confirmed without a complete valve outline. SUI 138479 (Fig. 6.9), which is 22 mm high and at least 32 mm long (based on a minimum ratio), preserves unevenly preserved larger pits, about 150 μm in diameter, on the outer surface, as well as pits about one-third this size, similar to those on the smaller specimens. A fragment of a third specimen (SUI 138475, not figured: largest dimension 21 mm parallel to the hinge, but clearly much larger) also preserves pits of two sizes as well as traces of an anastomosing ornament along part of the margin. Although the marginal ornament is reminiscent of that in *Decoracaris hildebrandi*, the surface of the valves in that taxon is smooth and these smaller pitted specimens show no evidence of an anterior projection.

Etymology.—*Collisio* (L.), impact, referring to the arthropod's occurrence in a meteorite crater.

Remarks.—The specimens we assign to *Iosuperstes collisionis* include considerable variation in the degree and distribution of ornamentation, from none visible (Fig. 6.4, 6.6, 6.7), through pitting on the rim (Fig. 6.5), on part of the surface (Fig. 6.3), to dense pitting over most of the surface (Fig. 6.8). While some of this variation is real, in other cases it is likely to be taphonomic (i.e., the result of processes such as exfoliation or decortication (Rolfe, 1962b, p. 916). While the idea of using this variation to distinguish separate species is attractive, ornamentation can vary significantly even within species of bivalved arthropod (Rolfe, 1962b) and other crustaceans (Waugh et al., 2009) particularly with growth and molting. Thus, we have grouped shields of otherwise similar morphology together in the one taxon pending evidence to the contrary.

Iosuperstes collisionis is similar in size and valve outline to the phyllocarid *Arenosicaris* from the late Cambrian of Wisconsin (Collette and Hagadorn 2010b), but it lacks the concentric ridges that parallel the valve margins in that taxon. The outline of the valves is also similar to that in a diversity of Cambrian arthropods occupying different positions on the stem (Legg et al., 2012; Legg and Caron, 2014) such as *Canadaspis laevigata* (Hou and Bergström, 1997), *Pectocaris eurypetala* (Hou et al., 2004) and *Jugatacaris agilis* (Fu and Zhang, 2011) from the Chengjiang biota, and *Canadaspis perfecta* (Briggs, 1978), *Perspicaris dictynna* (Briggs, 1977), and *Loricicaris spinocaudatus* (Legg and Caron, 2014) from the Burgess Shale. Some of these forms, however, show a somewhat more pronounced posterior projection of the hinge and none of them preserve the pitting characteristic of the Winneshiek form. On this basis we assign it to a new genus and species here. The comparisons with other bivalved forms simply serve to emphasize the difficulty of assigning *Iosuperstes collisionis* to a particular group.

?Crustacea Brünnich, 1772
?Order Leperditicopida Scott, 1961
?Leperditiidae Jones, 1856
Genus and species indeterminate
Figure 7.1–7.10

Material.—SUI 138480-138483 (WL), SUI 138484-138489 (WS).

Description.—This taxon is represented only by the bivalved shield, which has a mineralized cuticle. The majority of the specimens are preserved with the valves articulated but splayed in a 'butterfly' fashion (Fig. 7.1–7.10). The valves are sub-oval in outline, with a very narrow ridge along the margin. In most cases the ventral margin is folded beneath the valve itself (e.g., Fig. 7.5, 7.6). Only when the paired valves are flattened in a somewhat oblique attitude to bedding is the outline of one of the valves evident (Fig. 7.1, 7.2 right valve, on left in figure; Fig. 7.5, 7.6 right valve). The maximum height lies to one side

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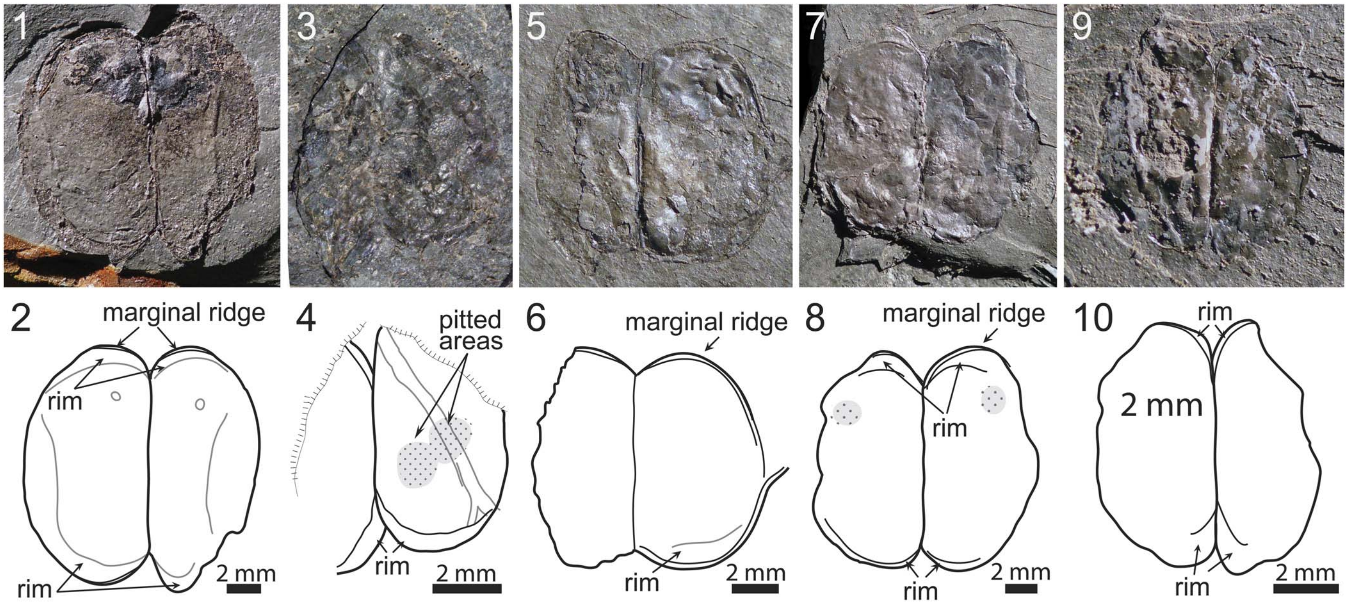

Figure 7. Undetermined ?leperditiid: (**1, 2**) SUI 138488; (**1**) internal view; (**2**) explanatory drawing; (**3, 4**) SUI 138482; (**3**) valves incomplete anterolaterally; (**4**) explanatory drawing, pitted areas are poorly defined; (**5, 6**) SUI 138489; (**5**) left valve fold underneath; (**6**) explanatory drawing; (**7, 8**) SUI 138486; (**7**) specimen; (**8**) explanatory drawing, circular areas are poorly defined; (**9, 10**) SUI 138480; (**9**) specimen; (**10**) explanatory drawing.

of the midlength (Fig. 7.5, 7.6); the valves are presumably postplete; i.e., the more expanded part is posterior. The fact that one valve generally appears higher (the dimension orthogonal to the hinge line) than the other may reflect different dimensions, as in leperditicopid arthropods (Berdan, 1976, 1984). Inside the marginal ridge is a rim ('brim' in the terminology of Berdan, 1976, text fig. 3) which narrows to a point at the hinge line (Fig. 7.1–7.10). The rim appears to taper out along the ventral margin. Some specimens preserve possible nodes (perhaps even eye tubercles: Fig. 7.1, 7.2), in some cases with hints of pitting in subcircular areas (Fig. 7.3, 7.4, 7.7, 7.8), but node-like features are not present in a consistent position from specimen to specimen. The valves are irregularly crumpled (e.g., Fig. 7.9) making such relief difficult to characterize. The surface of the valves is smooth. Due to the flattened preservation, it is not possible distinguish any features of the ventral margin (see Vannier et al., 2001, figs. 1, 13).

The valves range in length from 8.8 mm (SUI 138489, Fig. 7.5, 7.6) to 17.5 mm (SUI 138485, not figured).

Remarks.—This bivalved arthropod is similar to leperditicopes in the size and external appearance of the valves (Berdan, 1984; Vannier et al., 2001). Vannier et al. (2001) noted that the earliest leperditiid is *Eoleperditia ambigua* Berdan, 1976 from the early Llanvirn of Utah—a similar age to the Winneshiek occurrence. The best preserved leperditicopes from other localities are uncrushed and in the round, preserving significant relief (Williams and Siveter, 2008). Silicified specimens can be released from limestone by dissolution; calcitic specimens have to be cracked out of limestones. The Winneshiek shields, in contrast, are flattened and diagenetically altered, eliminating relief, and features of the internal surface of the valves are not evident, all of which make diagnostic characters difficult to observe (Berdan, 1984, p. 3). Even though leperditicopid arthropods range from Ordovician to late Devonian (Vannier et al., 2001) unequivocal flattened specimens (requiring demineralization and preservation in shale) are essentially unknown but this may be, in part, because they are difficult to identify. The absence of the rim around the ventral margin in the Winneshiek form indicates an affinity with Leperditiidae rather than Isochilinidae (of the two major groups recognized by Berdan, 1984) but the lack of diagnostic features prevents the identification of this taxon with a genus (it is similar to a number of smooth forms of leperditiids with a wide marginal rim).

The affinities of leperditicopes are uncertain and will only be resolved with the discovery of preserved soft parts (Becker, 2005). Although traditionally assigned to ostracods (e.g., Berdan, 1984), such a relationship is controversial (Becker, 2005) and most authors now refer them only to arthropods (Vannier et al., 2001; Williams and Siveter, 2008). Frustratingly (in contrast to the small phyllocarids), no soft parts are preserved in the Winneshiek specimens.

Vannier et al. (2001, p. 75) observed that leperditicopes 'preferentially occupied very shallow marginal habitats … that were subjected to environmental stress,' including salinity (see also Knox and Gordon, 1999; Knox, 2001). Berdan (1984, p. 17) considered them to be euryhaline and shallow water. They are generally considered to be benthic (Vannier et al., 2001, p. 91). The low oxygen bottom conditions within the Winneshiek basin would not have suited them, implying that they lived beyond the crater and were washed in following death (this would be consistent with their 'butterflied' configuration and the absence of preserved soft parts).

Flattened leperditicopes occur elsewhere where they are similarly difficult to identify. Large numbers of leperditicopids are known from the Lower Silurian Waukesha lagerstätte (Telychian) of Wisconsin, some of them 'butterflied' (Mikulic

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et al., 1985). Large numbers of *Leperditia* also occur in association with eurypterids in the Upper Silurian Tonoloway Formation (Upper Ludlow-Přídoli) of Pennsylvania (Vrazo et al., 2014) and leperditicopes are associated with eurypterids from the Bertie Group (Přídoli) of New York State in the collections of the Yale Peabody Museum of Natural History.

Crustacea Brünnich, 1772
Ostracoda Latreille, 1802
?Palaeocopida Henningsmoen, 1953
cf. *Lomatopisthia* (Guber and Jaanusson, 1964)
Figure 8.1–8.3

Material.—SUI 138490 (WS), SUI 138491 (WL).

Description.—SUI 138490 (Fig. 8.1, 8.2) is preserved as two articulated valves, opened in butterfly fashion and affording a view of the interior. The right valve (the lower one in Fig. 8.1, 8.2) shows the suboval outline, with some loss of the anterior margin. The maximum height lies at or slightly anterior of the mid length, i.e., the valve is assumed to be preplete. The left valve is folded on itself longitudinally exposing the exterior of the ventral part. A narrow ridge runs around the margin, which is particularly evident on the right valve. The relief on the valves is somewhat obscured by flattening and the features appear negative. The right valve preserves evidence of four lobes (shaded in Fig. 8.2). Lobe 1 is anterodorsal, subcircular in outline, and appears discrete; a similar somewhat larger structure lies ventral to it. Lobe 2 is poorly defined, similar in height to Lobe 1, but extends dorsally to merge with Lobe 3. Lobes 3 and 4 extend to the dorsal margin and merge ventrally into a raised area along the ventral margin (?ventral lobe). The surface of the valves is granular, with a covering of unevenly spaced tubercles that are 30–40 µm in diameter and appear as pits on the interior surface; they may, in part, be evident due to exfoliation. SUI 138491 (Fig. 8.3) is slightly larger than the better-preserved specimen. It is flattened, obscuring the relief, and much of the posterior part of the valves is lost.

The length of the valves is ~4 mm in SUI 138490 (Fig. 8.1, 8.2) and 5.5 mm in SUI 138491 (Fig. 8.3).

Remarks.—The long straight dorsal margin and pronounced lobes identify this form as an ostracod of the Order Palaeocopida. It appears comparable to species of *Lomatopisthia* that occur in the Sandbian/Katian of Oklahoma (Harris, 1957; Kraft, 1962; Williams, 1991; Williams and Siveter, 1996). *Lomatopisthia* shows a pattern of four dorsoventral lobes (Guber and Jaanusson, 1964) although the described species are much smaller than the Winneshiek form. *Lomatopisthia* is unusual among ostracods from the middle Ordovician Bromide Formation in that its ecological range is not confined to open marine but extends to shore face (Williams and Siveter, 1996). The ostracods of Late (and presumably mid) Ordovician Laurentia tend to be highly endemic (Mohibullah et al., 2012). Better-preserved material of the Winneshiek taxon would likely allow its status as a separate species (and possibly genus) to be confirmed. Hairapetian et al. (2011) extended the range of *Lomatopisthia* to the early Silurian of Iran.

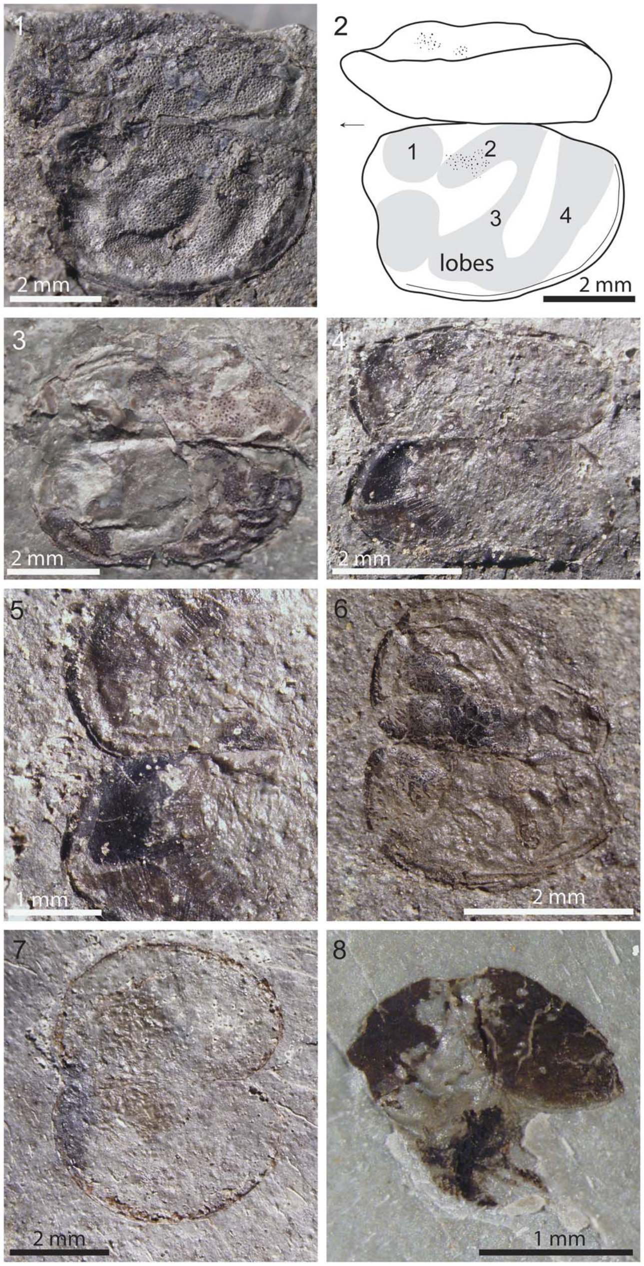

Figure 8. Ostracods: (**1–3**) cf. *Lomatopisthia*; (**1, 2**) SUI 138490; (**1**) internal view; (**2**) explanatory drawing, shaded areas approximate positive relief on the exterior of the valve; (**3**) SUI 138491, external view, much of the valves lost posteriorly; (**4, 5**) unidentified ?palaeocopid, SUI 138492; (**4**) internal view; (**5**) ?posterior showing radiating structures; (**6–8**) unidentified ?podocopid; (**6**) SUI 138497 showing some relief; (**7**) SUI 138498 shell demineralized, relief lost; (**8**) SUI 138499, oblique compaction, ?trunk and limbs projecting ventrally

Ostracoda Latreille, 1802
?Palaeocopida Henningsmoen, 1953
Genus and species indeterminate
Figure 8.4–8.5

Material.—SUI 138492, SUI 138493 (WS).

Description.—SUI 138492 preserves both valves in a butterflied configuration (Fig. 8.4). The valves are suboval in outline and

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there is little relief except on the periphery. The margins are marked by a narrow ridge and in places a marginal rim is evident. The surface of the valves (Fig. 8.5) is unusual in displaying arrays of radiating straight lines, the sets converging at high angles. The cuticle appears absent over much of the valves and there is evidence of wrinkling implying flexibility, perhaps because of demineralization. SUI 138492 is about 4 mm long. A second, somewhat larger specimen (SUI 138493), is incomplete anteriorly.

Remarks.—The radiating structures are reminiscent of ridges on the surface of *Bulbosulculus fragilis* (Kanygin, 1971) although the latter are coarser and more robust. The structures on the Winneshiek specimens also resemble the striae on the fringes of some palaeocopes, but such striae are usually oriented normal to the valve margin and the valves show no evidence of a fringe. The radiating structures are too straight to represent the anastomosing ridges that occur within the valves of some leperditicopids and living myodocopes (Vannier et al., 2001). Nor is their arrangement like that of the calcified radiate microstructures, polygonal to circular in outline, which are characteristic of Recent myodocopes where they represent platelets of calcium carbonate growing in the valves. Such platelets have also been described in Ordovician, Silurian and Carboniferous myodocopes (Siveter et al., 1987, 2014; Briggs et al., 1991a) where they may be modified by diagenesis. Although the radiating structures in this Winneshiek specimen differ in appearance, they may be similar in nature.

Ostracoda Latreille, 1802
?Podocopida Henningsmoen, 1953
Genus and species indeterminate
Figure 8.6–8.8

Material.—SUI 138494-138495 (WL), SUI 138496-138502 (WS) (138500 may not belong here).

Description.—A number of small bivalved specimens are characterized by a straight hinge line, inflated oval outline and narrow marginal ridge. SUI 138497 (Fig. 8.6) preserves two valves preserved in a butterflied configuration with a smooth surface and narrow marginal rim. The valves appear carbonaceous but there are traces of mineralized structures. Most of these have the appearance of polygonal cracks but in places there are hints of a radial arrangement similar to that in the calcified platelets of myodocopes. Other specimens show hints of such a radial arrangement even where the cuticle is largely lost, and there is little or no relief (Fig. 8.7). Yet other specimens preserve the mineralized valves with little relief and a smooth surface. SUI 138496 (not figured), a small distorted specimen, shows short projections beyond the hinge line which are reminiscent of antennae, but their nature is uncertain. SUI 138499, preserved in an oblique attitude to bedding, also shows traces of structures that may represent part of the trunk and some thoracic limbs (Fig. 8.8).

Remarks.—Bivalved taxa, including ostracods, are difficult to assign taxonomically in the absence of appendages (Siveter et al., 2013). We assign this provisionally to Podocopida based on the long straight hinge line, valve outline, and smooth surface.

Discussion and conclusions

There is limited evidence on which to base an interpretation of the mode of life of the Winneshiek bivalved arthropods. The combination of finely laminated sediment, abundant organic matter, and the presence of pyrite indicates low oxygen conditions in the substrate (Liu et al., 2006). The closed setting of the meteorite crater may have restricted water circulation at depth. The most abundant fossils are conodonts, which were presumably nektonic. *Ceratiocaris winneshiekensis* is the most common arthropod in the fauna and the only one preserving traces of the appendages, albeit rarely. It may have been tolerant of low-oxygen conditions as is the recent phyllocarid *Nebalia*, perhaps likewise feeding on organic matter in the sediment (Vannier et al., 1997).

It has been suggested that the Decorah impact structure is one of several associated with the same meteorite shower (Liu et al., 2009), in which case other craters might harbor similar sediments and fossils. In addition to Decorah, this meteorite shower may have generated the Ames structure in Oklahoma (Johnson and Campbell, 1997) to the south west, the Rock Elm structure (French et al., 2004) to the north and possible the Slate Islands crater in Lake Superior. Only Ames structure fossils have been described in detail and the conodont biostratigraphy of the sequence (Repetski, 1997) is consistent with the age of the Decorah Impact. Ames fossils extracted from black shale in cores (presumably yielding only a proportion of the potential diversity) include abundant phyllocarids representing two taxa, one of them closely similar to the most common arthropod in the Winneshiek fauna. The Ames fauna also includes rare brachiopods (including rhynchonellids) and ‘small phosphatic masses’ (Hannibal and Feldmann, 1997), the latter perhaps equivalent to bromalites from Decorah (Liu et al., 2006; Hawkins et al., 2013). Thus, aspects of the Ames fossil assemblage are similar to that in the Winneshiek Shale. The Rock Elm fauna is less well documented, but the assemblage is reported to contain brachiopods, molluscs (including gastropods), trilobites, crustaceans, annelids (as scolecodonts), and conodonts (Peters et al., 2002; French et al., 2004). Here too the apparent absence of some fully marine taxa (e.g, crinoids, bryozoans) suggests possible similarities with Winneshiek.

Two other Ordovician faunas, Airport Cove and William Lake, from Manitoba in Canada of Katian age also represent restricted shoreline settings (Young et al., 2007). There medusae, lingulids, eurypterids, horseshoe crabs, and conodonts are preserved in carbonate muds. The Winneshiek assemblage includes some of the elements of these faunas but apart from rare ostracods at William Lake (Young et al., 2007), bivalved arthropods have not been reported from them. A number of Silurian Lagerstätten also represent restricted settings (Kluessendorf, 1994). The Llandoverian Waukesha Lagerstätte of Wisconsin yields phyllocarids, thylacocephalans and leperditicopids (Mikulic et al., 1985; Haug et al., 2014) as well as conodonts. Xiphosurids are present but not eurypterids, and the Waukesha biota includes marine taxa such as trilobites and

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graptolites although most normal shelly marine taxa are absent. Eurypterids and giant phyllocarids are also present, with trilobites, in the poorly known Wenlockian Scotch Grove Lagerstätte of eastern Iowa (Hickerson and Sivill, 1997; John et al., 2010; Moore et al., 2011). The mid-Silurian Bertie Group of New York State (Nudds and Selden, 2008) yields a diversity of well-preserved eurypterid exuviae (Tetlie et al., 2008) as well as phyllocarids and occasional leperditicopids, but we can find no reports of conodonts. The occurrence of abundant eurypterids in some of these restricted faunas has been explained because of their congregating to molt (Braddy, 2001) in nearshore hypersaline settings. The setting of the Winneshiek Lagerstätte indicates that some eurypterids may also have favored brackish settings for this purpose. However, even a simple comparison of the Winneshiek biota with those of other Ordovician and Silurian Lagerstätten representing restricted settings shows that while individual faunas and their settings may show similarities, those separated in time and space are unique in character.

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