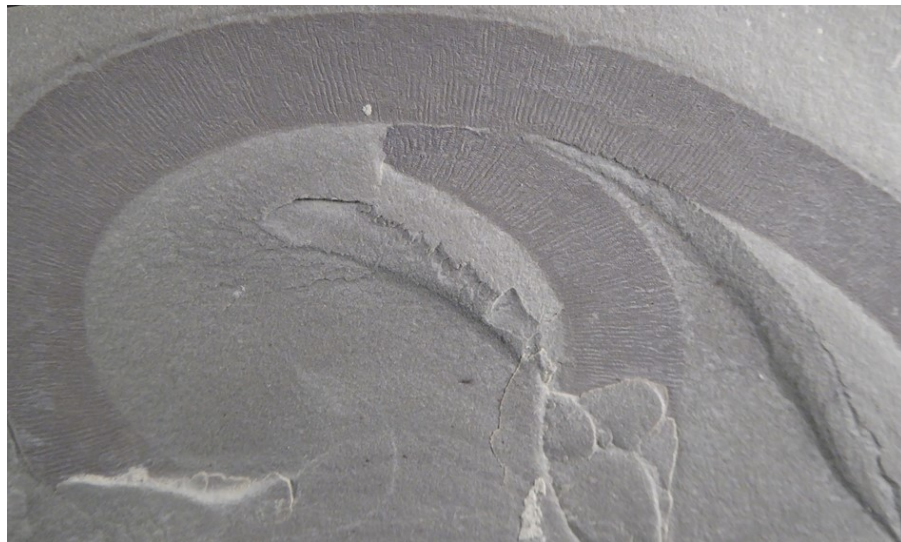# Enigmatic worm-like fossils from the Silurian Waukesha Lagerstätte, Wisconsin, USA

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(15 hp/ECTS credits)**

# Enigmatic worm-like fossils from the Silurian Waukesha Lagerstätte, Wisconsin, USA

Bachelor's thesis
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**Cover Picture:** Fossil from the Waukesha Lagerstätte, interpreted as a Palaeoscolecid in this study. Photo by Andrew Wendruff and Mats E. Eriksson.

# Enigmatic worm-like fossils from the Silurian Waukesha Lagerstätte, USA

MÄRTA WESTBERG

**Abstract:** The lower Silurian Waukesha Lagerstätte of Wisconsin, USA, is a Konservat-Lagerstätte which has yielded a diverse assemblage of exceptionally well-preserved soft-bodied organisms. This study comprises first-hand descriptions and assessments of 23 enigmatic worm-like specimens from the Waukesha Lagerstätte, alongside a literature review. The study focuses on the depositional environment in which the strata of the Waukesha Lagerstätte was formed, as well as which morphologies, mode of preservation and taxonomic affinities of the fossils. In total, eight different worm-like taxa have been identified, not only including annelids, but probably also arthropods and a poriferan. This suggests that worms and worm-like organisms formed an important and diverse component of the past biotas that are now preserved in the Waukesha Lagerstätte. Despite their exceptional preservation, the worm-like fossils of Waukesha Lagerstätte are difficult to interpret and unambiguously assign to specific taxa. Specimens previously interpreted to represent leeches are herein rather considered to be palaeoscolecid worms, based on detailed scanning electron microscopy (SEM)-studies which revealed the presence of external plates and nodes, closely similar to those reported from other palaeoscolecidans. One of these taxa could belong to Wronasco-lex because of its raspberry-like plates. SEM-based elemental mapping of one specimen shows enrichment of calcium and phosphorous in the fossil compared to the surrounding host rock, suggesting that the Waukesha fossils might be preserved as calcium phosphate. Future studies that could be of interest regarding this collection of fossils include more detailed investigations of fine structures in SEM in the specimens interpreted as palaeoscolecidans.

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# Enigmatiska masklika fossil från Waukesha Lagerstätte, Wisconsin, USA

MÄRTA WESTBERG

**Sammanfattning:** Den äldre siluriska Waukesha Lagerstätte från Wisconsin, USA, är en Konservat-Lagerstätte som uppvisar en diverse samling av exceptionellt välbevarade mjukvävnadsorganismer. Den här studien innefattar förstahandsbeskrivningar och bedömningar av 23 gåtfulla masklika fossila exemplar från Waukesha Lagerstätte, tillsammans med en litteraturstudie. Studien fokuserar på avsättningsmiljön i vilken strata av Waukesha Lagerstätte bildades, såväl som vilka morfologier, bevaringstillstånd och taxonomiska tillhörigheter som fossilerna har. Totalt har åtta olika masklika taxa identifieras, inte bara inkluderande annelider, men förmodligen även arthropoder och en poriferan. Detta tyder på att maskar och masklika organismer utgör en viktig och diverse komponent av det dåtida biota som nu är bevarat i Waukesha Lagerstätte. Trots de masklika fossilernas exceptionella bevaring, är de svåra att tolka och att entydigt tilldela ett specifikt taxa. Fossiler som tidigare har tolkats tillhöra iglar är i denna studie snarare tolkade till att vara palaeoscolecid maskar baserade på detaljerade scanning electron microscopy (SEM)-studier som visar förekomsten av yttre plattor och noder, mycket lika dem rapporterade från andra palaeoscolecider. Ett av dessa taxa kan möjligtvis tillhöra *Wronascolex* på grund av dess hallonliknande plattor. SEM-baserad elemental mapping på ett av fossilexemplaren visar en anrikning av kalcium och fosfat i fossilet jämfört med den omkringliggande stenen, vilket tyder på att Waukesha fossilerna kan vara bevarade som kalciumfosfat. Framtida studier som kan vara av intresse att utföra med avseende på denna fossilsamling inkluderar fler detaljerade undersökningar av finstrukturer i SEM i fossilerna tolkade som palaeoscolecider.

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# 1 Introduction

The fossil record is dominated by preserved hard parts of organisms, such as shells, teeth and bone, as soft-bodied taxa require very special environments and taphonomic pathways in order to become preserved as fossils (Mikulic et al. 1985a). Konservat-Lagerstätten are localities which have been formed in such type of environments (Kluessendorf 1994). They contain exceptionally well-preserved fossils in which soft-bodied, as well as lightly sclerotized organisms, have escaped post-depositional destructive forces and become fossilized (Mikulic et al. 1985a).

There are relatively few Silurian Lagerstätten in the geological rock record and the Waukesha Lagerstätte is one of them (Kluessendorf 1994; Briggs et al. 1996). Other examples of Silurian Lagerstätten include the Herefordshire Lagerstätte from the UK and the Eramosa Lagerstätte from Ontario, Canada (Siveter et al. 2018; von Bitter et al. 2017). Additionally, a few less known examples from the North America are reviewed by Kluessendorf (1994). This Lagerstätte preserves diverse soft-bodied fossils and, in rare cases, shelly organisms primarily including trilobites and conulariids (Wendruff 2016). The scarcity of shelly organisms is in fact unusual for normal Silurian biotas, i.e., those recorded outside of Lagerstätten (Moore et al. 2005).

There is a wide range of fossilized soft-bodied organisms in the Waukesha Lagerstätte (Mikulic et al. 1985a; Wendruff 2016). One conspicuous but still largely unexplored group includes fossils deriving from worm-like (vermiform) organisms. Specimens that possess a worm-like morphology include annelids but also different types of arthropods and even unusual sponge-like forms. Anatomical features that are "worm-like" in this context comprise a segmented and elongated body.

Annelida is an extensive phylum including animals with soft and elongated bodies; they can either be marine or terrestrial and are usually distinctly segmented (Lehmann & Hillmer 1983). This phylum has existed at least since the early Cambrian (Conway Morris & Peel 2008) but the fossil record is still relatively poorly known due to the difficulties in preserving the soft body tissues. Annelid fossils can be represented in the form of burrows, body impressions or carbonaceous films, and/or as parts of the jaw apparatuses. The jaws of polychaete annelid worms (known as scolecodonts) are most easily fossilized since they normally comprise the hardest and most resistant parts of the organism (Parry et al. 2019). Other worm-like phyla include the Arthropoda, the members of which also possess segmentation but additionally an exoskeleton (cuticle), with plates protecting each segment. Arthropods comprise, for example, the extinct trilobites, chelicerates (containing arachnids) and myriapods (e.g. centipedes and millipedes) (Lehmann & Hillmer 1983).

As Lagerstätten can preserve both soft and hard parts of organisms, they demonstrate a more accurate picture of the once living biota in ancient environments (Mikulic et al. 1985a). Examining the fossils from the Waukesha Lagerstätte can thus help in understanding what type of biota lived during that time, in that location and type of depositional environment.

The purpose of this paper is to analyze well-preserved worm-like fossils from the Waukesha Lagerstätte in order to increase our knowledge of the fossil diversity and faunal composition of the once-living biota. In this paper, the published literature on the Waukesha Lagerstätte, as well as selected coeval (or nearly so) Lagerstätten, is reviewed and evaluated. In addition, a collection comprising 23 different enigmatic specimens, all with a worm-like anatomy, from the Waukesha Lagerstätte is studied in order to address the following questions:

1. What characterized the depositional environment of the area that subsequently formed the strata of the Waukesha Lagerstätte?
2. What specific morphologies and mode of preservation characterize the worm-like fossils?
3. Which taxonomic affinities do the worm-like fossils have and how diverse were those faunas?

# 2 Materials and methods

In addition to first-hand descriptions and assessments of fossil materials from the Waukesha Lagerstätte as detailed below, this report also includes an extensive literature study. Previous work on Lagerstätten from the Silurian Period has been reviewed, alongside the records of worms and worm-like fossils. Analyses and classification of the fossils at hand have been made with the help of published literature dealing with similar types of organisms.

The studied fossils have been collected from the Waukesha Lagerstätte in the Brandon Bridge Formation at the Waukesha Lime and Stone Company Quarry in Wisconsin, USA. The samples were provided by Prof. Loren E. Babcock and Dr. Andrew Wendruff (both of the School of Earth Sciences, Ohio State University, USA). The 23 different specimens preserved in dolomite were macroscopically photographed in high resolution, primarily by Dr. A. Wendruff and Prof. Mats E. Eriksson (Lund University, Sweden) and these photographs have been the target for thorough examination in this paper. Moreover, one specimen was imaged by Dr. A. Wendruff using a FEI Quanta Field Emission (FEQ) Scanning Electron Microscope (SEM) at the Ohio State University (see Fig. 7B–C). In addition, another specimen was coated with platinum/palladium and subsequently imaged using a Tescan Mira3 High Resolution Schottky Field Emission Scanning Electron Microscope (FEG-SEM) and a pilot analysis of the chemical composition was performed through a SEM-based elemental mapping at the Department of Geology in Lund, Sweden (see Fig. 7D–L). Those latter analyses were performed by BSc Gabriel Zachén and the author (both of Lund University).

# 3 Geological setting and stratigraphy

The Waukesha Lagerstätte can be found in southeastern Wisconsin, USA, close to the city of Waukesha (see Fig. 1). This Lagerstätte forms part of the Brandon Bridge Formation, which overlies the Burnt Bluff carbonates (i.e., including the Manistique Formation sensu Wendruff 2016; Fig. 2) and consists of thinly laminated argillaceous dolomite and mudstone (Moore et al. 2005). Wisconsin was part of the Laurentian pa-

laeocontinent during the Silurian Period and located close to the equator (Fig. 3; Cocks & Scotese 1991). It was during this time that Laurentia collided with Baltica, which resulted in the Caledonian orogeny that gave rise to the Scandinavian mountain chain (Torsvik et al. 1996). In the oceans, prominent coral reefs expanded and the first vascular plants started to colonize land, at least based on the macroscopic fossil record (Briggs & Crowther 2003). Large parts of Laurentia were covered by epeiric seas and the today well-known Great Lakes region was dominated by carbonate platforms (Shaver 1996). These platforms are comprised of both reef and non-reef environments (Copper 1994).

The Waukesha Lagerstätte was deposited along the western margin of the intracratonic sedimentary Michigan Basin (Kluessendorf & Mikulic 1996). Non-reef facies are made up of argillaceous lime mudstone and are apt to be abundant in brachiopods, trilobites and rooting faunal elements such as pelmatozoans (i.e. crinoids and other stalk-bearing echinoderms), and graptolites (Feldman 1989). Multiple Konservat-Lagerstätten belong to these lime mudstone facies of

the Great Lakes region, in which Waukesha Lagerstätte is one of them (Kluessendorf 1994).

The sedimentation of the strata that would eventually form the Waukesha Lagerstätte occurred during a transgression (Kluessendorf & Mikulic 1996), which was caused by melting of the Gondwanan Ice Sheet (Spengler & Read 2010). The overall environment during which the sediments of the Lagerstätte were deposited was a tropical and shallow marine environment (LoDuca et al. 2003). The Lagerstätte is characterized by sedimentary features and structures resulting from intertidal processes, such as flat-topped and interference ripples, intraclasts and fenestral porosity (Kluessendorf 1994).

The underlying Burnt Bluff carbonates (i.e., including the Manistique Formation), which consist of different types dolomites (Biggs 1987), were uplifted and subaerially exposed during the Aeronian–early Telychian (early Silurian) together with older Silurian strata. This resulted in erosion and karstification (Moore et al. 2005). This event created a regional ridge with an elevation exceeding 50 m. The ridge forms an 8 m high scarp at its southern edge in Wau-
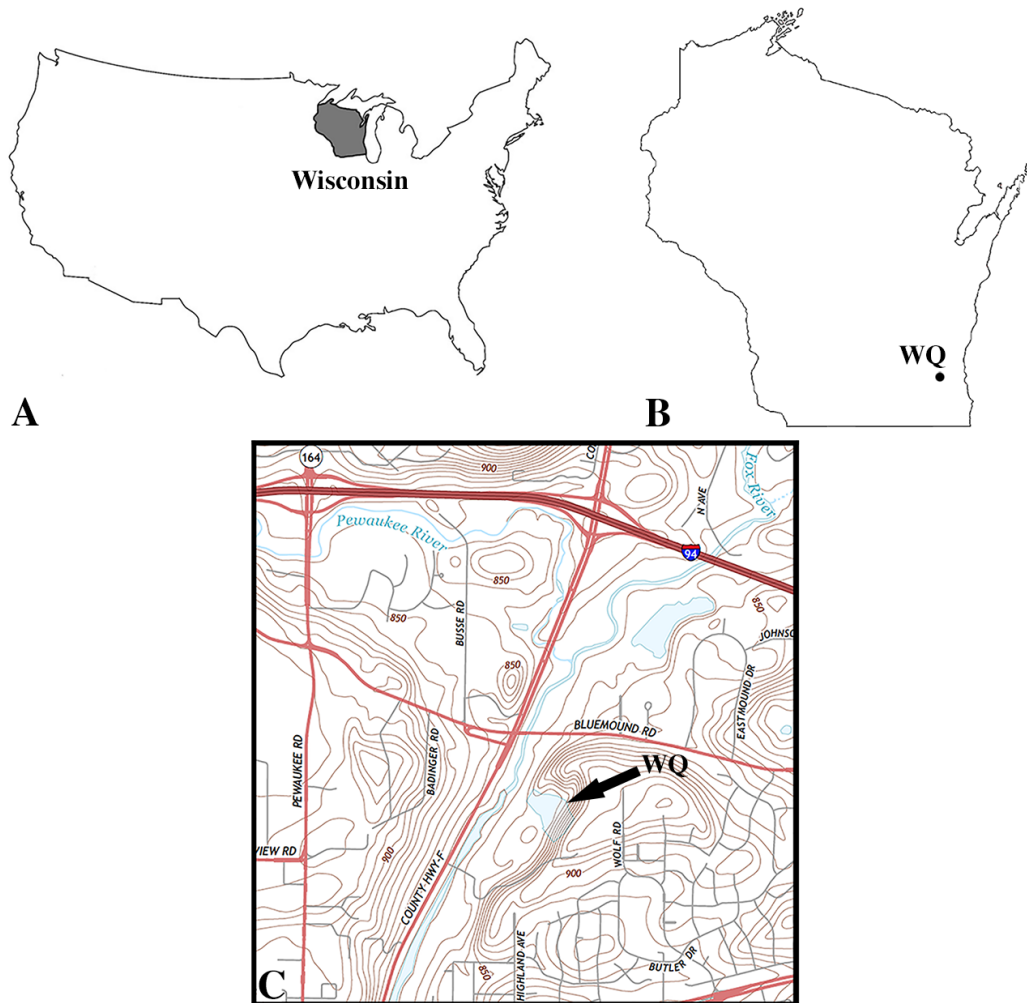


Fig. 1. **A.** Map of the USA with the position of the state of Wisconsin highlighted. **B.** An enlargement of Wisconsin showing the location of the Waukesha Lime and Stone Company Quarry (WQ). **C.** A part of the Waukesha 7.5' topographic quadrangle map, Wisconsin (U.S. Geological Survey 2013, 1:24,000) showing the location of the Waukesha Lime and Stone Company Quarry (WQ). The figure was kindly provided by Andrew Wendruff, modified, and used with permission.

kesha (Fig. 2; Kluessendorf and Mikulic 1996). The scarp, a steep slope, restricted water circulation and remains of organisms were washed into its lowest part from adjacent areas, making it act as a sediment trap (Wendruff 2016).

The Brandon Bridge Formation is dated to the late Llandovery to early Wenlock using conodonts and graptolites (Moore et al. 2005). The age of the Waukesha Lagerstätte is dated to early to mid Telychian (late Llandovery) with conodonts as biomarkers (Moore et al. 2005). Most of the Waukesha Lagerstätte consists of dolomitized, rhythmically bedded plattenkalk (Wendruff 2016).

It should be noted that whereas older literature defines the formation directly underlying the Brandon Bridge Formation as Burnt Bluff, more recent studies (e.g. Wendruff 2016) suggest that the Manistique Formation overlies the Burnt Bluff carbonates and underlies the Brandon Bridge Formation (see Fig. 2). The Manistique Formation, as Burnt Bluff carbonates, consists of different types of dolomite (Biggs 1987).

# 4  Taphonomy and fossil preservation

Different ideas for the exceptional fossil preservation in the Waukesha Lagerstätte have been suggested (see Mikulic et al. 1985a,b; Kluessendorf & Mikulic 1996; LoDuca et al. 2003; Moore et al. 2005). The strata reveal that the depositional environment was stagnant and that obrution took place (Mikulic et al. 1985b). The low water energy setting was a consequence of the abovementioned paleoscarp (LoDuca et al. 2003). There are signs of obrution but also anoxic conditions in the form of fine lamination, limited bioturbation and limited decay (Mikulic et al. 1985b). Recently Wendruff (2016) proposed that the obrution was not an effect of a rapid deposition of sediments, as there was a presence of microbial mats (today seen as variously developed fossil features) that cannot grow effectively during such conditions (Leinfelder et al. 1996). Furthermore, Wendruff (2016) noted that obrution can result from rapid growth by microbial mats which cover the seafloor. Organisms can then get stuck onto their sticky surfaces, which might inhibit processes of decay and also predation (Gehling 1999; Wendruff 2016). The microbial mats probably also promoted dysoxic to anoxic conditions to develop in the lower layers of the sea floor (Wendruff 2016). The presence of microbial mats and scarcity of relatively large trace fossils suggest that the habitat was unsuitable for much of the macroscopic organisms. As mentioned earlier, most macroorganisms were probably transported to, and stuck in, a sediment trap. One evidence for this is that a much higher amount of body fossils of arthropods is present compared to Diplichnites trace fossils (Wendruff 2016). The oxygen level was low on the seafloor which might have made the living situation difficult for trilobites. Many factors can create an unsuitable environment, for example limited circulation, high/low salinity and oxygen levels, and rapid changes in temperature (Riding 2000).

Most of the Waukesha biota was transported to the sediment trap as indicated by an assortment of tapho

nomic features (Mikulic et al. 1985a,b). Articulated trilobites together with no fossil alignment or changes in orientation suggest that the transportation was gentle and of a short distance (Mikulic et al. 1985a). Thus, the assemblage can be regarded as parautochthonous.

Except for the trilobites, the arthropods are highly compressed and preserved as organic impressions or substituted by fluorapatite (Kluessendorf 1994). Lightly sclerotized organisms and soft-bodied organisms are flattened apart from when they are infilled by diagenetic fluorapatite (Mikulic et al. 1985a). The shelly fossils that can be found are decalcified (Kluessendorf 1994; Mikulic et al. 1985a).
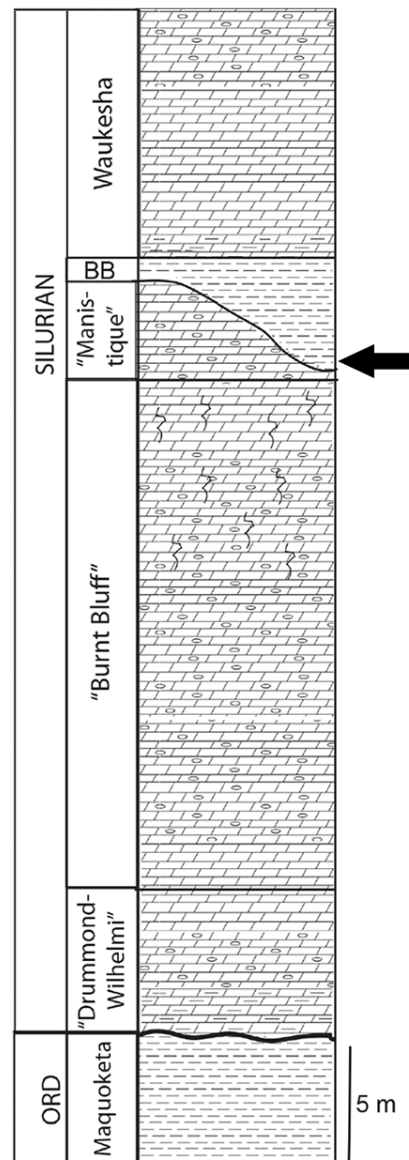


*Fig. 2.* General stratigraphy and lithological column of the latest Ordovician–mid-Silurian strata in southeastern Wisconsin, USA. The black arrow points at the position of the Waukesha Lagerstätte in the Brandon Bridge Formation (BB). The figure is adopted from Wendruff (2016), and was originally created by Joanne Kluessendorf and Don Mikulic (see Wendruff 2016, fig. 1.2).
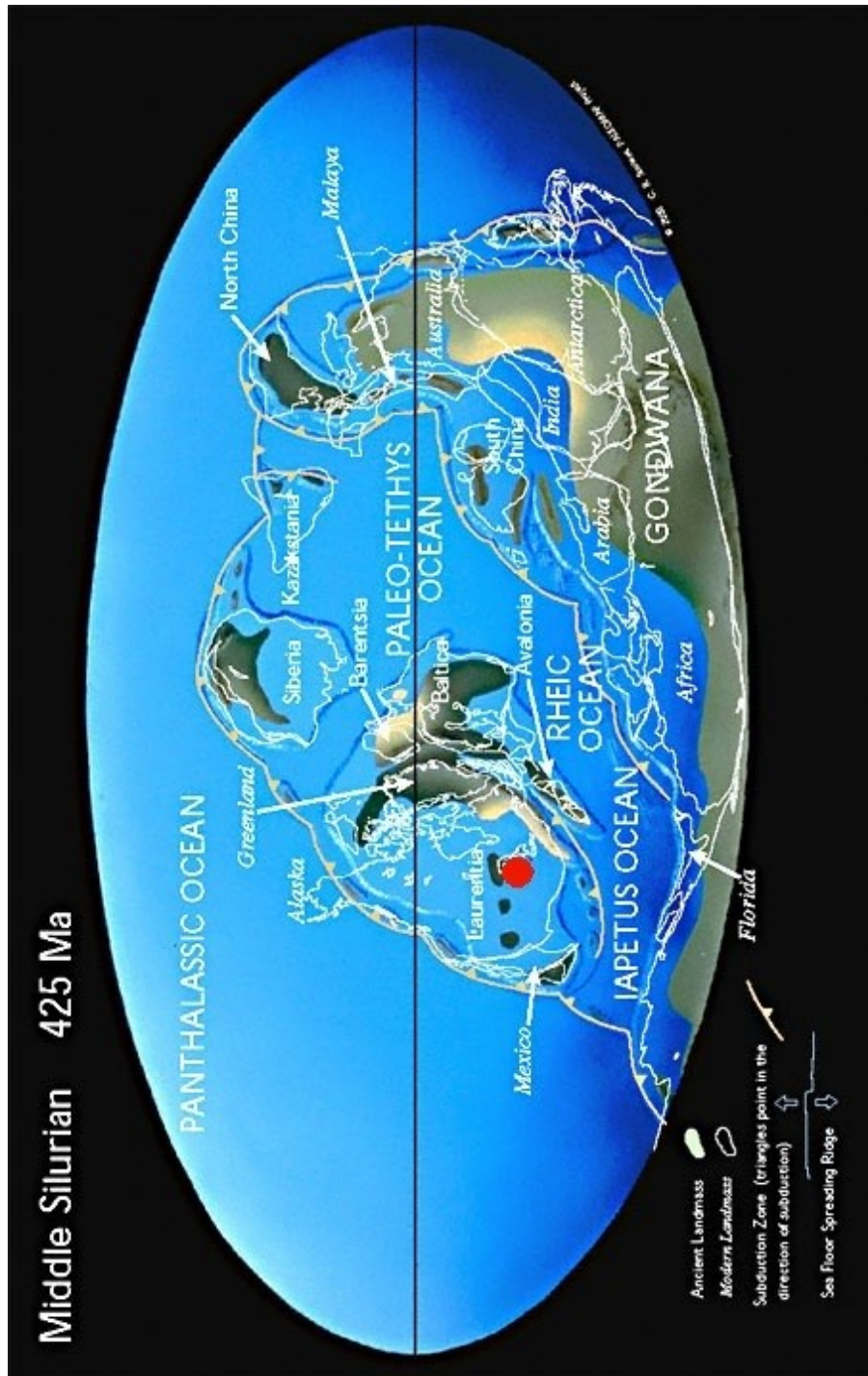
*Fig. 3.* Global paleogeography during the Silurian Period, ca 425 million years ago. Laurentia (which included most of present-day North America) was located close to the equator and the red dot indicates where Wisconsin was at the time. The image is adopted from Scotese (2001) and modified.

# 5 A brief overview of the Waukesha Lagerstätte fossil assemblage

The Waukesha biota is represented by more than 50 genera distributed over 12 phyla and organisms that usually range between 1 mm to 20 cm in length (Wendruff 2016). The biota includes a diverse assemblage of arthropods, alongside enigmatic and non-biomineralized organisms. The arthropods include 13 genera of trilobites, but also xiphosurans, phyllocarids, crustaceans, and ostracods. Biomineralized taxa, besides trilobites and conulariids, are uncommon and the non-biomineralized organisms include lobopodians, palaeoscolecid worms and great appendage arthropods (Wendruff 2016). At least four worm-like taxa have been identified based on the published literature. The Lagerstätte is also rich in graptolites, ostracods and conulariids in places (Mikulic et al. 1985b). Some organisms in the Waukesha Lagerstätte could be viewed as "holdovers", such as great appendage arthropods, palaeoscolecid worms and lobopodians, more typically found in older Lagerstätten, such as the Cambrian Burgess Shale (Wendruff 2016; A. Wendruff, pers. comm., 2019). Other unusual faunal components include a box jellyfish (cubozoan), an early arachnid and a possible leech (Wendruff 2016). Fossilized digestive tracts of different species from both worms and arthropods have been also been identified (Babcock et al. 2016). Shelly faunas, which are typical for other Silurian biotas (i.e., the "normal" or non-Lagerstätte fossil record), are rare or absent in the Waukesha Lagerstätte. Typical Silurian shelly fossils include molluscs (bivalves and cephalopods), brachiopods, corals, echinoderms and bryozoans (Moore et al. 2005).

# 6 Systematic paleontology

## 6.1 Phylum – Arthropoda Lar, 1904.

### 6.1.1 Vermiform arthropod sp. 1
Figures 4A–B

| Description and measurements | |
| --- | --- |
| Length: | 3.4–3.9 cm |
| Width: | 0.6 cm |
| Overall morphology: | Elongated, worm-like fossil with tapering ends, one of which has a blunter termination than the other. The segmentation in the middle part of one specimen (Fig. 4A) is less clearly pronounced. |
| Structure: | Distinctly segmented except for its putative head |
| Number of segments: | 40–45 |
| Segment width: | 0.08–0.1 cm |

*Remarks* – The organism is worm-like in the sense of its segmentation and overall elongated morphology with tapering terminations. However, its putative head region is not segmented which suggests that it probably represents an arthropod rather than an annelid. Annelids commonly show distinct segmentation throughout the body length and in cases where a well-defined head is present, it is usually considerably shorter related to body length than what is seen in the specimens at hand (cf. Beesley et al. 2000; Parry et al. 2019. The same specimen as here shown in Fig. 4B was referred to as a "vermiform arthropod with large headshield and small grasping appendage" by Wendruff (2016, p. 59 fig. 2.5M), which strengthens the interpretation made herein. Another closely similar fossil was described by Mikulic et al. (1985a, fig. 2C) from the Waukesha Lagerstätte, and referred to as a worm-like arthropod with an antenna-like appendage and 30–40 trunk tergites.

In one specimen (Fig. 4B) a putative appendage can be seen attached to the presumable head. The specimen shown in Fig. 4A probably belongs to the same taxon as the one shown in Fig. 4B and is herein treated as such. Also, this specimen might have an appendage preserved at its head region, but the overall state of preservation makes it difficult to see and therefore difficult to interpret unambiguously. The segmentation in the middle part of the specimen in Fig. 4A is less clearly pronounced than that of the other specimen (Fig. 4B).

The specimens assigned to the Vermiform arthropod sp. 1 resemble the group "great appendage arthropods" in the sense that the appendage is attached to the head, but not necessarily in the sense of the appendages size (Kühl et al. 2009).

*Material* – Two specimens from the Silurian Waukesha Lagerstätte of Wisconsin, USA.

## 6.2 Phylum – Annelida Lamarck, 1809
## Class – Polychaeta Grube, 1850

### 6.2.1 Tubeworm? sp. 1
Figures 4C–E

| Description and measurements | |
|---|---|
| Coiled size: | 0.4–0.5 cm |
| Uncoiled size: | 1.8–2.0 cm |
| Width: | 0.1–0.15 cm |
| Overall morphology: | Worm-like and coiled |
| Direction of coiling: | Obligatory trochospiral coiling (the direction of the coiling can both be clockwise and anti-clockwise) |
| Structure: | Thinly segmented |

*Remarks* – The fossils shown in Fig. 4C–E visually resemble the calcareous tube worms spirorbins, that belongs to the Serpulidae family of the order Sabellida (Ippolitov et al. 2014, fig. 2J, 2U–W). Tubes of serpulid worms are typically attached to hard surfaces, but there also exist a few free-living forms (Ippolitov et al. 2014). Species that are similar to the Tubeworm? sp. 1 include, for example, the unattached Nogrobs grimaldii (Ippolitov et al. 2014, fig. 2J) from alongside the attached species Bushiella (Jugaria) kofiadii, Circeis armoricana and Paradexiospira vitrea, all of which are living today (see Ippolitov et al. 2014, fig. 2U–W).

The direction of the coiling differs between the specimens at hand, either because they belong to different species or, more likely, that they exhibit obligatory trochospiral coiling, i.e., the direction of the coiling can both be clockwise and anti-clockwise (Ippolitov et al. 2014). Worms which live in the tubes are segmented, but since the tube is not integrated with the soft tissue of the organism, the tube itself will not reflect its structure (Weedon 1994). This can complicate classification of the fossils of tube worms. It is also difficult to distinguish possible opening ends in the fossils described here (Fig. 4C–E), due to their insufficient state of preservation. If opening ends are not present in the fossils it could be an indication that they are not fossils of tube worms.

The earliest known serpulids are from the Middle Triassic (Vinn et al. 2008). Records of serpulids from the Cambrian and Ordovician do exist in literature (e.g. Dalvé 1948; Clausen & Àlvaro 2002), but they do not clearly show the skeletal properties typical for serpulids or calcareous polychaetes (Vinn & Mõtus 2008; Vinn & Mutvei 2009). Therefore, Vinn & Mutvei (2009) referred to these as the Palaeozoic problematic tubeworms. Recent studies have shown that spirorbiform tubeworms from the Palaeozoic to Middle Jurassic, previously described as the polychaete Spirorbis, now have been reclassified as microconchids (Weedon 1994). Microconchids also build calcitic tubes but belong to an extinct group of lophophorates, perhaps the stem group phoronids (Taylor et al. 2010).

The tubes of serpulids consist of calcium carbonate and the Waukesha specimens do not appear as if they are made up of such material (cf. Vinn & Mutvei 2009), or if so, the original calcium carbonate component has been lost during the fossilization process. However, also other types of material are known to be used by worms to build tubes. This includes organic materials such as proteins or chitin (Merz 2015), but also agglutination of shell fragments or sediment particles (Parry et al. 2019). The Waukesha Tubeworm? sp. 1 specimens dealt with herein (Fig. 4C–E) rather give the appearance of representing the remains of originally soft-bodied worms and could therefore be the result of tubes made of organic material. Thus, the specimens probably do not belong to serpulids or microconchids, as these construct their tubes out of calcium carbonate. Instead, they might belong to the spionids (Order Spionida) or oweniids (Order Canipalpata; Suborder Sabellida), annelids whose tubes can consist of organic material (Parry et al. 2019).

The fossils herein assigned to Tubeworm? sp. 1 could alternatively be interpreted as juvenile, younger, forms of palaeoscolecid worms, such as the specimens described below (see Fig. 5F–H). Both of these groups show distinct coiling, although to different degrees (the specimens in Fig. 5F–H are, for example, only partially coiled). However, one argument against this idea is that there are no specimens of a size that are between these two types (i.e., the Tubeworm? sp. 1 and the Partially coiled palaeoscolecid sp. 1; see below) present in the collection, but only the two distinctly separated size classes. Therefore, for the time being, they are treated as separate taxa.

*Material* – Three specimens from the Silurian Waukesha Lagerstätte of Wisconsin, USA.
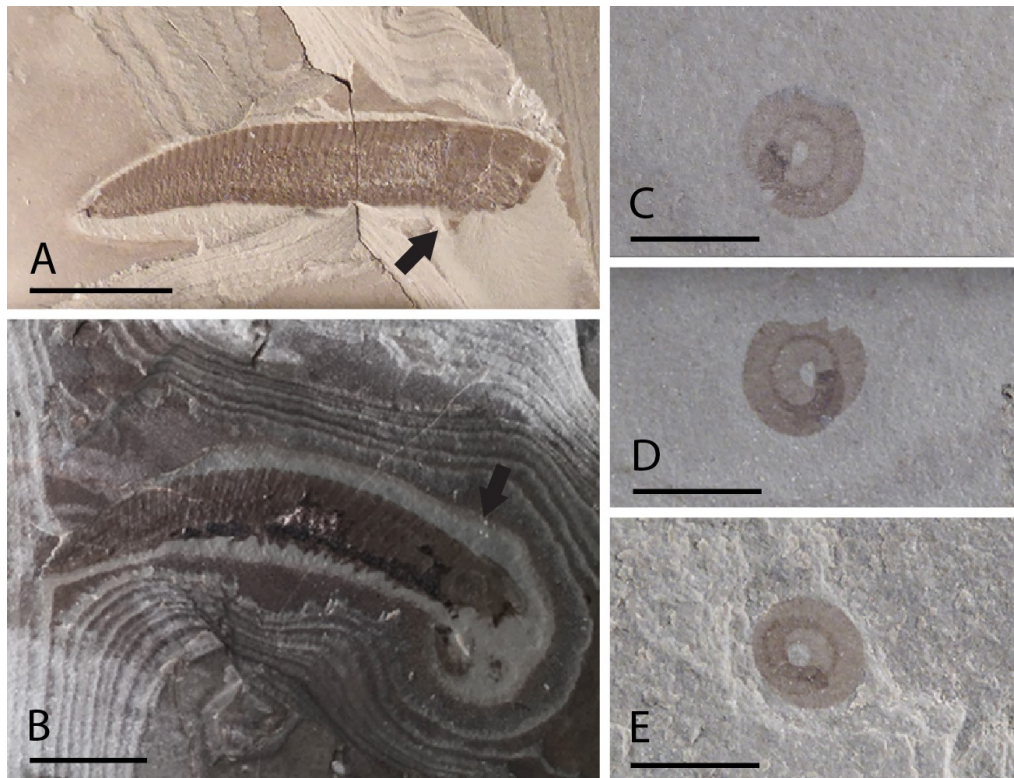
*Fig. 4.* Photographs of selected worm-like fossils from the Waukesha Lagerstätte of Wisconsin, USA. **A.** Vermiform arthropod sp. 1, with an appendage that can be vaguely seen on its lower side (indicated by the black arrow). **B.** Vermiform arthropod sp. 1, with a jaw-like structure or a grasping appendage attached to its headshield. The arrow points at a putative decay halo. **C–E** Small coiled tube worms(?) that exhibit very fine segmentation. Scale bars: 1 cm for A–B, 0.5 cm for C–E.

## 6.3 Phylum – Annelida Lamarck, 1809
## Class – Polychaeta Grube, 1850
## Family – Aphroditidae Malmgren, 1867

### 6.3.1 Aphroditid polychaete sp. 1
Figures 5A–D

| Description and measurements | |
|---|---|
| Length: | 0.8–3.2 cm |
| Width: | Approx. 0.3–0.6 cm |
| Overall morphology: | The specimens are wide and two of the specimens (Fig. 5B–5C) ends have the same rounded shape. |
| Structure: | Segmented |
| Number of segments: | Approx. 8–44 |
| Segment width: | Approx. 0.1 cm (the specimen in Fig. 5C–D) |

*Remarks* – The specimens are overall rather wide and those shown in Fig. 5B–D appear to be somewhat dorso-ventrally flattened. In the central part of the most well-preserved specimen (shown in Fig. 5C) an elongated structure can be distinguished which runs throughout most of the length of the fossil. This central structure measures approximately 2.3 mm in maximum width and tapers slightly towards the anterior and posterior part of the fossil. The structure is herein interpreted as representing the remains of the gastrointestinal tract, because of its size, morphology and placement.

This same specimen (Fig. 5C) has been interpreted to be an aphroditid polychaete also by Wendruff (2016, fig. 2.7F), which strengthens the affinity assignment of the fossil. Another specimen from the Silurian Eramosa Formation of Ontario, Canada, with similar morphological features, such as an oval body shape and a dorso-ventrally flattened aspect has been interpreted as an aphroditid-like polychaete by von Bitter et al. (2007, fig. 2G).

Modern-day aphroditid polychaetes have a broad and sub-flattened body suitable for their crawling lifestyle (Mettam 1971; Beesley et al. 2000). The Waukesha fossils show resemblance to members of the now-living aphroditid genus Aphrodita, also known

under their common name sea mouse, because of their resemblance to the terrestrial rodent. The specimen shown in Fig. 5C especially resembles the species Aphrodita aculeata (for example when comparing the illustrative drawing, Fig. 5D, with the segmentation of an Aphrodita aculeata). However, despite their overall similarities, the Waukesha specimens do not taxonomically belong to the same genus as the now-living forms.

*Material* – Three specimens from the Silurian Waukesha Lagerstätte of Wisconsin, USA.

## 6.4 Phylum – Lobopodia Snodgrass, 1938

**6.4.1 Lobopodia sp. 1**
Figure 5E

| *Description and measurements* | |
|---|---|
| Length: | 1.1 cm |
| Width: | 0.3–0.4 cm |
| Overall morphology: | A curved body and narrow limbs. The specimen tapers to the lower right in the sample slab (Fig. 5E) which probably happened during preservation and is not part of the anatomy. |
| Structure: | Thinly segmented |
| Number of segments: | Approx.18 |
| Viewing angle: | The animal is viewed from its side in a right lateral view. |

*Remarks* – There is a single specimen from the Waukesha Lagerstätte (Fig. 5E) which looks similar to both lobopodians (see von Bitter et al. 2007, fig. 2.E and 2.F; Wendruff 2016, fig. 2.5D and 2.5E) and myriapods (see Mikulic et al. 1985a, fig. 2B; Briggs 1991, fig. 9) described from the fossil record. Lobopodians are a diverse group of organisms with worm-like morphology (Ortega-Hernádez 2015). They are uncommon in the fossil record apart from the Cambrian from which about 20 species are known. Representatives of lobopodians occur from the Cambrian to the Carboniferous, but depending on their definition they could encompass a larger period of time. For example, if one would include onychophora which exist also in post-Palaeozoic strata (Siveter et al. 2018). Lobopodians have unsegmented limbs and a thin, annulated sclerotized cuticle (Ortega-Hernádez 2015). The specimen studied herein has the strongest resemblance to the specimen interpreted as a lobopodian by Wendruff (2016, fig. 2.5E) which has narrow limbs and a length of about 1.3 cm. It should be noted that the fossil shown in Fig. 5E is incomplete and there are parts missing at the right end of the fossil in the picture.

There are 40 different myriapod-like species from the Waukesha biota according to Wilson et al. (2004), with bodies that reach up to 4 cm in length. These specimens were first thought to be true myriapods but have later been reevaluated to more likely belonging to the lobopodians because of their circular muscles (Wilson et al. 2004). The fossil discussed here is not sufficiently well preserved to distinguish possible circular muscles. Nevertheless, its close similarity to the specimen illustrated by Wendruff (2016, fig. 2.5E) is the reason why it is being interpreted as a lobopodian.

*Material* – One specimen from the Silurian Waukesha Lagerstätte of Wisconsin, USA.

## 6.5 Phylum – uncertain
## Class – Palaeoscolecida Conway Morris & Robinson, 1986

**6.5.1 Partially coiled palaeoscolecid sp. 1**
Figures 5F–H

| *Description and measurements* | |
|---|---|
| Uncoiled length (incomplete fossil): | 2–7.3 cm |
| Width: | 0.2–0.9 cm |
| Overall morphology: | Partially coiled. The specimen shown in Fig. 5F has an odd appearance resulting from its mode of preservation. |
| Structure: | Thinly segmented |

*Remarks* – The fossils shown in Fig. 5G–H are part and counterpart of one and the same specimen. This same specimen was previously interpreted as a palaeoscolecid worm with partial preservation of the gut tract by Wendruff (2016, fig. 2.7D). Palaescolecidans are a group of long, slender vermiform organisms that are in the millimeter to decimeter size range. Their cuticle is annulated and covered by transverse rows of phosphatic microscopic plates (García-Bellido et al. 2013; Smith 2015). Representatives of the class Pal-
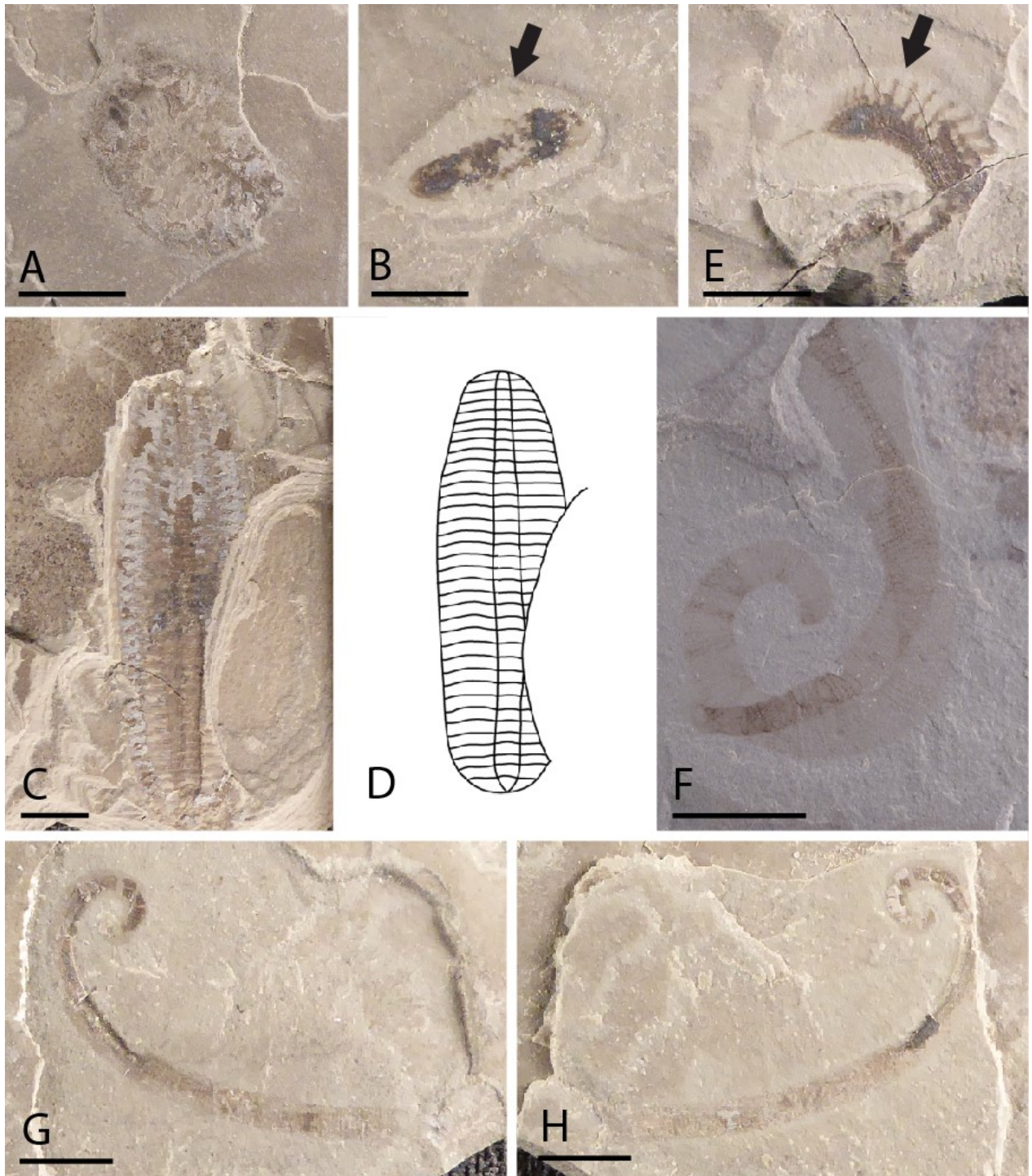
*Fig. 5.* Photographs and an illustration of selected worm-like fossils from the Waukesha Lagerstätte of Wisconsin, USA. **A–C** Three different specimens of a putative aphroditid polychaete assigned to the taxon Aphroditid polychaete sp. 1. **D.** An illustrative and interpretive drawing of the specimen photographed in C. **E.** Lobopodia sp.1, note that the whole body does not seem to be preserved. **F–H** Partially coiled palaeoscolecid worms, where G and H are the part and counterpart of the same individual. The arrows in B and E show the delimitations of the putative decay halos. Scale bars: 1 cm for A and F, 0.5 cm for remaining specimens.

aeoscolecida have been recorded from the Cambrian Series 2 to the upper Silurian. However, the systematic position of paleoscolecidans has been widely debated and their phylogeny is not yet resolved (Martin et al. 2016). For example, the paleoscolecid genus *Palaeoscolex* is well known as a so-called wastebasket taxon. This means that a whole range of fossils, even such just having few of the features characterizing this genus, have previously been lumped there. Over the recent years there has been a reevaluation of some species from this genus (e.g. García-Bellido 2013) but thorough work remains to be done. The unresolved phylogeny of the Palaeoscolecida makes the classification of fossils belonging to the group difficult.

The specimen shown in Fig. 5F resembles a partially coiled worm-like fossil interpreted as a *Palaeoscolex? tenensis* from Lower Ordovician Fezouata Lagerstätte of Morocco (Martin et al. 2016, fig. 2F) in that their length, overall morphology and segmentation are similar. One difference is that the specimen described by Martin et al. (2016) is considerably thinner; approximately 2 mm in width, compared to the maximum width of 9 mm in the Waukesha specimen.

The Waukesha specimen shown in Fig. 5F looks a bit puzzling in its present state of preservation. Either one and the same specimen has been twisted and folded just prior to, or during, early burial, or there are actually parts of two different specimens preserved together, one on top of the other. Both of these scenarios could result in the strange appearance with seemingly doubled soft-body tissue in places.

The specimens in Fig. 5F–H grossly resemble some palaeoscolecid worms in that they are partially curled, worm-like and thinly segmented. Since the specimen shown in Fig. 5F differs from the one in Fig. 5G–H they might belong to different taxa, but both are still assigned to palaeoscolecidans. One possible way to further test the paleoscolecidan affinity of these specimens would be to analyze them in a scanning electron microscope in search of the characteristic minute plate-like scales that are known to cover the external cuticle of these worms (e.g., García-Bellido et al. 2013; see also below and Fig. 7). This was however beyond the scope of the present study.

*Material* – Three specimens (one of which is represented by part and counterpart) from the Silurian Waukesha Lagerstätte of Wisconsin, USA.

## 6.6 Phylum – uncertain
## Class – Palaeoscolecida Conway Morris & Robinson, 1986

### 6.6.1 Palaeoscolecid sp. 2
Figures 6A–F

| *Description and measurements* | |
| --- | --- |
| Length: | 13–21 cm |
| Width: | 0.5–1.0 cm |
| Overall morphology: | Same shape at both ends of the organism. The specimens are curved and one of them (Fig. 6E) seems to lay curled on top of itself. |
| Structure: | Thinly segmented |

*Remarks* – Fossils of this particular type have been classified as leeches (i.e., annelid worms belonging to the subclass Hirudinea) in previously published literature (Mikulic et al. 1985a, fig. 2F; Briggs 1991, fig. 10; Wendruff 2016, fig. 2.7A and 2.7C). Their overall morphology and particularly the distinctive and fine segmentation match those of leeches. In particular one very well-preserved specimen from the Waukesha Lagerstätte has been figured by Briggs (1991, fig. 10). It comprises a large annulate worm that terminates in a sucker-like structure and was suggested to represent a fossil leech. Importantly Briggs (1991) also noted that if the fossil indeed is a leech it pushes back the first appearance of Hirudinea by approximately 280 million years; the oldest previous findings are only 150 million years old, specimens from the Jurassic Period. The fossil record of leeches is unsurprisingly overall scarce and patchy. Today they comprise a successful group of predatory or parasitic worms that are primarily confined to freshwater environments, although rare terrestrial and marine forms also exist (Davies & Govedich 2001).

One main argument for why these types of fossils are being classified as leeches simply relates to their striking morphological similarity with the now-living forms (again, particularly the specimen figured by Briggs 1991, fig. 10, with the sucker-like termination). However, general morphology does not necessarily indicate affinity. A major argument against this interpretation is the presence of microscopic plates on the external surface of the body discovered when studying specimens in high magnification using a SEM (Fig. 7B–F). One of these specimens (Fig. 6E–F and 7A) has on its external surface two different types of plate-like structures; smooth plates (cf. square 1 in Fig. 7B) and in some places instead horn-like structures (cf. square 2 in Fig. 7B). Where a close-up of, perhaps the same, horn-like structure can be seen in Fig. 7C. The smooth plates are approximately 17 µm in diameter and the horn-like structures (Fig. 7C) 13.5 µm.

Also, a second specimen belonging to these types of palaeoscolecid worms (Fig. 6) was imaged using SEM. It is only a fragment (Fig. 7G) but based on the highly characteristic segmentation and overall morpho-

logy it can be assigned to the Paleoscolecid sp. 2 taxon with confidence. Alongside its segmentation (Fig. 7D), small (approximately 17 μm in diameter), round plates with nodes that give rise to a raspberry-like morphology can be observed (Fig. 7E–F). Such external plates are not present in leeches, but in palaeoscolecid worms (García-Bellido et al. 2013). The plates observed in one of the specimens (Fig. 7C) are slightly similar to the so-called "node" microstructures of a palaeoscolecid worm, Gamascolex vanroyi, described from the earliest Late Ordovician strata of the Tafilalt Konservat-Lagerstätte in Morocco (Gutiérrez-Marco & García-Bellido 2015, fig. 4). Moreover, the overall body segmentation of another specimen (Fig. 6B–C) closely resembles that of G. vanroyi (see Gutiérrez-Marco & García-Bellido 2015, fig. 4A–B). They both share a segmentation characterized by thin stripes running perpendicular to the segments.

Raspberry-shaped plates can be seen in a specimen interpreted as the palaeoscolecid worm, Wronascolex antiquus, from the Cambrian Series 2 of the Emu Bay Shale in South Australia, but the nodes are not as distinctly marked as in the specimen discussed herein (Fig. 7E–F; cf. García-Bellido et al. 2013, fig. 5). Wronascolex are long and slender worms with circular phosphatic plates with 3–10 nodes arranged in a single circle sometimes including a central node (García-Bellido et al. 2013). This fits well with the SEM-images shown in Fig. 7E–F. Even if the specimens from the Waukesha Lagerstätte are not congeneric to Wronascolex, their similarities, including the presence of microplates, suggest that the material studied herein comprises a palaeoscolecid species rather than representing a leech.

*Chemical composition* – In order to assess the chemical composition of the Waukesha specimens, a pilot investigation by means of SEM-based elemental mapping was performed on one specimen assigned to the Paleoscolecid sp. 2 taxon (Fig. 7G). The result of this analysis is summarized in Fig. 7G–L and shows the distribution and relative abundance of different elements by the brightness of the tone. The distribution maps of phosphorous (Fig. 7H) and calcium (Fig. 7I) clearly show an enrichment of these elements in the fossil, compared to the surrounding host rock. This suggests that the worm was preserved mainly as calcium phosphate. This fits well with the general interpretation of the mode of preservation of the Waukesha Lagerstätte fossils (see Wendruff 2016), but also specifically with regards to palaeoscolecid worms, the plates of which typically are preserved in calcium phosphate (Martin et al. 2016).

By contrast, there is a slight depletion of silica in the fossil (Fig. 7J) compared to that of the matrix which reflects the siliciclastic component of the host rock. The carbon map (Fig. 7K) reveals very low concentrations within the rock suggesting little to no organic matter left in the fossil specimen (the halo of elevated levels of carbon is an artefact caused by the carbon tape used to keep the specimen in place). Sulphur (Fig. 7L) shows elevated levels in an area in the center of the fossil specimen. Microscopic irregular roundish structures (ca 0.1 mm in diameter) can be seen in this same area in SEM-images (vaguely visible in Fig. 7G). The irregular shapes of the structures indicate that they are not part of the fossil but instead comprise inorganic sedimentary particles and of which the elevated level of sulphur is suggestive of pyrite.

*Material* – Three specimens (and some small fragments) from the Silurian Waukesha Lagerstätte of Wisconsin, USA.

## 6.7 Other fossil material
Figure 8

*Remarks* – In addition to the specimens described above, the studied Waukesha collection of "worm-like fossils" include a number of enigmatic specimens that are very difficult to interpret and classify in terms of biological affinity. However, in order to present the full representation of the study assemblage these specimens are shown in Fig. 8 and briefly addressed below. This also provides for a better estimation of the taxonomic diversity of the Waukesha Lagerstätte, and opens up for the possibility of improved identifications in the future.

The elongated specimen shown in Fig. 8A is vermiform in its shape and has a distinct segmentation, at least for ca three-fourths of the body length. However, it lacks segmentation at its presumable head (seen to the left in Fig. 8A) which indicates that it could be some arthropod species with a relatively large head shield. It is uncertain whether or not the arched, sinusoidal line close to the outer termination of the head, and perpendicular to length axis of the body, is part of the body morphology or not (that is, simply representing a physical crack). Its smooth and near symmetrical architecture, however, indicate that it is an anatomical feature.

The fossilized organism shown in Fig. 8B has a larger head relative to the rest of its body and barely visible body segmentation. The overall shape of the fossil is slightly reminiscent of a specimen from the Waukesha Lagerstätte found by Meyer & Gunderson (1986, fig. 11), which they, together with similar fossils, called a "helmet animal". Meyer & Gunderson also noted that the "helmet animal" has been interpreted by Mikulic et al. (1985a,b) as a xiphosuran. One difference between the fossil discussed herein (Fig. 8B) and the "helmet animal" of Meyer & Gunderson (1986, fig. 11) is that the number of segments is fewer in the latter.

One of the specimens in the collection of worm-like taxa from the Waukesha Lagerstätte is truly enigmatic (Fig. 8C) and shows little resemblance to the remaining specimens described in this paper. It has a faint, barely visible and very thin annulations throughout the length of the specimen. It does not look like it belongs to any worm phylum, but instead might represent a sponge (Porifera). There is a swollen round structure to the right in the image (Fig. 8C), shown by an arrow, which could be the osculum of a sponge. The organism appears to be divided into two parts, both of which are oval in shape and of which one part, seen to the left in Fig. 8C, is considerably thinner (representing ca half the maximum width) than the other part. If the round shape to the right in the photo-
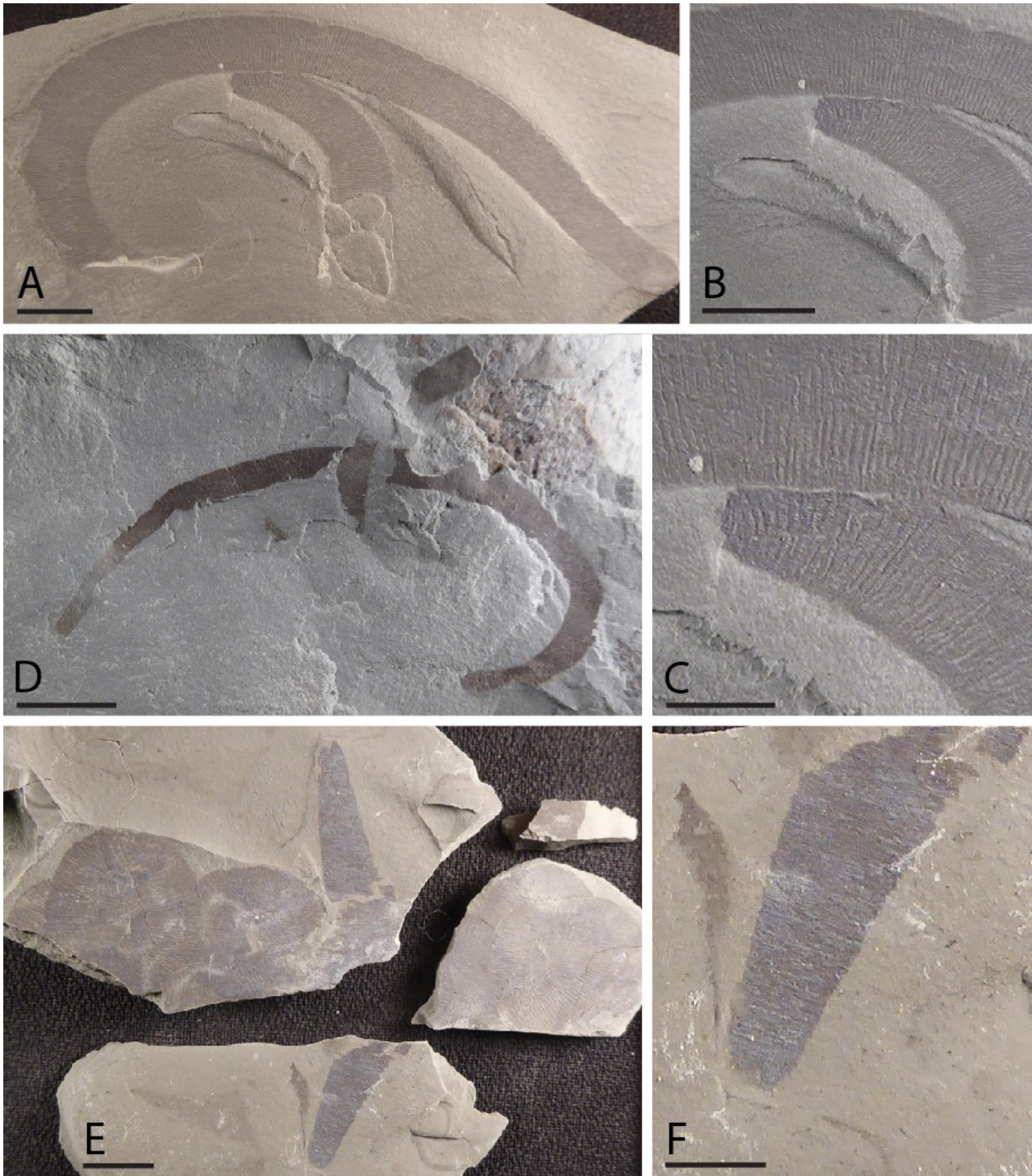
*Fig. 6.* Photographs of three different specimens assigned to Palaeoscolecid sp. 2. from the Waukesha Lagerstätte of Wisconsin, USA. Figures A, D, and E shows the different specimens and the remaining images are close-ups. **A–C** An exceptionally well-preserved specimen shown in different magnifications; in the detail images **B–C**, thin stripes can be seen running perpendicular to the segments. **D.** A second specimen assigned to Palaeoscolecid sp. 2. **E–F** Slabs showing parts of and jumbled bodies of Palaeoscolecid sp. 2. With the close-up photograph **F** showing the fine segmentation. Scale bars: 1 cm for A, B, D and E, 0.5 cm for the remaining.
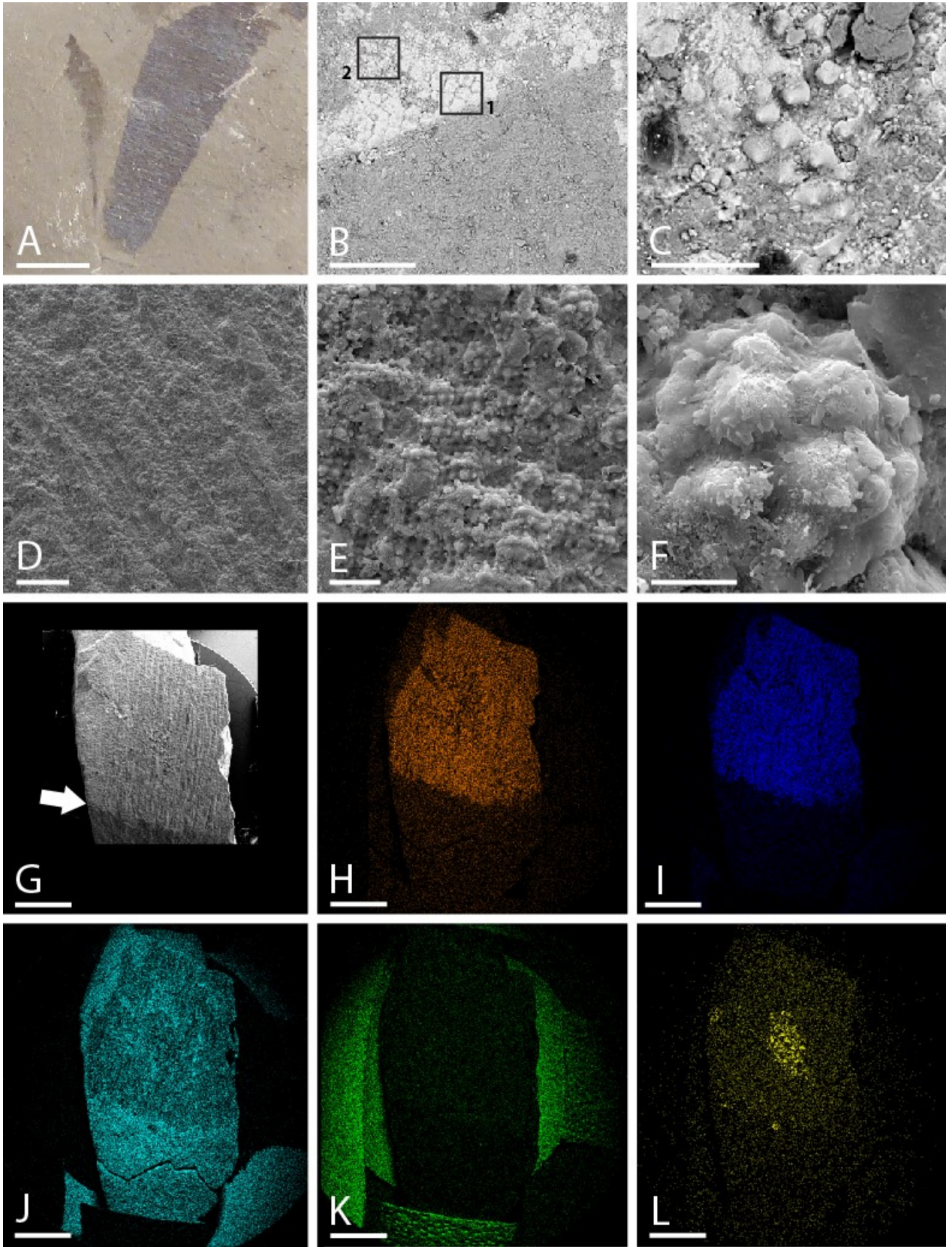
graph is an osculum, then the left part represents the lower part where the sponge would be attached to the sea floor. However, the entire organism might not be preserved as a fossil, but parts may be, and likely are, missing from the lowermost portion (i.e., to the left in Fig. 8C). This suspicion is strengthened further when studying both sides of the specimen, as they are preserved as part and counterpart. If the specimen is a sponge, its faint segmentation indicates that it could belong to the sphinctozoan sponges which are segmented (Reitner & Keupp 1991).

The vermiform specimen shown in Fig. 8D is only 0.8 cm in maximum length. It somewhat resembles a lobopod and might otherwise represent an annelid (possibly even an aphroditid form due to its sub-oval and dorso-ventrally flattened shape).

Fig. 8E shows the fossil of a wide-bodied putative annelid which could belong to the same group as the Palaeoscolecid sp. 2 discussed above (cf. Fig. 6). There is a whitish substance to the right that is present in some of the fossils (e.g. Fig. 5C, 5H, 6E–F, 8A and 8H) which probably is phosphate. The elemental mapping on one of the palaeoscolecid worms (Fig. 7G) furthermore showed an enrichment of calcium phosphate.

The specimens shown in Fig. 8F–H are segmented throughout the length of (what is left of) their entire bodies. They are all incomplete and the strongly tapering end which still seems to be intact could be the head region. There are two fossils on the slab shown in Fig. 8F which are of different overall size and style of segmentation. These two fossils might both represent annelids, but they clearly are different species. The larger specimen (seen to the left in Fig. 8F) has a darker area running through the body which could be remains of the gastrointestinal tract.

The specimens in Fig. 8G–H visually resemble Oligochaeta (a subclass of Annelida), but since most oligochaetes are terrestrial and the Waukesha Lagerstätte clearly is of marine origin this seems unlikely (cf. Brinkhurst & Gelder 2001). The rolled-up one of these two specimens (Fig. 8H) is, unlike most other specimens, covered by a whitish matter which probably represents calcium carbonate and/or phosphate coating. As it differs from many other specimens in this aspect it could also indicate a unique biological affinity of the fossil itself.

*Material* – Eight specimens from the Silurian Waukesha Lagerstätte of Wisconsin, USA.

# 7 Discussion

In some of the specimens analyzed herein there is a distinct whitish border present in the host rock immediately surrounding the actual fossil (see Figs. 4B, 5B, 5E and 8A), and similar structures have been reported also from other fossils from the Waukesha Lagerstätte (Wendruff 2016). These are interpreted as so-called decay halos which in turn are the evidence of microbial activity related to the taphonomic processes. These types of halos are created around decaying organic material and consist of a microbial consortium which enables authigenic mineralization (Borkow & Babcock 2003; Briggs 2003). It might be these microbes that mediate precipitation of some minerals such as calcium phosphate, silica and pyrite and enabling exceptional preservation in the Waukesha Lagerstätte, as well as in other Konservat-Lagerstätten (Borkow & Babcock 2003; Briggs 2003; Wendruff 2016).

The Waukesha Lagerstätte includes fossils from a wide range of life-forms, most notably including various arthropods and worm-like organisms. The fossils specifically addressed in this paper all comprise well-preserved, soft-bodied worm-like organisms. Because many worm groups have no or very few hard parts included in their anatomies, they obviously have a limited potential of preservation. This can complicate interpretation of the fossils as there might be, and often are, important anatomical structures which cannot be seen in the fossils. Collectively, this also explains why their fossil record is scant and patchy (Parry et al. 2019). Full body fossils of worms and worm-like phyla are therefore almost exclusively recorded from Konservat-Lagerstätten, which is also why new discoveries – such as the Waukesha specimens described herein – are of great importance for our understanding of their evolution and ecology in a deep time perspective.

Even though annelids and arthropods belong to different phyla, they possess many similar traits. These include distinct segmentation and sometimes also a correspondence in size and an overall vermiform morphology. These similarities result in Waukesha specimens that are difficult to classify, even at a relatively high taxonomic level. Specimens in this study have mostly been taxonomically assessed by comparisons to similar types of fossils or extant organisms described in the published literature. However, as referenced at above, there is a dire need of more fossils of worm-like animals in general to be unearthed, ca-

*Fig. 7.* Different images of specimens assigned to Palaeoscolecid sp. 2. from the Waukesha Lagerstätte of Wisconsin, USA. **A-C** The same specimen as shown in Fig. 6F; **A.** Photographic representation. **B.** Backscattered SEM-image (BSE-image) of the specimen in which the lighter part represents the fossil and the darker area represents the matrix. Two different plate structures can be seen in the black squares, there are polygonal smooth looking plates in square 1 and horn-like structures in square 2 that could be the same structures as in C. **C.** Close-up SEM-image of some of the plates or nodes seen in C. **D–F** SEM-images of another specimen belonging to Palaeoscolecid sp. 2 (an overview of the small fragment is shown in G); **D.** The fine external segmentation in which small rounded plates can be observed. **E.** The plates are show in greater magnification. **F.** Enlargement of one of the raspberry-shaped plates, also seen in the upper right corner of Fig. E. **G–L** BSE-image and elemental maps of the same specimen as shown in Fig. D–F. The arrow in G points at the border between the fossil and the matrix. **H–L** Elemental maps showing the distribution and relative abundance of different elements and the brighter the tone, the higher the level of a certain element; H) Phosphorus, I) Calcium, J) Silica, K) Carbon, and L) Sulphur. Scale bars: 0.5 cm for A, 100 μm for B, 50 μm for C, 200 μm for D, 20 μm for E, 5 μm for F, 2 mm for G–L.
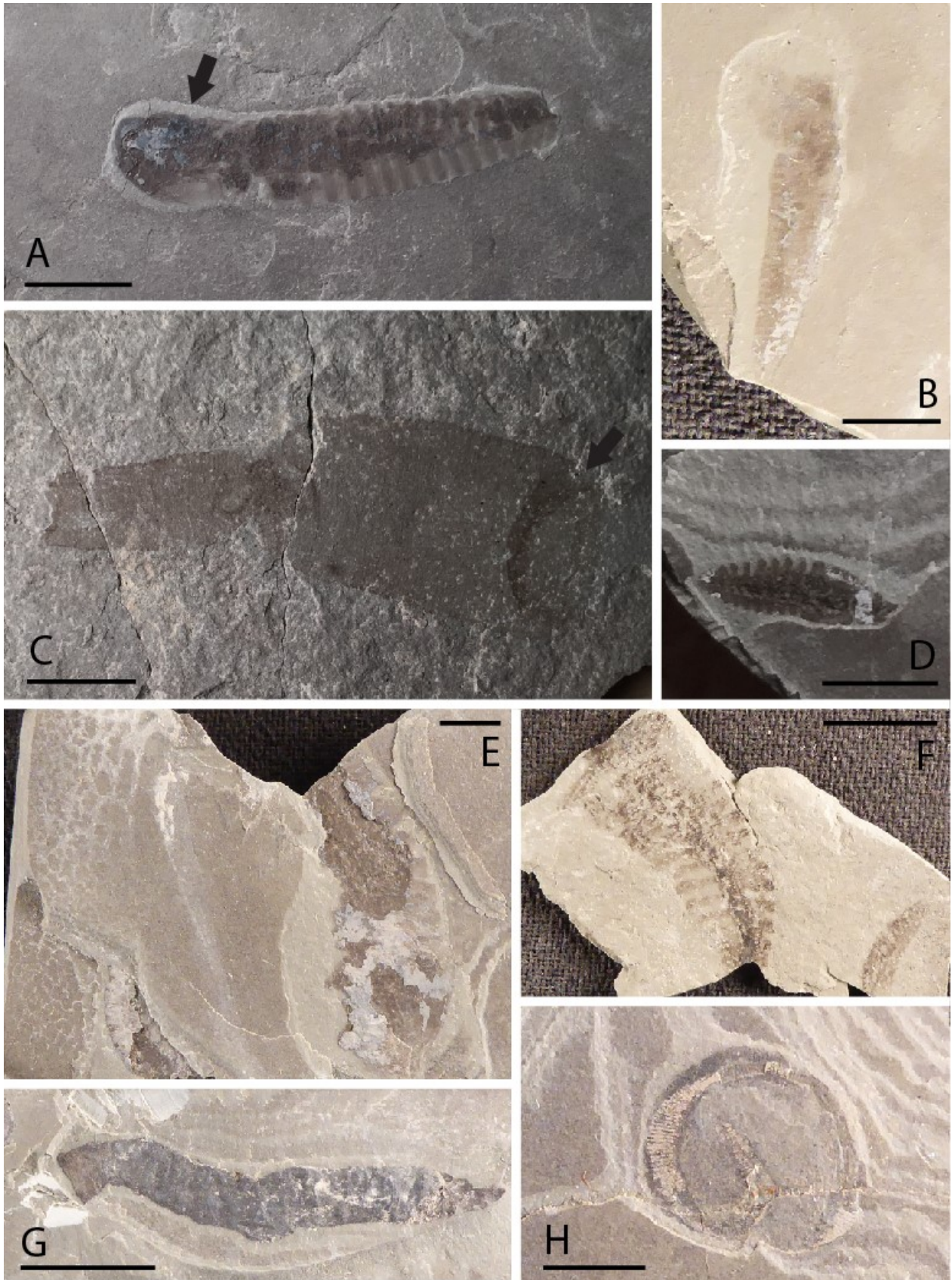
*Fig. 8.* Photographs of selected enigmatic fossils from the Waukesha Lagerstätte of Wisconsin, USA, in the main text referred to as "other fossil material". **A.** A putative arthropod with a suture line or crack in the left side of the head region which might suggest an anatomical structure. The black arrow shows the presence and delimitation of, a decay halo. **B.** Another putative arthropod specimen. **C.** A sponge-like organism, the black arrow points at its presumable osculum. **D.** A worm-like fossil. **E.** Possibly a wide-bodied annelid, perhaps a palaeoscolecid worm. **F–H** Other worm-like fossils. Scale bars: 1 cm for A, C, F and G, 0.5 cm for B, D and E.

refully examined, and published upon in order to facilitate more robust systematic classifications. Another complicating factor regarding specifically to the Waukesha fossils is the limited number of published studies dealing with similar material of co-eval (or at least, nearly so) age.

The classification of palaeoscolecid worms is especially tricky because Palaeoscolex has acted as a wastebasket taxon. Many people have in recent time try to work out how the different worms/worm-like organisms in this group are related to one another and where they belong in the phylogeny (e.g. Hou & Bergström 1994; Conway Morris 1997; Harvey et al. 2010). Some specimens that have previously been placed in Palaeoscolex have in recent years been reclassified (e.g. García-Bellido 2013). The relationships between the different animals will become better understood the more work that goes into this. It is therefore important to describe and analyze additional fossils of palaeoscolecid worms from different ages and localities. Moreover, this is not limited to species similar to, or placed in, Palaeoscolex (Conway Morris 1997), but also other Palaeoscolecida genera such as Mafangscolex (Vannier & Martin 2017), Wronascolex, Guanduscolex, and Wudinscolex (García-Bellido et al. 2013). However, even with robust studies of such specimens there would probably still be many worm-like fossils that would be classified with open nomenclature. This because of to the relative few morphological traits that are diagnostic for the separate taxa, which in turn is due to poor preservation, of these organisms, even in Lagerstätten. It would require exceptionally well-preserved material in order to obtain an unambiguous systematic placement, which is not the case with all the material from the Waukesha Lagerstätte.

# 8 Conclusions

- In total, eight different worm-like taxa have been identified in the studied collection of fossils from the Silurian Waukesha Lagerstätte of Wisconsin, USA. The fossils constitute a variety of vermiform fossils, of which not all belong to Annelida, but probably also Arthropoda as well as Porifera. This suggests that worms and worm-like organisms formed an important component of the past biotas that are now preserved in the Waukesha Lagerstätte.

- Despite their exceptional preservation, the worm-like fossils of Waukesha Lagerstätte are complicated to interpret and unambiguously assign to specific taxa. This partly also results from the scarcity of published comparative material of a similar age.

- The specimens previously interpreted to represent leeches are herein rather considered to be palaeoscolcid worms (Fig. 6; cf. Wendruff 2016). This assessment was primarily based on detailed SEM-studies which revealed the presence of plates and nodes, closely similar to those reported from other palaeoscolecidans. There were two different plate structures of which the raspberry-shaped one (Fig. 7E–F) have the right number of nodes to place the specimen in the genus Wronascolex.

- Future studies that would be of interest to conduct on the collection at hand include more detailed investigations of fine structures in SEM, and from a wider range of specimens. This could most specifically help in interpretations of the suspected palaeoscolecidans.

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