Paleobiology and Taphonomy of Exceptionally Preserved Organisms from the Brandon Bridge Formation (Silurian), Wisconsin, USA

Dissertation

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

Andrew J. Wendruff, M.Sc.

Graduate Program in Geological Sciences

The Ohio State University

2016

Dissertation Committee:

Loren E. Babcock, Advisor

William I. Ausich

Steven K. Lower

John P. Hunter

Rodney M. Feldmann
Copyrighted by

Andrew J. Wendruff

2016
Abstract

The Waukesha Lagerstätte in the Brandon Bridge Formation (Silurian: Llandovery Series, Telychian Stage) hosts a diverse, exceptionally preserved fauna. Similar to a number of other Silurian Lagerstätten in Laurentia, it was deposited on a warm, shallow-marine carbonate platform. The Waukesha Biota includes an interesting assemblage of organisms, some of which are characteristic of Silurian epeiric seas, others of which are expected but rare in the Silurian, and still others that could be considered “holdovers” of groups more characteristic of the Cambrian.

The Waukesha Lagerstätte hosts a diverse biota of metazoans that are mostly marine but also probably some terrestrial forms. Taxa include biomineralized trilobites, conulariids, *Sphenothallus*, and a variety of non-biomineralized or lightly skeletonized arthropods, lobopodians, ‘worms,’ a cubozoan, chordates, and graptolites. Echinoderms, cephalopods, brachiopods, gastropods, bivalves, bryozoans, and corals, which are biomineralized and normally common in Silurian shelf lithofacies, are rare or unknown.

The Waukesha Lagerstätte substantially increases our understanding of the biota of Silurian carbonate platform ecosystems. Many of the taxa are represented by similar organisms in other less well-known Silurian Lagerstätten. The existence of the diverse Waukesha Biota is the result of specific taphonomic processes related to localized and atypical depositional conditions. Microbial processes contributed in important ways to exceptional preservation in this deposit.
Dedication

This work is dedicated to my wife, Diana.
Acknowledgments

First and foremost, I would like to thank my loving wife Diana who has listened to me ramble on about rocks for as long as I have known her. She has constantly encouraged me when I needed it. Special thanks are in order to those who collected the material I have spent the last five years examining: notably Don Mikulic, Joanne Kluessendorf, Steve LoDuca, Gerry Gunderson, Ron Meyer. I would also especially like to thank Carrie Eaton for loaning out numerous specimens, accessioning new specimens and photographing others when we were unable to make the trip. Don Mikulic and Joanne Kluessendorf have been especially helpful with discussion and information on the Silurian of Wisconsin. They helped me get access to this material, and I am most grateful for the opportunity. I would like to thank friends and colleagues including Wade Jones, Jessie Kastigar, Aaron Leblanc, and many others for discussions, support and encouragement throughout the years. Scott McKenzie, my first mentor, has always been willing to listen, offer support, and provide the occasional comparative specimen for that I am always thankful. I would also like to thank my committee members, Bill Ausich, Steve Lower, Rod Feldmann and John Hunter, for their time and expertise. Stig Bergstrom, though you were unable to serve on my committee, I have benefited from your breadth of knowledge and stories. Angie Rogers without you I am fairly certain nothing would ever get done, and I am thankful for all of your help. Finally, I would like
to thank my advisor, Loren Babcock, who has helped me grow as a scientist. I have
learned immensely from you in the last five years. I look forward to our continued work
and what I will learn from you in the future.
Vita

May 2003 ......................................................Toms River High School South

2008..............................................................B.S. Geology, Mercyhurst University

2011..............................................................M.Sc. Biology, University of Alberta

2011 to present ...........................................Graduate Teaching Associate, Department

of Earth Sciences, The Ohio State

University

Publications


**Fields of Study**

Major Field: Geological Sciences
## Table of Contents

Abstract ........................................................................................................................................... ii  
Dedication ........................................................................................................................................ iii  
Acknowledgments ............................................................................................................................... iv  
Vita .................................................................................................................................................... vi  
List of Tables .................................................................................................................................... ix  
List of Figures .................................................................................................................................... x  
Chapter 1: Overview ......................................................................................................................... 1  
Chapter 2: Palaeobiology and Taphonomy of the Waukesha Biota ............................................... 11  
Chapter 3: A Silurian ancestral scorpion ........................................................................................... 73  
Chapter 4: Paleobiology and taphonomy of an early scorpion ....................................................... 92  
Chapter 5: New cheloniellid arthropod from the Silurian of Wisconsin ....................................... 143  
Chapter 6: Silurian lobopodians from the Waukesha Lagerstätte ................................................. 168  
Chapter 7: A non-biomineralized chordate from the Waukesha Lagerstätte ............................... 184  
References ....................................................................................................................................... 202
List of Tables

Table 4.1 Characters and character states present in some of the most completely known Paleozoic scorpions .......................................................... 125

Table 4.2 Comparison of data used to infer habitats of some Paleozoic scorpions ...... 127

Table 6.1 Paleozoic lobopodians known from articulated material ............................... 180
List of Figures

Figure 1.1 Location of Waukesha Lime and Stone Company quarry and Franklin Aggregate Inc. quarry .............................................................. 7

Figure 1.2 General stratigraphic section of uppermost Ordovician into mid-Silurian strata of southeastern Wisconsin ................................................................. 9

Figure 2.1 Location of Waukesha Lime and Stone Company quarry and Franklin Aggregate Inc. quarry .............................................................. 51

Figure 2.2 General stratigraphic section of uppermost Ordovician into mid-Silurian strata of southeastern Wisconsin ................................................................. 53

Figure 2.3 Large trilobites from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................. 55

Figure 2.4 Small trilobites from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................. 57

Figure 2.5 Non-mineralised and lightly skeletonised arthropods from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................. 59

Figure 2.6 Shelly organisms from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................. 61

Figure 2.7 ‘Worms’ from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................. 63

Figure 2.8 Hemichordates and chordates from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................. 65

Figure 2.9 Dalmanitid trilobites preserved on flinz from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin (UWGM 5581) showing bidirectional alignment in rose diagram .............................................................. 67

Figure 2.10 Sedimentary and microbial structures from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................. 69
Figure 2.11 Microbial obrution explanatory diagram ............................................................. 71

Figure 3.1 Parioscorpio venator gen. et sp. nov., Brandon Bridge Formation (Silurian), Wisconsin, USA .................................................................................................................. 84

Figure 3.2 Medial structures associated with the pulmonary-cardiovascular system in Silurian and Holocene scorpions ............................................................................................. 86

Figure 3.3 Reconstruction of Parioscorpio venator gen. et sp. nov. ........................................... 88

Figure 3.4 Hypothesis of relationship among some of the more completely known Paleozoic scorpions, with geologic time scale at left .............................................................. 90

Figure 4.1 Parioscorpio venator, n. gen., n. sp., holotype, part, UWGM 2162, Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin preserved in dolomudstone ............................................. 129

Figure 4.2 Parioscorpio venator, n. gen., n. sp., holotype, UWGM 2162, Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin ......................................................... 131

Figure 4.3 Parioscorpio venator, n. gen., n. sp., paratype, UWGM 2163, a specimen preserving some ventral anatomy but split through the body, Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin ................................................................. 133

Figure 4.4 Circulatory and respiratory system of a Holocene scorpion ..................................... 135

Figure 4.5 Chronostratigraphic positions of Silurian to Carboniferous (Mississippian) scorpions ................................................................................................................................. 137

Figure 4.6 Reconstruction of Parioscorpio venator n. gen., n. sp. ........................................... 139

Figure 4.7 Hypothesis of relationship among some of the more completely known Paleozoic scorpions, with geologic time scale at left ................................................................. 141

Figure 5.1 Latromirus tridens, n. gen. sp. from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin preserved in dolomudstone ................................................. 166

Figure 6.1 Undetermined lobopodians from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin .............................................................................................. 182

Figure 7.1 Location of Franklin Aggregate Inc. quarry ............................................................ 196

Figure 7.2 Incomplete chordate from the Brandon Bridge Formation (Silurian, Llandovery, Telychian), Franklin Aggregate Inc. quarry, Franklin, Wisconsin, showing
trunk and caudal regions .......................................................................................................................... 198

Figure 7.3 Slab with incomplete chordate, unidentified arthropods and ‘worms’ from the Brandon Bridge Formation (Silurian, Llandovery, Telychian), Franklin Aggregate Inc. quarry, Franklin, Wisconsin ........................................................................................................... 200
Chapter 1: Overview

Introduction

Studies of Paleozoic Lagerstätten, or deposits of exceptional preservation, have in recent years concentrated on the Cambrian. With some exceptions, less well studied are a number of post-Cambrian deposits, and as a result the evolutionary fate of certain clades and fossilization mechanisms are often more speculative. Lagerstätten have been shown to have a tendency to be time specific (e.g., Allison and Briggs, 1993; Zhu et al., 2006; Babcock et al., 2015). In the Paleozoic, the Cambrian, Silurian and Carboniferous systems are host to a large number of localities yielding exceptionally preserved fossils. They provide a series of time slices documenting widely separated points in the evolution of life on Earth, and documenting the expansion of life forms from the marine realm to terrestrial habitats.

One of the more diverse Silurian biotas known at present is preserved in the Waukesha Lagerstätte of the Brandon Bridge Formation (Llandovery, Telychian) in southeastern Wisconsin (Mikulic et al., 1985a, b; Figs. 1.1, 1.2). This deposit records life forms from a shallow, tropical carbonate platform environment and associated islands. It provides insight into biodiversity of marine forms in the early Paleozoic as well as providing details about nascent terrestrial habitats at the time when metazoans were first
colonizing them.

Strata yielding exceptionally preserved biota of the Waukesha Lagerstätte are present in two quarries, located about 32 km apart, in southeastern Wisconsin (Fig. 1.1). Most previously documented material, and much of that documented here, was collected from the Waukesha Lime and Stone Co. quarry at Waukesha, Wisconsin (see Mikulic et al., 1985a, b; Smith et al., 1987; Kluessendorf, 1994; Kluessendorf and Mikulic, 1996; Mikulic and Kluessendorf, 1998; LoDuca et al., 2003; Moore et al., 2005; Haug et al., 2014; Jones et al., 2016). Some material reported here is from the Franklin Aggregate Inc. quarry at Franklin, Wisconsin.

This dissertation involves varied studies of the biota and fossilization history of the Waukesha Lagerstätte. Chapters are formatted as papers to be submitted to a number of specialty journals. The Waukesha deposit yields a diverse biota of non-biomineralized and lightly skeletonized organisms in association with typical biomineralized Silurian organisms such as trilobites and conulariids. Some members of the biota have been described previously (e.g., Smith et al., 1987; Moore et al., 2005; Haug et al., 2014; Jones et al., 2016), and others are documented here. In addition to the metazoan body fossils, trace fossils and evidence of prokaryotes (microbes) are documented here. Some microbes are shown to have played a leading role in the early taphonomic history of metazoans in this deposit.
Summary of Contents

This dissertation is organized with papers emphasizing two aspects of the Waukesha Lagerstätte. One is an overview of the biotic composition and taphonomy, and the other documentation of some new or poorly known taxa. Each of the chapters that follows is planned to be a separate paper and is formatted in the style of the journal for which it is intended. Some of the journals are published in the United States and others in Europe, and English language usage reflects journal preference.

Chapter 2 is a review of the Waukesha Biota with discussions of paleobiology and taphonomy. Members of the biota include a number of Burgess Shale-type taxa as well as exceptionally preserved Silurian arthropods and ‘worms.’ Trilobites and conulariids are common. Other Silurian organisms such as gastropods, corals, bryozoans and brachiopods are rare to absent. Examination of the depositional environment of the Brandon Bridge Formation allowed for the development of a model, involving microbial mediation, that helps explains the exceptional preservation of some organisms. This model may explain the abundance of Konservat-lagerstätte in the Silurian of Laurentia. This chapter is formatted for submission to *Lethaia*.

Chapter 3 is a description of a new fossil scorpion from the Brandon Bridge Formation (Waukesha Lagerstätte) in the Waukesha Lime and Stone Co. quarry, Waukesha, Wisconsin. It represents the earliest arachnid in the fossil record. Anatomical structures are preserved that help to shed light on the evolution of early land-dwelling arthropods and how they achieved terrestrialization. Elements of the respiratory and
circulatory systems allowed for comparisons with extant chelicerates, scorpions and horseshoe crabs. These comparisons show that essentially no structural changes have occurred in the main elements of the respiratory and circulatory systems since the Silurian and that arachnids were ‘predapted’ for life on land. This paper is formatted for Nature.

Chapter 4 is a more detailed description of the new scorpion from the Brandon Bridge Formation. Arguments for a terrestrial or aquatic origin of scorpions (and arachnids in general) are systematically reviewed. This chapter is formatted for submission to Palaeontology.

Chapter 5 is a description of a non-biomineralized arthropod from the Brandon Bridge Formation in the Waukesha Lime and Stone Co. quarry, Waukesha, Wisconsin. Although previously illustrated (Mikulic et al., 1985a, b), new specimens indicate a range of taphonomic issues that hindered full interpretation previously. More complete specimens suggest morphological reinterpretation and an affinity with the rather enigmatic Cheloniellida. This chapter is formatted for the Bulletin of Geosciences.

Chapter 6 documents two lobopodians from the Brandon Bridge Formation in the Waukesha Lime and Stone Co. quarry, Waukesha, Wisconsin. They are left in open nomenclature because key anatomy is absent or indistinctly preserved. These forms represent the first described lobopodians from the Silurian and add considerably to their scant post-Cambrian record. This chapter is formatted for the Journal of Paleontology.

Chapter 7 documents non-biomineralized chordates from the Brandon Bridge Formation in the Franklin Aggregate Inc. quarry, Franklin, Wisconsin. They are left in
open nomenclature because cranial regions are unknown at present. Otherwise, these specimens preserve typical chordate features including v-shaped muscle blocks and a notochord. This chapter is formatted for the *Journal of Paleontology*.

**References**


Fig. 1.1. Location of Waukesha Lime and Stone Company quarry and Franklin Aggregate Inc. quarry. A, map of the United States showing the location of Wisconsin. B, map of Wisconsin showing the locations of the Waukesha Lime and Stone Co. quarry (WQ) and Franklin Aggregate Inc. quarry (FQ). C, part of Waukesha 7.5’ topographic quadrangle map, Wisconsin (U.S. Geological Survey, 2013, 1:24,000) showing position of Waukesha Lime and Stone Company quarry (WQ). D, part of Greendale 7.5’ topographic quadrangle map, Wisconsin (U.S. Geological Survey, 2013, 1:24,000) showing position of Franklin Aggregate Inc. quarry (FQ).
Fig. 1.1
Fig. 1.2. General stratigraphic section of uppermost Ordovician into mid-Silurian strata of southeastern Wisconsin. Arrow indicates position of Waukesha Lagerstätte within the Brandon Bridge Formation. Figure provided by Joanne Kluessendorf and Don Mikulic.
Fig. 1.2
Chapter 2: Palaeobiology and Taphonomy of Exceptionally Preserved Organisms from the Waukesha Biota (Silurian), Wisconsin, USA

Introduction

The Brandon Bridge Formation hosts the Waukesha Biota, an important Silurian Konservat-lagerstätte yielding a diverse assemblage of arthropods, non-biomineralised organisms and enigmatic creatures (Mikulic et al., 1985a, b). The biota includes members characteristic of the Laurentian shelf in the Silurian (Weller, 1900; Weller, 1907; Feldman, 1989; Peters & Bork, 1999) but also has organisms that could be considered ‘holdovers’ or novelties better known from Cambrian Burgess Shale-type deposits. Some taxa, including a conodont retaining soft tissues (Smith et al., 1987), an early synzipsosurine (Moore et al., 2005) and an early thylacocephalan crustacean (Haug et al., 2014), have been described and descriptions of others are in preparation. Biomineralising taxa, apart from trilobites, are rare. Palaeoscolecid worms, great-appendage arthropods, lobopodians and a chordate comprise some of the non-biomineralised fauna. Other notable taxa include an early arachnid, leech and box jellyfish (cubozoan). Several ‘worm’ and arthropod species preserve digestive tracts. The Waukesha Biota is among the earliest Silurian Konservat-lagerstätten, representing a taphonomic window into the evolutionary recovery following the end-Ordovician extinction.
In this paper, we address the overall biotic composition of the Waukesha Lagerstätte and explore its taphonomic history. New information highlights the importance of microbial processes, among other factors, in promoting exceptional preservation in the deposit. A depositional model is presented for the Waukesha Lagerstätte that also may explain exceptional preservation in other Silurian deposits of exceptional preservation of Laurentia.

Significance of the Waukesha Lagerstätte

The stratigraphic record is dotted with Konservat-lagerstätten (or simply ‘Lagerstätten’), yielding exceptionally preserved fossils (Seilacher, 1970). Exceptional preservation commonly refers to fossils in which non-biomineralised parts, such as chitin (arthropod cuticle) and internal organs are preserved, not merely hard parts such as bones, teeth and shells. Hard part preservation dominates much of the fossil record (Kidwell & Flessa, 1995), and exceptional preservation is a relatively uncommon occurrence. These deposits (e.g., Burgess Shale, Chengjiang, Hunsrück Slate, Mazon Creek and Solnhofen) are celebrated and intensely studied because they provide important glimpses into, among other things, evolutionary history, palaeoecology, palaeobiology, palaeoenvironments and the processes of fossilisation (taphonomy). Some Lagerstätten have attracted an enormous amount of interest because they offer insight into the evolution of animals during a critical time in Earth history.

Two intervals of the Paleozoic seem to have a disproportionately large number of
non-concretionary Lagerstätten, the Cambrian and Silurian. With few exceptions (e.g., eurypterids; Clarke & Ruedemann, 1912; Andrews et al., 1974; Kluessendorf, 1994; Ciurca & Tetlie, 2007; Tetlie et al., 2007; Vrazo et al., 2016), exceptionally preserved fossils from Silurian deposits are not as well known and less studied than those of the Cambrian. Strictly from a large-scale perspective, Cambrian and Silurian Lagerstätten share some interesting similarities but differ in some fundamental ways. Similar to the Cambrian deposits, those of the Silurian record biotic events during a critical interval of Earth history: it was the time during which, for example, jawed fishes evolved, the Mid-Paleozoic Marine Revolution (Signor & Brett, 1984) was in early stages, coral-stromatoporoid reefs became common and widespread, vascular land plants were evolving, and arthropods first became fully terrestrial. In contrast with the Cambrian, many Silurian Lagerstätten are in dolomitised carbonate platform deposits. Some examples of Silurian Lagerstätten have obrution (or sediment-smothering) beds (e.g., Rochester and Waldron Shales). Exceptional preservation is commonly attributed to dysoxic or anoxic conditions or sediment smothering in the Cambrian (e.g., Whittington, 1971; Conway Morris, 1986; Caron & Jackson, 2006; Gaines, 2014). Predominantly, these Silurian Lagerstätten of the palaeocontinent Laurentia occur in shallow carbonate platform settings (Kluessendorf, 1994), including tidal flats, sabkhas, and inter-reef patches (e.g., Shaver, 1991; 1996). Preservational mechanisms responsible for exceptional preservation in the Silurian may have occurred locally, involved fluctuating environmental conditions, even perhaps time-specific facies (compare Brett et al., 2012; Babcock et al., 2015).
Konservat-lagerstätten, such as the Brandon Bridge Formation, preserve non-biomineralised and lightly mineralised organisms that are typically absent from the fossil record (Seilacher, 1970; Seilacher et al., 1985). A large proportion of Holocene marine ecosystems comprises organisms lacking hard tissues with poor preservational potential (Conway Morris, 1986). For this reason, Konservat-lagerstätten are thought to provide glimpses into biotic diversity that is commonly lost from the stratigraphic record (Conway Morris, 1986, Conway Morris et al., 1987; Conway Morris, 1989; Butterfield, 1995). Much of the focus on Burgess Shale-type localities (Hagadorn, 2002) has been on matters related to the the ‘Cambrian Explosion’ and the presence of presumed short-lived enigmatic groups, such as the anomalocaridids that seemingly disappeared shortly after they appeared (Allison & Briggs, 1993; Zhang et al., 2001; Butterfield, 2003). Recently, several Ordovician Konservat-lagerstätten were reported to yield classic Burgess Shale-type taxa (see Farrell et al., 2010; Van Roy et al., 2010; Botting et al., 2011; Young et al., 2012; Botting et al., 2015) that were previously thought to have become extinct at the end of the Cambrian (Conway Morris, 1989). Some Burgess Shale-type taxa are also present in the Waukesha Lagerstätte. Kluessendorf (1994) provided an analysis of North American Silurian Konserat-lagerstätten, and concluded that they have a predictable pattern of occurrence and provide information about the less commonly preserved components of Silurian epeiric seas.
Material and Methods

This study is based mostly on specimens collected from dolostone of the Waukesha Lagerstätte in the Brandon Bridge Formation (Silurian), Waukesha Lime and Stone Company quarry, Waukesha, Wisconsin (see Mikulic et al., 1985a, b; Kluessendorf and Mikulic, 1996). Specimens were collected in quarry blast piles; none were collected in situ. Additional specimens were collected from blast piles in the Franklin Aggregate quarry, Franklin, Wisconsin, which exposes the same unit. Specimens from the Waukesha Lime and Stone Company Quarry are deposited in the University of Wisconsin Geology Museum, Madison, Wisconsin, USA (UWGM). Specimens from the Franklin Quarry are deposited in the Field Museum of Natural History, Chicago, Illinois, USA (FMNH).

Specimens were photographed with a Canon EOS Rebel T3i Digital SLR with a Canon MP-E 65 mm macro lens and full spectrum lighting. Images were stitched using Adobe Photoshop CC.

Geological Setting and Stratigraphy

Geological Setting.—During the Silurian Period, present-day Wisconsin was part of the Laurentian palaeocontinent, which lay astride the equator and was largely covered by epeiric seas. The present-day Great Lakes region was dominated by carbonate platforms and associated carbonate lithofacies (Shaver, 1996). Platform lithofacies included
extensive reef and non-reef subtidal environments (Copper, 1994), as well as low-profile islands, arranged as an archipelago (Shaver, 1991). Subtidal, intertidal and supratidal settings hosted microbial communities manifested as crusts, mats, microbialites and as interstitial components of the sediment (compare Riding, 2000).

Exceptionally preserved fossils from the Brandon Bridge Formation near Waukesha, Wisconsin, occur in finely laminated carbonate mudstone that was deposited along the western edge of the Michigan Basin (Kluessendorf & Mikulic, 1996). The Michigan Basin is an intracratonic sedimentary basin bounded by the Wisconsin Arch along the west and the Kankakee Arch along the southwest (Howell & van der Pluijm, 1990: fig. 1; Shaver, 1996). Hundreds of fossilised reefs occur along the margin of the basin (Shaver, 1991; Copper, 1994). Large reef communities, such as the Thornton Reef (Ingels, 1963; Mikulic, 1987; McGovney, 1989), tend to align along changes in slope of the Michigan Basin. Small patch reefs occur in deeper water along the outer margins (Obermajer et al., 2000, fig. 1) and in platform areas bounding larger reef complexes (Ingels, 1963, fig. 5). Reef faunas were rich in rugose and tabulate corals and stromatoporoid sponges (Copper, 1994). Inter-reef facies consist of argillaceous lime mudstone and tend to be rich in trilobites, brachiopods and rooting organisms such as benthic graptolites, pelmatozoans (crinoids, rhombiferans, diploporans; e.g., Weller, 1900; Weller, 1907; Feldman, 1989; Peters & Bork, 1999).

The Waukesha deposit is one of a number of Konservat-lagerstätten preserved in lime mudstone facies of the Great Lakes region (Kluessendorf, 1994; von Bitter et al., 2007). They include sites in the Bertie Formation or Group (New York and Ontario),
Eramosa Formation (Ontario), Waubakee Dolomite (Wisconsin), *Lecthaylus* Shale (Illinois), Kokomo Limestone (Indiana) and Pointe-aux-Chenes Shale (Michigan). These Lagerstätten record a great diversity of organisms, including some that are lightly and non-biomineralised, and add considerably to the overall known biodiversity of the Silurian.

*Stratigraphy.*—The Waukesha Lagerstätte consists predominately of a dolomitised, rhythmically bedded plattenkalk. Barthel et al. (1990) used the terms flinz and fäule to describe endmember petrographic variation in the Solnhofen (Jurassic) plattenkalk. We follow their terminology here. Flinz (plural, flinzen) refers to sheets of pure micritic carbonate that often show conoidal fracture. Fäule (plural, fäulen) refers to fossiliferous, shaly carbonate layers. Bedding surfaces of the flinz layers are not normally smooth, but slightly crenulated (probably due to the influence of microbial mats), whereas bedding surfaces of the fäule layers are normally smooth. Lithologies intermediate between fäule and flinz may be known by terms such as blättenflinz (fissile flinz) and zähe fäule (tough or tenacious fäule).

In the Waukesha Lagerstätte, fossils are preserved predominately in thinly laminated (mm scale), non-fissile, silt-sized dolomudstone (flinz) or thinly laminated (< 1 mm thick), fissile, organic-rich, clay-sized argillaceous dolomudstone (fäule). Overall, flinz predominates in thickness and fäule layers form thin intercalations. The two lithologies are readily distinguishable by colour and occur in an alternating rhythmic-like pattern. Flinz layers are a light-grey to tan-grey. Fäule layers are commonly medium to
dark grey or greenish-grey and rarely pinkish-grey. Both lithologies occur with lighter and darker sedimentary couplets. Intermediate lithologies, blättenflinz and zähe faule, occasionally occur as well. Uncommon beds rich in skeletal debris are present. Above the most productive layers, the Brandon Bridge Formation commonly occurs as weakly laminated, crystalline dolomudstone (LoDuca et al., 2003).

The Brandon Bridge Formation in southeastern Wisconsin (Fig 2.1) has a maximum thickness of 8 m and is composed mostly of dolomudstone (Fig. 2.2). The Brandon Bridge overlies a Type 2 sequence boundary, which is manifested at the Waukesha Lime and Stone Company quarry as a scarp (Kluessendorf & Mikulic, 1996, fig. 3). The Brandon Bridge Formation wedges out over the Manistique Formation in southeastern Wisconsin (McLaughlin et al., 2013) and is overlain by the Waukesha Formation (Kluessendorf & Mikulic, 1996).

There are at least two intervals of exceptional preservation in the Waukesha Lime and Stone Company quarry. The lower interval, which is the most productive one, is a ≤12 cm layer of the Brandon Bridge Formation approximately 2 m above the disconformity with the Manistique Formation (Kluessendorf & Mikulic, 1996). This interval has yielded a variety of exceptionally preserved fossils and is referred to as the Waukesha Lagerstätte. The upper interval begins approximately 60 cm above the lower interval (LoDuca et al., 2003). Exceptional preservation in the upper interval is limited primarily to non-calcified green algae and graptolites. A variety of sedimentary structures including rill marks, wrinkle structures, intraclasts, interference ripples and Chondrites trace fossils have been reported above the lower interval (Kluessendorf & Mikulic, 1996;
LoDuca et al., 2003).

Most of this work is based on material from the lower interval of the Brandon Bridge Formation in the Waukesha quarry, and unless otherwise specified, statements refer to this material. Supplementary information comes from material collected from the upper interval of the Brandon Bridge Formation in the Waukesha Lime and Stone Company quarry, or from the nearby Franklin quarry.

Collecting in the Franklin Quarry was less extensive than in the Waukesha Lime and Stone Quarry (Fig. 2.1). Exceptionally preserved fossils are in blocks from an interval inferred to be correlative with the lower part of the Brandon Bridge Formation at the Waukesha Quarry. Exceptionally preserved fossils include a variety of non-biomineralised and lightly skeletonised organisms present in the Waukesha Lime and Stone Quarry, though at Franklin they occur in more concentrated accumulation (Fig. 2.5G). Missing members include the trilobites. Unique members include a chordate. The most abundant sedimentary structures present include fine lamination and hummocky structures.

The Konservat-lagerstätte layers were deposited as part of a transgressive systems tract (Kluessendorf & Mikulic, 1996). This episode of eustatic rise is attributed to partial melting of the Gondwanan Ice Sheet (see Spengler & Read, 2010). The Lagerstätte layers contain graptolites indicative of the *Oktavites spiralis* Zone (Mikulic et al., 1985a, b; Saunders et al., 2009) and conodont elements indicative of the *Pterospathodus celloni* Zone (McLaughlin et al., 2013). Both graptolite and conodont guide fossils suggest a Silurian (Llandovery, Telychian) age.
Biota

More than 50 genera, representing at least 12 phyla, are present in the Waukesha Biota. The Brandon Bridge Konservat-lagerstätte preserves organisms typically ranging from 1 mm to 20 cm in maximum dimension. Whereas many Konservat-lagerstätten display greater biological diversity by preserving soft and hard tissue (shelly) organisms, shelly organisms other than trilobites and conulariids are uncommon in the Brandon Bridge lagerstätte.

Trilobites.—At least 13 trilobite species are present in the Waukesha Biota (Figs. 2.3, 2.4) Common forms are an undescribed dalmanitid, *Stenopareia* and a harpид (*Scotoharpes?*). Less common forms include *Arctinurus*, *Calymene*, *Eophacops?*, *Meroperix*, *Otarion*, *Leonaspis*, *Acidaspis?* and three unidentified lichids. The dalmanitid, *Stenopareia*, *Arctinurus*, *Meroperix* and *Leonaspis* are known from articulated specimens. Some of the trilobites preserve mineralised gut tracts. Digestive tracts are common in the undescribed dalmanitid but are also known from *Arctinurus* and *Meroperix*.

Non-trilobite arthropods.—At least 14 non-trilobite arthropods are present (Fig. 2.5). They include synziphosurines (see Moore et al., 2005), a scorpion (Chapters 3, 4), three species of *Ceratiocaris* (Jones et al., 2016) and leperditicopid ostracods. Arthropods of
uncertain affinity include three great-appendage arthropods, a myriapod-like animal, two enigmatic bivalved arthropods and a number of others, mostly represented by fragmentary material.

*Lobopodians.*—At least two lobopodian taxa are present in the Waukesha Biota. They include a small ‘armored’ lobopodian with round dorsal ‘plates’ (Fig. 2.5F) and a large stout-limbed ‘xenusiid’ lobopodian (Fig. 2.5E).

*Problematica.*—Two conulariids, *Conularia niagarensis* Hall, 1852 (Fig. 2.6B) and *Metaconularia* cf. *manni* Roy, 1935 (Fig. 2.6A), plus *Sphenothallus* are present. *Sphenothallus* is known from complete tubes (Figs. 2.6C) and holdfasts, which are attached to specimens of both conulariid species. Conulariids are among the best preserved shelly fossils, and likely due to their phosphatic composition.

*Brachiopods.*—Orbiculoids, phosphatic inarticulate brachiopods, are rare (Fig. 2.6E). Several poorly preserved, undetermined articulate brachiopods, which originally had calcite shells, are present. They include possible orthids (Fig. 2.6D) and rhynchonellids (Fig. 2.6F).

*Cephalopods.*—At least two, poorly preserved cephalopods are present in the Waukesha Biota. One form (Fig. 2.6I) shows characteristics of the family Kionoceratinae (compare Holland, 2000: fig. 1h). The other specimen is an internal mold (Fig. 2.6J).
Cnidaria.—A partial tabulate coral, possibly *Favosites*, is known from a single incomplete specimen (Fig. 2.6G). One specimen of a cubozoan is known.

Worms.—Several ‘worms’ with soft tissue present, including at least two palaeoscolecid (Figs 2.7D, E), an aphroditid polychaete (Fig. 2.7F), a spiny polychaete worm (Fig. 2.7G, H), a wide-bodied annelid (Fig. 2.B7) and a ‘leech’ (Fig. 2.7A, C). Scolecodonts have also been recovered (Mikulic et al., 1985a, b).

Hemichordates.—Graptolites, often carbonised, are common in this biota. Taxa present include *Oktavites spiralis* (Fig. 2.8D), cf. *Desmograptus* (Fig. 2.8A), cf. *Dictyonema* (Fig. 2.8B), *Thallograptus* sp. (Fig. 2.8E) and a possible mastigograptid (Fig. 2.8C).

Echinoderms.—Disarticulated pelmatozoan ossicles are scattered (Fig. 2.10D) through a number of slabs from the Waukesha quarry. An undetermined articulated crinoid is known (Fig. 2.6H).

Chordates.—A partial conodont with an assemblage of phosphatised elements and decayed soft tissue was described from the Waukesha Lime and Stone Quarry (Smith et al., 1987). The Franklin Quarry has produced numerous specimens of a well-preserved chordate, which is unknown from the Waukesha Quarry, that preserves a notochord, v-shaped myomeres and caudal fin-like marginal structures (Figs 2.8F, G). Conodont
elements were not preserved in direct association with these specimens. The soft tissue remains of the Franklin Quarry chordate resembles the soft tissues of the conodont *Clydagnathus windsorensis* (Carboniferous; compare Sweet & Donoghue, 2001, fig. 3) and the cephalochordate *Cathaymyrus diadems* (Cambrian; compare Shu et al., 1996; Donoghue & Keating, 2014, fig. 2e).

**Microbial structures.**—Mudcracks coated with an elephant skin texture are present (Fig. 2.10A, B) and indicates the buildup of microorganisms in a mat-influenced sedimentary environment (compare Bottjer & Hagadorn, 2007, fig. 4(a)-6b). Additional microbial structures are visible in cross-sections of rock, and they include dark, crinkled, and wavy, laminae and domal structures (Figs. 2.10C, E; compare Pflüger, 1999, fig. 6D). Torn and ruptured laminae (Fig. 2.10C) indicate the presence of microbial mats (compare Pflüger, 1999, fig. 6d; Schieber, 1999, fig. 5). Decay halos (Fig. 2.5D, E, M) around some non-biomineralised and lightly skeletonised organisms indicate the former presence of microbial activity (see Borkow & Babcock, 2003). Possible microbial-induced gas escape structures (Fig. 2.10F) are also present (compare Dornbos et al., 2007, fig. 4(d)-2c, d; 4(d)-3b).

**Trace Fossils.**—Trace fossils are rare and observed only in the Fäule layers. The lower interval of the Waukesha Lagerstätte has an ichnofabric index (Droser & Bottjer, 1986) of 1. Vertical burrows are not evident. Traces observed are horizontal or bedding-plane-parallel. They include a few examples of *Diplichnites* (Fig. 2.10G) and *Gordia*-like
pyrite-infilled burrows (compare Babcock & Peel, 2007) on the cuticle of a phyllocarid. has been reported (Jones et al., 2016, figs. 2.2, 2.5).

**Taphonomy**

*Biotic composition.*—The Waukesha Lagerstätte provides a skewed view of Silurian biodiversity. Animals characteristic of normal marine salinity communities are rare or absent (e.g., corals, echinoderms, bryozoans). Preserved organisms likely represent a death assemblage (taphocoenosis) washed in from nearby marine and possibly non-marine environments. The Waukesha Lagerstätte favors preservation of organisms poorly known from other Silurian marine deposits and helps fill in our perception of biodiversity during the Silurian.

*Anatomical composition.*—Fossils of the Waukesha Lagerstätte display a range of taphonomic styles that are related in part to the organisms’ original compositions and lithologies in which they are preserved. Typically, faule layers yield finer preservation of non-biomineralised and lightly skeletonised anatomy, whereas flinz layers primarily yield trilobites with occasional examples of poorly preserved non-biomineralised and lightly skeletonised arthropods.

Preservation involving calcium phosphate is common in the Waukesha Lagerstätte, and organisms originally incorporating phosphate often preserve differently from those that were secondarily phosphatised. Organisms having phosphatic hard parts such as
conulariids (see Babcock & Feldmann, 1986; Fig. 2.6A, B), an inarticulate brachiopod (Fig. 2.6E), annelid worms (see Gibbs & Bryan, 1984; Briggs et al., 1985; Figs. 2.7) and ceratiocaridid phyllocarids (see Baird, 1978; Fig. 2.5N) tend to be well-preserved and without apparent secondary mineral overgrowth. Commonly non-biomineralised organisms are compressed and secondarily phosphatised with an organic carbon film beneath (Fig. 2.5F). Secondary phosphatic overgrowths tend to be thicker and crinkled on non-biomineralised and lightly skeletonised organisms. Calcium phosphate also appears to have infilled and coated anatomical structures preserving but often distorting or obscuring morphological details (see Moore et al., 2005).

Organisms originally having calcium carbonate skeletons are commonly preserved as ghost-like fossils, or they preserved mouldically. Trilobites are most numerous in the Fäule layers, and exoskeletons tend to be preserved in various stages of decalcification (Mikulic et al., 1985b). Most examined specimens retain a thin carbonate overgrowth or film that is likely the result of dissolution within or under a microbial mat (see Babcock & Peel, 2007). Trilobite exoskeletons also show a range of states of compression with most being nearly flat and without marginal fractures related to sedimentary compaction. Trilobites possessed an exoskeleton composed of calcium carbonate with an external chitinous layer (Towe, 1973; Mutvei, 1981; Dalingwater & Mutvei, 1990; Wilmot, 1990). The absence of fractures on nearly flat trilobites suggests that carbonate was removed early in their fossilisation history, leaving the more pliable chitin. Phosphatised gut tracts are present in some trilobites, but preserved appendages and hypostomes are rare. Gut tracts are moderately common in dalmanitids (Fig 2.3F), which are the most numerous
trilobites, but are also observed in the lichid \textit{Arctinurus} (Fig. 2.3C) and the bumastine \textit{Meroperix} (Fig. 2.3A, B; Babcock et al., 2016). Echinoderms are represented mostly by disarticulated ossicles, preserved as moulds (Fig. 2.10D). Mollusks and articulate brachiopods are mostly mouldic.

Organisms with carbonised preservation include graptolites, non-calcifying algae, ‘worms.’ and some arthropods. Graptolites occur in the lower and upper Waukesha Lagerstätten beds, non-calcified green algae occur in the upper Waukesha beds. Especially at the Franklin Aggregate Inc. quarry, chordates, ‘worms’ and non-biomineralised arthropods are commonly preserved with carbon, and little or no phosphate is evident (Fig. 2.5G, I).

\textit{Disarticulation and transportation}.—Many of the examined dalmanitid and bumastine trilobites are articulated and fully outstretched. A few specimens are loosely folded in a post-mortem posture (see Babcock & Speyer, 1987). Tightly enrolled trilobites have not been observed. Assemblages of dalmanitids are present on several slabs. The loss of limbs, antennae and hypostomes on the trilobites indicates that they disarticulated somewhat prior to deposition. Taphonomic experiments have shown that extant arthropods can remain at the sediment surface for weeks before complete disarticulation occurs (Babcock & Chang, 1997; Babcock et al., 2000). Limbs and gills are among the first structures to be lost, and they begin disarticulating in about one week (Babcock & Chang, 1997; Babcock et al., 2000; McCoy & Brandt, 2009). Transportation seems to have little, if any effect on disarticulation (Babcock & Chang, 1997; Babcock et al.,
2000). However, alignment of trilobite exoskeletons on slabs, commonly bidirectional, suggests current transport and alignment (Fig. 2.9). It is likely that these fossils were allochthonous.

Evidence that macroorganisms were alive at or close to the time of burial in the lower Brandon Bridge Formation is scant. The presence of Diplichnites on several slabs denotes the activity of some live arthropods, but it is uncertain which arthropods made the tracks and whether they routinely lived at the burial site or were infrequent or accidental visitors to it (washed in). Tightly enrolled trilobites are an indicator of inhospitable environmental conditions (Henry & Clarkson, 1974; Babcock & Speyer, 1987). Lacking enrolled trilobites suggests that rapidly changing conditions did not contribute to their deaths. All observed dendroid graptolites lack their rooted holdfasts indicating that they were not preserved in place (Fig. 2.8A). Stemmed echinoderms, mostly preserved as moulds, are nearly exclusively known from fragmentary remains having disarticulated prior to burial (compare Ausich & Sevastopula, 1994; Ausich et al., 1999). Evidence indicates that most macroorganisms in the Waukesha Lagerstätte were transported, from nearby areas, often as moults and carcasses (Mikulic et al., a, b; Mikulic & Kluessendorf, 1998; LoDuca et al., 2003).

_Microbial environments and microbial obrution._—Fluctuating environmental parameters are often the cause of chemically or physically stressed environments in the Holocene. Stressed carbonate platform environments (e.g., tidal flats, lagoons, inter-reef) tend to inhibit macroorganisms while allowing microorganisms to flourish. In some
circumstances, these microorganisms develop into diverse stratified microbial communities, known as microbial mats (e.g., Paerl et al., 2000; Riding, 2000). Fluctuating environmental parameters such as salinity, temperature and circulation (stagnation) are common factors leading to stressed carbonate platform settings (Riding, 2000). Other factors commonly associated with salinity-stressed environments include nutrient-depletion and periodic subaerial exposure (Paerl et al., 2000). Any of these fluctuating parameters could limit or prevent macroorganisms such as burrowers (e.g., worms) and grazers (e.g., gastropods) that would have interrupted or prevented the buildup of microbes into mat structures. Instead, microorganisms, such as cyanobacteria, that can tolerate stressed environmental conditions tend to dominate and thrive. These microbial-rich communities are crucial components in a variety of biological and geochemical processes including the trapping and stabilisation of sediment (see Decho, 2000; Paerl et al., 2000; Riding, 2000). Cyanobacterial mats biologically mediate sediment stabilisation through the secretion of a sticky film known as extracellular polymeric substance (EPS) that binds sediment and through the precipitation of calcium carbonate that lithifies sediment (Decho, 2000).

Microbial structures have been observed or inferred in Ediacaran and Cambrian deposits (e.g., Gehling & Droser, 2009; Ahn & Babcock, 2012; Cai et al., 2014), and Gehling (1999) was the first to draw attention to the importance of microbial mats (laminar sheets of microorganisms) in the preservation of the unusual non-biomineralised organisms during this period. He referred to characteristic Ediacaran fossils as “death masks,” or replicas of the external morphology produced when thin microbial mats
coated bodily remains. It is thought that the microorganismal consortia comprising the mats mediated early diagenesis, ultimately leading to fossilisation.

Microbial-stabilised marine sediment environments declined in abundance during the Phanerozoic due to the appearance of burrowers and grazers that disrupted and devoured the mats (see Gehling, 1999; Pflüeger, 1999; Seilacher, 1999; Bottjer et al., 2002; Gehling & Droser, 2009; Stal, 2012). Although microbial mats are thought to have played an important role in fossilisation during the Proterozoic Eon (Gehling, 1999; Hagadorn & Bottjer, 1999; Seilacher, 1999), they are not conventionally thought of as exerting as much influence in Phanerozoic deposits of exceptional preservation and, instead, were restricted to stressed environments. Microbial “death mask” preservation is largely undocumented in the Cambrian and Ordovician, but it seems to reappear in certain unusual marine environments during the Silurian.

Evidence indicating the former presence of a microbial mat is not always straightforward because mats do not normally retain their integrity through the fossilisation process (see Gehling, 1999). The microbes that comprise the mat may be preserved as fossils (Ahn, 2010; Ahn and Babcock, 2012), but they are rarely reported. In the absence of preserved or reported fossilised microbes, other more subtle evidence, such as sedimentary structures, is commonly used to infer the former presence of a microbial mat. Microbial decay halos are direct evidence of microorganismal activity (Borkow & Babcock, 2003; Robison & Babcock, 2011) and are present around several specimens (Figs. 2.5D, E, M). Borkow & Babcock (2003) demonstrated that halos, which form around decaying organic matter, are composed of a microbial consortium that
facilitates authigenic mineralisation. Such microbes may be responsible for mediating the precipitation of early diagenetic minerals including pyrite (e.g., Briggs et al., 1996; Borkow & Babcock, 2003), calcium phosphate (e.g., Babcock et al., 2005; Briggs et al., 2005), and silica (Ciampaglio et al., 2006; Babcock & Ciampaglio, 2007; Babcock & Peel, 2007; Strang et al., 2016) leading to exceptional preservation in Konservat-lagerstätten.

Varied explanations have been offered for the mechanisms of preservation in the Waukesha Lagerstätte (see Mikulic et al., 1985a, b; Kluessendorf & Mikulic, 1996; LoDuca et al., 2003; Moore et al., 2005; Haug et al., 2014). Rapid burial coupled with anoxia may have helped facilitate the fine preservation (Mikulic et al., 1985b; LoDuca et al., 2003; Moore et al., 2005). However, microbially mediated rock such as a plattenkalk (microbialite) probably reflects moderate sedimentation rates because high sedimentation rates would have inhibited growth and development of microbial mats (see Leinfelder et al., 1996). In this context, it is important to distinguish between sediment smothering (obrution in the classic sense) as a form of rapid burial and rapid covering by a microbial mat. Classic obrution is generally understood to mean rapid (or event) burial under a layer of sediment grains. Rapid covering of organic remains or traces at the sediment surface by a living microbial layer is also a form of obrution, and we term this process “microbial obrution” (see Fig. 2.11). Organisms can become trapped in the sticky surface of a microbial mat and decay, predation and other forms of biogenic disruption may then be limited (compare Allison & Briggs, 1991a, b; Gehling, 1999; Briggs, 2003b).

Some microbial structures were previously noted within the Brandon Bridge
Formation (see Kluessendorf & Mikulic, 1996). The presence of crinkled (compare Pflüeger, 1999: fig. 6d), wrinkled (compare Hagadorn & Bottjer, 1999: fig. 1; Schieber, 1999: fig. 2) and domal layers, torn up and rolled up mat layers (compare Simonson & Carney, 1999: fig. 3), fenestral fabric (compare Kennard & James, 1986; Ahn & Babcock, 2012), decay halos (compare Borkow & Babcock, 2003) and shrinkage cracks (Gehling, 1999) are all direct macroscopic indicators of microbial activity in the Waukesha Lagerstätte. Indirect evidence includes finely laminated layers and the paucity of large trace fossils, which indicates that most burrowing and vagile macroorganisms were not thriving in this ancient environment. Some tiny burrows are present and interpreted to have been formed by small organisms ‘mining’ the mat (compare Seilacher, 1999).

The rarity of large trace fossils and presence of a developed microbial mat indicate an environment hostile to most macroscopic lifeforms. The high number of arthropod fossils compared to the low number of Diplichnites trace fossils suggests that most organisms were washed in as carcasses or moults. These organisms likely were transported from nearby areas and have accumulated in sedimentary traps or tidal pools. Below the Brandon Bridge Formation, the Schoolcraft and Burnt Bluff carbonates were subaerially exposed prior to the time of Brandon Bridge sedimentation, creating an 8-m scarp with a gentle slope and epikarstic features. Tidal pools, which formed along the base of the scarp in the intertidal or supratidal zones, would have collected the remains organisms washed in from nearby areas.

The inferred presence of microbial mats and mat-influenced sedimentation in the
Waukesha Lagerstätte indicates deposition in a rather hostile environment, not conducive to macroorganisms that would have interrupted microbial buildup. Such environments can be caused by factors including high salinity, temperature fluctuations and stagnation from restricted circulation, which can prevent most large metazoan life from thriving (Riding, 2000). The presence of the Burnt Bluff Scarp may have served to restrict local circulation of water (Kluessendorf & Mikulic, 1996: fig. 3). Almost certainly sediment below the mat reached dysoxic or anoxic conditions, and this could have helped facilitate carbonate dissolution in skeletons and facilitated authigenic mineralisation of calcium phosphate or other minerals. The presence of sporadic, scattered pyrite cubes tends to support the hypothesis that sulfate reduction was occurring.

*Early diagenesis.*—Precipitation of calcium phosphate and dissolution of calcium carbonate (shelly biota) are processes facilitated by microbial mats (Briggs, 2003a, b). Modern microbial mats are complex stratified ecosystems in which different consortia of microorganisms occupy different layers (Paerl et al., 2000; Puckett et al., 2011). Upper mat levels typically are aerobic and dominated by photoautotrophs, whereas lower levels tend to be anaerobic and dominated by chemoautotrophs and heterotrophs (Puckett et al., 2011). Upper layers, commonly dominated by cyanobacteria, provided a sticky surface (EPS) for organisms to adhere (Gehling, 1999). Organisms trapped in the mat would have quickly become enveloped through microbial obrution (Fig. 2.11B).

Once exposed to lower mat levels, organisms endured localised microbial-mediated chemical microenvironments (semi-closed systems) under which dissolution and
precipitation could occur, depending on pH conditions, oxygen levels, and ion concentrations (Fig. 2.11C). Dysoxic or anoxic microenvironments can yield differential preservation of biomineralised parts and non-biomineralised tissues (e.g., Dick & Brett, 1986; Babcock & Speyer, 1987; Briggs et al., 1993; Wilby et al., 1996; Briggs et al., 2005; Moore et al., 2005; Moore et al., 2011; Zatoń et al., 2014). Below the mat surface, decaying organisms produce free phosphorus ions that can accumulate (Briggs et al., 1993; Briggs, 2003a, b) and become the source for calcium phosphate precipitation; pH is the primary driver of this process (Allison, 1988; Wilby et al., 1996). A drop in pH, which is commonly associated with dysoxia or anoxia, can promote dissolution of calcium carbonate and precipitation of calcium phosphate. These microbially mediated processes likely facilitated mineralisation leading to the preservation of non-biomineralised and lightly skeletonised organisms in the Waukesha Lagerstätte and possibly other Silurian Lagerstätten in Laurentia (e.g., Bertie and Eramosa formations). The rarity of organisms with original calcium carbonate hard parts, other than trilobites, is likely the result of a combination of original restriction or low abundance of certain shelly biota (e.g., bivalves, brachiopods, cephalopods, gastropods, echinoderms, corals, bryozoans, stromatoporoids) as well as post-depositional dissolution. Moulds of disarticulated pelmatozoans are moderately common in cross sections of Fäule layers but have not been observed in the Flinze layers. Much like modern carbonate platform environments (e.g., San Salvador; Puckett et al., 2011), Fäule layers would have cemented quickly, via microbial mediation, into a hardground.
Discussion

One salient aspect of the Waukesha Lagerstätte is that the exceptional preservation occurs in a non-concretionary carbonate Lagerstätte (NCCL). In fact, a large proportion of Paleozoic non-concretionary Konservat-lagerstätten, either siliciclastic or carbonate, are hosted in fine-grained, laminated rock. Babcock (2011) and Babcock et al. (2011) emphasised that non-concretionary carbonate Lagerstätten are commonly underreported or receive less study than Lagerstätten hosted in concretions or siliciclastic deposits. Some important non-concretionary carbonate Lagerstätten are certainly well known (e.g., Solnhofen, Green River), but many others (e.g., Huaqiao Formation, Trenton Limestone, Hamilton Quarry) provide important glimpses into an array of sedimentary environments where exceptional preservation has occurred and where taphonomic processes are poorly understood. Three depositional models have been proposed for NCCL; tidal deposition, storm deposits and sediment-gravity flows (Babcock, 2011). Evidence of storm deposition or sediment-gravity flow (obrution) preservation is absent. The presence of mud cracks (subaerial exposure), microbial-influenced sedimentation (microbial obrution) and fine laminations of dark-light couplets in the Waukesha Lagerstätte indicates cyclicity expected in a tidally influenced environment (Mikulic et al., 1985b; see also Feldman et al., 1993).

We establish a model, which we term microbial obrution, to explain how microbial mats and microbially stabilised sediment contribute to the preservation of non-biomineralised organisms and the non-preservation (or rarity) of shelly organisms.
Conventionally, microbial mats were thought to have exerted significant influence in Ediacaran lagerstätte (Gehling, 1999; Hagadorn & Bottjer, 1999; Seilacher, 1999), but little influence in the Phanerozoic. However, stressed conditions such as high salinity would have contributed to the growth and development of a microbially-rich environment that would lead to conditions favorable for this type of exceptional preservation. Rapid sediment smothering was not necessary to prevent organismal decay. Organisms were initially coated in a microbial covering, and this was followed by mat-stabilised sedimentation. Finally remains were preserved (often through mineral precipitation) or partly destroyed (through dissolution) in microenvironments below the mat surface. Microbial obrution applies not only to the Waukesha Lagerstätte but probably also other Silurian Konservat-lagerstätten preserved in dolostone (e.g., Bertie and Eramosa formations) and could also apply in part to other carbonate Lagerstätten preserved in shallow, warm waters (e.g., Bear Gulch Limestone, Solnhofen Plattenkalk) of the Phanerozoic.

References


Ahn, S.Y. & Babcock, L.E. 2012: Microorganism–mediated preservation of Planolites, a common trace fossil from the Harkless Formation, Cambrian of Nevada, USA.


Babcock, L.E., Peng, S., Wasserman, G.J. & Robison, R.A. 2011: Exceptionally preserved biota from a carbonate lithofacies, Huaqiao Formation (Cambrian:


Bottjer, D. & Hagadorn, J.W. 2007: Mat features in sandstones: mat growth features. *In*


Von Nostrand Reinhold, New York.


McGovney, J.E. 1989: Thornton reef, Silurian, northeastern Illinois. *Canadian Society of


Robison, R.A. & Babcock, L.E. 2011: Systematics, paleobiology, and taphonomy of
some exceptionally preserved trilobites from Cambrian Lagerstätten of Utah.

*Paleontological Contributions* 5, 1–47.


Signor, P.W., III & Brett, C.E. 1984: The mid-Paleozoic precursor to the Mesozoic


Weller, S. 1900: The paleontology of the Niagaran Limestone in the Chicago area; the Crinoidea. *Chicago Academy of Sciences 4*, 1–152.


Young, G.A., Rudkin, D.M., Dobrzansku, E.P., Robson, S.P., Cuggy, M.B., Demski,


**Fig. 2.1. Location of Waukesha Lime and Stone Company quarry and Franklin Aggregate Inc. quarry.** A, map of the United States showing the location of Wisconsin. B, map of Wisconsin showing the locations of the Waukesha Lime and Stone Co. quarry (WQ) and Franklin Aggregate Inc. quarry (FQ). C, part of Waukesha 7.5’ topographic quadrangle map, Wisconsin (U.S. Geological Survey, 2013, 1:24,000) showing position of Waukesha Lime and Stone Company quarry (WQ). D, part of Greendale 7.5’ topographic quadrangle map, Wisconsin (U.S. Geological Survey, 2013, 1:24,000) showing position of Franklin Aggregate Inc. quarry (FQ).
Fig. 2.2. General stratigraphic section of uppermost Ordovician into mid-Silurian strata of southeastern Wisconsin. Arrow indicates position of Waukesha Lagerstätte within the Brandon Bridge Formation. Figure provided by Joanne Kluessendorf and Don Mikulic.
Fig. 2.2
Fig. 2.3. Large trilobites from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin. A, *Meroperix* sp (UWGM 2583). B, close-up of *Meroperix* gut tract (UWGM 2583). C, *Arctinurus* sp. preserved gut tract (UWGM 2582). D, multiple plate of dalmanitid trilobites (UWGM 2340). E, bitten cephalon of a dalmanitid trilobite, arrow denotes bite mark (UWGM 2338). F, close-up of dalmanatid from multiple plate preserving gut tract (UWGM 2340). G, bitten pygidium of *Arctinurus* sp., arrow denotes bite mark (UWGM 2335). Scale bar equals 2 cm for A–C, F–G, 5 cm for D; 1 cm for E.
Fig. 2.4
Fig. 2.7. ‘Worms’ from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin. A, putative leech preserving mouth (UWGM 2422). B, large wide bodied annelid worm (UWGM 2430). C, putative leech with detailed soft tissue (UWGM 2584). D, palaeoscolecid worm, form 1, preserving gut (UWGM 2431). E, palaeoscolecid worm, form 2 (UWGM 2578). F, aphrodite polychaete (UWGM 2434). G, spiny polychaete worm (UWGM 2433); H, spiny polychaete worm, as preserved resembles a choiid sponge (UWGM 2432). Scale bar equals 2 cm for A–C; 1 cm for D–H.
*Fig. 2.8. Hemichordates and chordates from the Brandon Bridge Formation,*

Fig. 2.9. Dalmanitid trilobites preserved on flinz from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin (UWGM 5581) showing bidirectional alignment in rose diagram. Complete trilobite exoskeletons (n=49) were measured along mean axial direction with cephalon pointed forward and plotted in 15º classes. Scale bar equals 20 cm.
Fig. 2.9
Fig. 2.10. Sedimentary and microbial structures from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin. A, mud cracks coated in microbial mat causing an elephant skin texture (UWGM 2457). B, closeup of microbially induced elephant skin texture (UWGM 2457). C, sliced cross section of plattenkalk with both fäule (top darker grey layer) and flinz (predominate lighter grey layer) with microbial mat structures (UWGM 2585). D, cross section showing molds of pelmatozoan stem fragments (UWGM 2585). E, domal microbial buildup (UWGM 2451). F, possible gas escape structure. G, *Diplichnites* trace fossil (UWGM 2456.) H, microbial dissolution of a dalmanitid trilobite (UWGM 2455). I, cross section of dalmanitid trilobite showing that no exoskeleton remains (UWGM 2455). Scale bar equals 2 cm for A, C–E, G; 1 cm for B, F, H–I.
Fig. 2.10
**Fig. 2.11. Microbial obrution explanatory diagram.** A, generalised diagram of microbial mat. B, washed in organisms (e.g., trilobites and crinoids) adhere to the sticky surface of the microbial mat. C, over time, the mat surface covers the organisms exposing them to the dysoxic/anoxic portions of the microbial mat, causing the formation of decay halos and both the dissolution (e.g., calcite) and precipitation of minerals (e.g., pyrite and phosphate). D, eventually the organisms are below the live portion of the microbial mat and no longer undergo further dissolution or precipitation of minerals. Yellow highlighting indicates which layer is being described.
Fig. 2.11
Chapter 3: A Silurian ancestral scorpion with fossilised internal anatomy

SCORPIONS are the oldest land-dwelling chelicerate arthropods, or arachnids, and among the first animals to have become fully terrestrialised\textsuperscript{1}. Their early fossil record is limited, and fundamental questions, including how they adapted to the terrestrial realm, have been difficult to answer\textsuperscript{2,3}. Here we describe a new exceptionally preserved fossil scorpion from the Waukesha Biota (early Silurian, ca. 435 Ma) of Wisconsin, USA\textsuperscript{4,5}. This is the earliest scorpion yet reported, and it has a combination of primitive and derived arachnid characteristics. Elements of the circulatory, respiratory and digestive systems are preserved, and they are essentially indistinguishable from those of present-day scorpions but also are similar to marine relatives. At this early point in arachnid evolution, there is no discernible evidence of structural changes in the circulatory or respiratory systems as might be expected with the marine-to-terrestrial transition.

Scorpions include some of the earliest animals to have become fully terrestrial\textsuperscript{1,6}. The earliest forms are Silurian in age\textsuperscript{7,8}, but because most Palaeozoic species are represented by only rare, fragmentary material, much of their early evolutionary history is speculative. Divergent views regarding the habitat of Palaeozoic scorpions have been published. Some have argued that the earliest scorpions were marine\textsuperscript{9,10}, whereas others
have claimed a terrestrial origin\textsuperscript{6,11}. It has also been argued that some Palaeozoic scorpions were secondarily aquatic\textsuperscript{12}. Arguments about whether early scorpions were terrestrial or marine have been based on 1, stratigraphic context\textsuperscript{13}; 2, the presence or absence of structures used for liquifying prey (coxapophyses or stomathecae)\textsuperscript{14}; 3, organs related to chemosensory function (pectines\textsuperscript{11}), mechanosensory function (trichobothria\textsuperscript{14}) or respiratory function (book gills or book lungs)\textsuperscript{11,12,15}; and 4, inferred locomotory stance based on limb morphology\textsuperscript{10}. All Silurian scorpion fossils and most from the Palaeozoic occur in nearshore to marginal-marine strata, yielding equivocal evidence of habitat, as bodily remains of arthropods are easily transported after death\textsuperscript{16}. Likewise, inferring locomotory stance and habitat from limb morphology in a fossil scorpion can yield equivocal results\textsuperscript{13}. Pectines, stomathecae, trichobothria, and respiratory structures are rarely preserved as fossils, and in many examples the non-preservation of such structures likely has a taphonomic origin\textsuperscript{2,17}.

Here we report exceptionally preserved remains of a new Silurian scorpion, \textit{Parioscorpio venator} gen. et sp. nov. (Figs 3.1, 3.2a, 3.3). The new species has a combination of primitive and derived characters, which supports an interpretation of this animal close to the base of the scorpion clade. Internal anatomy, including parts of the circulatory, respiratory and digestive systems (Figs 3.1, 3.2a), has been preserved, and provides insight into a group that terrestrialised early in its evolutionary history.
Material and Stratigraphic Context

Study material consists of two substantially complete specimens (Fig. 3.1) from the Waukesha Lagerstätte in the lower Brandon Bridge Formation near Waukesha, Wisconsin, USA\textsuperscript{4,5,18}. Remains are preserved as a combination of thin organic film and replication by thin calcium phosphate coating. Associated graptolites\textsuperscript{4,5,18} and conodont elements\textsuperscript{19} indicate an early Silurian age (Llandovery Series, mid-Telychian Stage).

The Waukesha Biota is diverse\textsuperscript{4,5} and includes biomineralised and non-biomineralising or lightly skeletonised taxa, of which macrofossils are assigned to at least 12 metazoan phyla. Articulated trilobites, ostracodes, conulariids, graptolites, non-biomineralised arthropods and ‘worms’ dominate the biota. Atypical marine conditions are suggested by the near lack of echinoderm, brachiopod, mollusk and coral remains. Fossils are preserved in a 12 cm layer of thinly laminated, fine-grained dolostone deposited during a transgressive episode over the eroded Schoolcraft and Burnt Bluff Dolomites\textsuperscript{19}.

Fossils of \textit{P. venator} are from marine sediments that accumulated in a sedimentary trap at the toe of an erosional scarp. The Schoolcraft and Burnt Bluff carbonates were subaerially exposed prior to the time of Brandon Bridge sedimentation, creating an 8-m scarp with a gentle slope and epikarstic features\textsuperscript{18,19}. Sedimentary traps which formed along the base of the scarp in the intertidal or supratidal zones received remains of both marine and terrestrial organisms washed in from nearby areas. Microbial mats coated and cemented bodily remains in place. Microbial processes are implicated in
the precipitation of thin phosphatic coatings on non-biomineralised or lightly skeletonised remains.

**Systematic Palaeontology**

Order Scorpiones

Family undetermined

*Parioscorpio* gen. nov.

**Etymology.** From Latin, *pario*, progenitor, and *scorpio*, scorpion.

**Type species.** *Parioscorpio venator* sp. nov.

**Distribution.** Silurian (Llandovery, early to mid-Telychian), Wisconsin, USA.

**Diagnosis.** As for *P. venator*, see below.

*Parioscorpio venator* sp. nov.

Figs 3.1, 3.2a, 3.3


**Types.** Holotype, University of Wisconsin Geology Museum, Madison, Wisconsin, UWGM 2162. Paratype, UWGM 2163.

**Location.** Waukesha Lime and Stone Company west quarry, north of State Highway 164, Waukesha, Wisconsin, USA.

**Horizon.** Lower Brandon Bridge Formation.
Diagnosis. Exoskeleton small; prosoma subtrapezoidal with large, possibly compound, eyes situated anterolaterally and ocelli situated anteromedially; pedipalps large, with tibia (fixed finger) elongate, swollen proximally in manus, narrow and recurved distally in ramus; mesosoma moderately wide and much longer than the metasoma, containing seven dorsal tergites and seven ventral sternites; sternites 1-2 short, length increasing posteriorly. Metasoma about 1/3 length of opisthosoma, containing five narrow, subequal, weakly bilobate segments. Telson swollen proximally, aculeus not preserved.

Comparative discussion. Parioscorpio venator gen. et sp. nov. has a unique array of characters suggesting both primitive and derived conditions for scorpions. At present, scorpions are identified by a combination of characters that include clawed pedipalps, metasomal tail terminating in a stinger and pectines\(^20\). A long mesosoma containing seven tergites and sternites (Fig. 3.1c, d) is interpreted as a plesiomorphic characteristic (Fig. 3.4). Scorpions show a trend toward reduction of the number of sternites through phylogeny. Six sternites are present in two Silurian species, which are younger and more derived, Proscorpius osborni\(^3\) and Eramoscorpius brucensis\(^10\). Most extant and extinct scorpions have five sternites\(^21,22\), a condition that had evolved by at least the Carboniferous Period. The large, anterolateral eyes and anteromedial position of the small medial eyes, are also regarded as plesiomorphic features, as they are present in younger Silurian species (Allopalaeophonus caledonicus\(^23\), Palaeophonous nuncius\(^24\), and Proscorpius osborni\(^3\)). Pectines, which are chemosensory structures present in all extant
scorpions, are unknown in most Palaeozoic forms including *P. venator*. This is probably a taphonomic artefact, as pectines are easily lost after death or moulting\(^2,17\). In other aspects of external morphology *P. venator* fits within the range of character states exhibited among other, more derived, scorpion taxa. A telson bearing an expanded area for a poison vesicle and a stinger is an apomorphic condition for scorpions\(^20\). The holotype of *P. venator* preserves an incomplete telson, which is folded under the fifth metasomal segment. The proximal portion shows a swelling close to the articulation with the metasoma, inferred to be a poison vesicle, but the more delicate terminal stinger is not evident.

Both specimens of *P. venator* preserve details of internal anatomy. In the paratype, parting of the rock through the fossil reveals a medial structure interpreted as the gut tract (Fig. 3.1c, d), and it resembles that of extant scorpions. It is a narrow, simple tube extending from the prosoma to the metasoma. It originates in the anterior prosoma, slightly forward of the inferred position of the mouth, suggesting that the mouth was forward-facing.

In the holotype of *P. venator*, internal structures of the mesosoma and metasoma have been impressed on the thin dorsal cuticle during sediment compaction. They consist of a series of narrow, hourglass-shaped medial structures extending much of the length of the mesosoma (Fig. 3.1a, b). Extending laterally from each of the medial structures is a pair of curved, strut-like elements. The hourglass-shaped structures of the mesosoma continue into the metasoma as a simple, narrow tube. Neither book lungs nor book gills have been preserved.
Detailed studies of the central architecture of the circulatory and respiratory systems in present-day scorpions\textsuperscript{25,26} reveal a strikingly similar arrangement, which we infer is homologous. The pericardium, which surrounds and houses the heart, comprises a series of narrow, medial hourglass-shaped structures in the mesosoma, and strut-like pulmo-pericardial sinuses projecting laterally from it (Fig. 3.2). In some extant scorpions, these internal medial structures are reflected externally on the dorsal cuticle (Fig. 3.2c). Pulmo-pericardial sinuses connect the book lungs with the circulatory system. The book lungs oxygenate the haemolymph (‘blood’) and deliver the oxygenated haemolymph to the pericardium\textsuperscript{25,26}.

Despite physiological differences between extant marine chelicerates (xiphosurans) and terrestrial chelicerates (scorpions), the structure of the circulatory and respiratory organs is fundamentally similar,\textsuperscript{26,27} apart from the means by which marine and terrestrial forms take up oxygen. Marine xiphosurans extract oxygen from water by means of book gills, and scorpions process oxygen from air by means of structurally similar book lungs.

Preserved elements of the circulatory and respiratory systems (Figs 3.1a, b, 3.2a) of \textit{P. venator} suggest that rather subtle morphological changes accompanied the marine-terrestrial transition in the arachnid clade and that the fundamental respiratory-cardiovascular architecture was evolutionarily conservative. These systems show remarkably little structural change from their appearance in \textit{P. venator} in the Silurian Period to present-day scorpions. The basic morphology of the pericardium and the pulmo-pericardial sinuses have little if any difference in marine xiphosurans, \textit{P. venator},
and extant terrestrial scorpions, indicating that relatively little morphological change in those organs occurred at the marine-terrestrial transition. Early arachnids may have been structurally ‘preadapted’ to life on land, and conceivably made occasional forays onto land before becoming fully terrestrialised.

References


FIG. 3.1. *Parioscorpio venator* gen. et sp. nov., Brandon Bridge Formation (Silurian), Wisconsin, USA. *a-b*, holotype, UWGM 2162; *a*, photographed under low-angle lighting; *b*, interpretive drawing. *c-d*, specimen split through middle, revealing segmental pattern and internal gut tract, UWGM 2163; *c*, photograph; *d*, interpretive drawing. Abbreviations: *cx*, coxa; *fe*, femur; *fr*, free finger; *fx*, fixed finger; *gt*, gut; *le*, lateral eye; *me*, median eyes; *mt*, metasomal segment; *pa*, patella; *pc*, pericardium; *pfm*, pedipalp femur; *pm*, pedipalp manus; *pmc*, pedipalp manus carina; *ppt*, pedipalp patella; *pr*, pedipalp ramus; *ps*, pulmo-pericardial sinus; *pv*, poison vesicle; *st*, sternum; *stn*, sternite; *tr*, trochanter; *wl*, walking leg. Scale bars 5 mm.
Fig. 3.1
FIG. 3.2. Medial structures associated with the pulmonary-cardiovascular system in Silurian (a) and Holocene (b, c) scorpions; a, Parioscorpio venator gen. et sp. nov., holotype, detail of medial region showing pulmo-cardiovascular structures; b, SEM of Centruroides exilicauda, corrosion cast of pericardium and associated pulmo-pericardial sinuses; c, Hadogenes troglodytes, male, dorsal surface, showing medial structure reflecting the position of the internal pericardium. Abbreviations: bl, book lungs; pc, pericardium; ps, pulmo-pericardial sinus. Scale bars 1 mm.
Fig. 3.2
FIG. 3.3. Reconstruction of *Parioscorpio venator* gen. et sp. nov. Structures outlined in grey are inferred based on *Proscorpius osborni*³. Position of structures known of the pulmonary-cardiovascular system are indicated with grey infill.
FIG. 3.4. Hypothesis of relationship among some of the more completely known
Paleozoic scorpions, with geologic time scale at left.
Fig. 3.4
Chapter 4: Paleobiology and taphonomy of an early scorpion from the Waukesha Lagerstätte (Silurian), Wisconsin, USA

Introduction

Scorpions are the oldest known fossil arachnids (Dunlop et al., 2013). Their fossil record extends to the Silurian (Selden and Dunlop, 1998), and much of their early history is uncertain. More than 100 fossil scorpion species have been described, of which about 80 are Paleozoic (Dunlop and Penney, 2012; Dunlop et al., 2012). Few of the Paleozoic species are known from more than a single incomplete, specimen (see Kjellesvig-Wearing, 1986; Dunlop and Penney, 2012; Dunlop et al., 2012). One exception is Proscorpius osborni, from the latest Silurian (Whitfield, 1885), which is commonly cited as a model for early scorpions (Werner, 1934; Sissom, 1990; Weygoldt, 1998; Dunlop and Braddy, 2001; Farley, 2001b; Dunlop et al., 2008, Poschmann et al., 2008; Dunlop and Penney, 2012). Differing interpretations of the morphology, ecology, and evolution of early scorpions, and arachnids in general, have emerged, in large part based on reference to, or contrast with, P. osborni (e.g., Jeram, 1998; Giribet et al., 2002; Shultz, 2007; Garwood and Dunlop, 2014; Waddington et al., 2015).

Here, we discuss an early fossil scorpion from the Silurian (Llandovery Series,
Telychian Stage) of Wisconsin, USA, that preserves elements of the circulatory and respiratory systems. This internal anatomy is crucial to our understanding of the earliest scorpions, and answering fundamental questions concerning the timing of arachnid terrestrialisation and anatomical changes that may be expected to be associated with the transition from water to land. The new form, *Parioscorpio venator* Wendruff, Babcock, Wirkner, Mikulic and Kluessendorf, 2016, is the oldest scorpion and earliest arachnid now known. It is represented by two well-preserved specimens that retain a mixture of primitive characters such as large compound eyes and derived characters such as the presence of respiratory and circulatory anatomy that are essentially indistinguishable from modern scorpions.

**Material and Methods**

This study is based on two specimens collected from dolostone of the Waukesha Lagerstätte in the Brandon Bridge Formation (Silurian), Waukesha Lime and Stone Company quarry, near Waukesha, Wisconsin (Figs 4.1, 4.2). Specimens are deposited in the University of Wisconsin Geology Museum, Madison, Wisconsin, USA (UWGM 2162, 2163).

Specimens were photographed with a Canon EOS Rebel T3i Digital SLR with a Canon MP-E 65 mm macro lens and full spectrum lighting. Images were stitched using Adobe Photoshop CC. Outline drawings were created using Photoshop on a tablet with a stylus, and measurements were made using ImageJ (Schneider et al., 2012).
Geological Setting and Stratigraphy

Exceptionally preserved fossils from the Brandon Bridge Formation near Waukesha, Wisconsin, occur in finely laminated dolostone deposited along the western edge of the Michigan Basin (Kluessendorf and Mikulic, 1996). During the Silurian Period, present-day Wisconsin was part of the palaeocontinent Laurentia, which lay astride the equator and was largely covered by epeiric seas. The present-day Great Lakes region was dominated by carbonate platforms and associated carbonate lithofacies (e.g., Copper, 1994; Kluessendorf and Mikulic, 1996; Shaver, 1996). Platform lithofacies included extensive reef and non-reef subtidal environments (Copper, 1994), as well as low-profile islands (Shaver, 1991). Subtidal, intertidal, and supratidal settings hosted microbial communities manifested as crusts, mats, microbialites, and as interstitial components of the sediment (compare Riding, 2000).

A number of Silurian Konservat-Lagerstätten preserved in lime mudstone facies of the Great Lakes and Midcontinent regions are now known (Kluessendorf, 1994). They include sites in the Bertie Formation or Group (New York and Ontario), Eramosa Formation (Ontario), Waubakee Dolomite (Wisconsin), Lecthaylus Shale (Illinois), Kokomo Limestone (Indiana), Pointe-aux-Chenes Shale (Michigan), Bertie Group (New York), Scotch Grove Formation (Iowa), and Brandon Bridge Formation (Wisconsin). These Lagerstätten record a great diversity of organisms, including some that are non-biomineralised or lightly skeleontised, and add considerably to the overall biodiversity of
the Silurian of Laurentia (see Kleussendorf, 1994; Feldmann and Hackathorn, 1996; Taylor and Brett, 1996)

The Brandon Bridge Formation in southeastern Wisconsin has a maximum thickness of 8 m and is composed predominately of dolomudstone. It overlies the Schoolcraft and Burntbluff dolomites and is overlain by the Waukesha Formation. The Brandon Bridge Formation overlies a Type 2 sequence boundary, which is manifested at the Waukesha Lime and Stone Company quarry as a scarp (Kluessendorf and Mikulic, 1996).

Within the Waukesha Lime and Stone Company quarry, exceptionally preserved fossils occur mostly in a 12 cm thick layer of the Brandon Bridge Formation approximately 2 m above the disconformity with the Schoolcraft and Burntbluff dolomites (Mikulic and Kluessendorf, 1998). The layers were deposited as part of a transgressive systems tract attributed to partial melting of the Gondwanan Ice Sheet (Spengler and Read, 2010). The lower Brandon Bridge Formation yields graptolites indicative of the *Oktavites spiralis* Zone (Mikulic et al., 1985a, b; Saunders et al., 2009) and conodont elements indicative of the *Pterospathodus celloni* Zone (McLaughlin et al., 2013). Both graptolite and conodont guide fossils indicate a Silurian (Llandovery, Telychian) age.

Fossils in the lower part of the Waukesha Lagerstätte are preserved in a dolomitised plattenkalk and occur either in thinly-laminated, fissile, organic-rich, argillaceous dolomudstone (fäule) or thinly laminated, non-fissile, dolomudstone (flinz; terminology follows Barthel et al., 1990). Although similar in lamination and composition, there are
distinct colour and preservational differences between the two lithologies. The fäule is commonly medium to dark grey or greenish grey and rarely pinkish grey. The flinz is light grey to a tan-grey. Finer preservation of non-biomineralised organisms predominately occurs in the fäule layers.

**Biota and Taphonomy**

The Waukesha Lagerstätte contains representatives of at least 12 metazoan phyla (see Chapter 2). Arthropods dominate the macrobiota, and there is evidence of an extensive microbiota. Trilobites, small bivalved arthropods, conulariids, and graptolites are among the most common animal fossils in the Brandon Bridge Formation (Mikulic et al., 1985a, b). Other organisms include phyllocarids, great appendage arthropods, lobopodians, scorpions, and ‘worms’. Conodonts, both isolated phosphatic elements and soft-tissue remains, have been reported (Smith et al., 1987). Brachiopods, corals, cephalopods, and articulated echinoderms are rare; bivalves, bryozoans, and gastropods are unknown (Mikulic et al., 1985b).

Most arthropod fossils are coated in blue-grey to white calcium phosphate. A dark grey to brown organic film has been detected beneath the phosphate (Jones et al., 2016). The two scorpion fossils are preserved as secondarily phosphatised, compacted remains. One is in fäule, and the other is in flinz. Preservation of the specimen in fäule is more detailed. A dark-brown, presumably organic, film is present in the specimen preserved in fäule (Figs. 4.1, 4.2). Some details of dorsal, ventral, and internal anatomy are visible as a
result of compaction.

Body fossils in the Waukesha Lagerstätte are inferred to be mostly allochthonous, derived from locations on the carbonate platform, and stranded in a sedimentary trap, adjacent to a carbonate island. The sedimentary trap was probably tidally influenced. Thinly laminated layers with inferred laminar microbial mats and mudcracks suggest intermittent wet and dry conditions. Occasional repichnial traces and layer-penetrative burrows associated with matground conditions indicate the presence of limited live macrofauna. Most bodily remains presumably represent moults or carcasses that were buried under tidally, microbially influenced, sedimentation.

Matground and microbial processes likely played a key role in sedimentation and taphonomic processes, helping to facilitate exceptional preservation in the Brandon Bridge Formation. Trilobites and other body fossils show evidence of decalcification and possible mouldic preservation, resulting in a ‘death mask’-like preservation under a microbial mat (compare Gehling, 1999). Evidence of microbially influenced environments include wrinkle structures and elephant skin texture. Many Brandon Bridge macrofossils rest outstretched on fäule layers. Trilobites occur outstretched in both the fäule and flinz layers, often in clusters. These attributes suggest a hostile environment with a thriving microbial community; one that could host few animals. Conditions in such an environment, perhaps a sabkha, limited rapid breakdown of washed-in carcasses and moults (compare Hagadorn and Bottjer, 1999; McIlroy and Logan, 1999; Tarhan et al., 2013). Sedimentation was moderately rapid, which helped ensure preservation of non-biomineralised and lightly mineralised remains.
Systematic Palaeontology

Varied classifications of early scorpions have been published (e.g., Kjellesvig-Waering, 1986; Stockwell, 1989; Dunlop et al., 2007; Jeram, 1998) and classification below the order level is contentious. Comparisons between fossil scorpions and extant scorpions suffer from incongruent character selection and interpretation, resulting in disparate evolutionary trees (Dunlop et al., 2008; Prendini and Wheeler, 2005). For these reasons, the infraorder and familial assignment of *Parioscorpio venator* is left open.

Phylum Arthropoda Siebold, 1848

Subphylum Chelicerata Heymons, 1901

Order Scorpiones Koch, 1837

Family undetermined


Figures 4.1–3; 4.6 (figures from this paper)

Synonomy

*Parioscorpio venator* Wendruff, Babcock, Wirker, Mikulic, and Kluessendorf, Chapter 3, figs. 3.1–3.
Diagnosis (from Chapter 3)

Exoskeleton small; prosoma subtrapezoidal with large, possibly compound, eyes situated anterolaterally and ocelli situated anteromedially; pedipalps large, with tibia (fixed finger) elongate, swollen proximally in manus, narrow and recurved distally in ramus; mesosoma moderately wide and much longer than the metasoma, containing seven dorsal tergites and seven ventral sternites; sternites 1-2 short, length increasing posteriorly. Metasoma about 1/3 length of opisthosoma, containing five narrow, subequal, weakly bilobate segments. Telson swollen proximally, aculeus not preserved.

Description

Prosoma is trapezoidal in outline; width of anterior margin is about half the width of posterior margin. Anterior margin slightly bowed, posterior margin straight. Large, presumably compound, eyes located anterolaterally; together occupying nearly 2/3 the width of anterior margin. Small paired median eyes located between ‘compound’ eyes near anterior edge of prosoma. Pair of median carinae present in posterior half of prosoma. Limbs are incompletely known, though evidence of four pairs of walking legs is present. Chelicerae and pedipalps present. Pedipalps with a tibia (fixed finger) that is recurved in distal half (ramus) and bulbous in proximal half (manus). Pair of dorsal carinae present on manus, tarsus (movable finger) narrow. Patella and femur elongate and cylindrical femur is slightly longer; trochanter short about half the length of femur. Coxae
of walking legs evenly spaced along lateral sides of sternum. Sternum is incompletely known; outline uncertain, bilobed along the posterior margin.

Mesosoma moderately wide and long, about 2/3 length of opisthosoma, containing seven dorsal tergites and seven ventral sternites, approximately half as wide as long. Widest at fourth and fifth segments. Hourglass-shaped structures located medially are interpreted as the pericardium (compare Wirkner and Prendini, 2007, fig. 1f; Wirkner et al., 2013; herein Fig. 4.4). At least four pairs of curved strut-like structures extend laterally from the medial structures and are interpreted as pulmo-pericardial sinuses, or channels that connect the circulatory system to the book lungs (compare with Wirkner and Prendini, 2007, fig. 1f). Along the ventral side, sternites have rounded lateral margins and slightly bilobate posterior margins; medial emargination present on posterior margin of sternite seven. The first two sternites are short and realigning sternites increase in length posteriorly. The pectines are unknown. Intrasternite spiracles are unknown. Neither book lungs nor book gills have been preserved.

The metasoma is short, comprising about 1/3 length of opisthosoma and contains five segments. Segments are subequal in length and tube-like. The hourglass-shaped structures of the mesosoma continue into the metasoma as a narrow, raised ridge. The first metasomal segment articulates with posterior mesosoma at a notch in the posterior margin of the last mesosomal segment. The fifth segment appears to have a bulbous dorsal structure, possibly a vesicle. The aculeus (stinger) is unknown. An incomplete gut tract is preserved in the paratype (Fig. 4.3). It comprises a simple narrow tube extending lengthwise from the prosoma through at least part of the mesosoma.
Discussion

*Parioscorpio venator* adds to a rather meager fossil record of Silurian scorpions. Six monospecific genera, including *P. venator*, are known. They include *Dolichophonus loudonensis* Laurie, 1899, *Allopalaeophonus caledonicus* Hunter, 1886, and *Palaeophonus nuncius* Thorell and Lindström, 1884, all of which are known from single specimens. *Proscorpius osborni* Whitfield, 1885 and *Eramoscorpius brucensis* Waddington et al., 2015 are known from multiple specimens. Two undetermined species, known from fragmentary material, were noted by Kjellesvig-Waering (1954) and Dunlop and Selden (2013). *P. venator* differs from all other known scorpions, Silurian or otherwise, in having seven sternites and a metasoma that is considerably shorter than the mesosoma. In addition, the combination of a trapezoidal prosoma, large anterolaterally situated compound eyes, anteromedially situated ocelli, strongly recurved fixed fingers of the pedipalps, and a moderately wide mesosoma distinguish *P. venator* from all other known Silurian species.

The trapezoidal (subtriangular) dorsal carapace is most similar to the Devonian *Waeringoscorpio* (Poschmann et al., 2008). Lateral compound eyes and anterior median eyes are also known from other Silurian scorpions (e.g., *Allopalaeophonus*: Petrunkevitch, 1953; *Palaeophonus*: Kjellesvig-Waering, 1986; *Proscorpius*: Dunlop et al., 2008).

The chela (manus) of the pedipalp is bulbous and similar to *Palaeophonus*.
(Petrunkevitch, 1953), *Waeringoscorpio* (Poschmann et al., 2008) and *Palaeoscorpius* (Kühl et al., 2012; Dunlop and Penney, 2012), but it differs in the degree of curvature. Pedipalpal patella and femur are elongate with a slightly longer femur most similar to *Waeringoscorpio* (Poschmann et al., 2008, fig. 2a) and *Compsoscorpius* (Legg et al., 2012, fig. 3-2, 3-5). Conversely, *Proscorpius* (Dunlop et al., 2008, pl. 1, figs. 1, 4) and *Eramoscorpius* (Waddington et al., 2015, fig. 1c) possess patellas that are significantly shorter than the femur, less than half its length.

The earliest scorpions tend to have a higher number of tergites than their extant relatives. Most extant and extinct scorpions have five sternites, four of which carry paired book lungs (Hjelle, 1990; Sissom, 1990). Six sternites have been reported in *Proscorpius* and *Eramoscorpius* (Dunlop et al., 2008; Waddington et al., 2015). Seven sternites are present in *P. venator* (Fig. 4.3A, B) signifying that primitively scorpions had an equal number of tergites and sternites.

Dunlop et al. (2008) cautiously suggested that pectines may be lacking in at least some of the early scorpion taxa, *Proscorpius* and *Waeringoscorpio*. There is no evidence of pectines in *P. venator* either. However, small reputed pectines were reported in *Eramoscorpius*, which would make them the earliest example (Waddington et al., 2015).

A long, narrow tail with a stinging telson is one of the most iconic features of scorpions. In extant and fossil scorpions, the posterior margin of the last mesosomal segment, where the first metasomal segment abuts, is straight (Waddington et al., 2015, fig. 1c) or slightly emarginate (Jeram, 1994b, fig. 2a; Dunlop et al., 2008, pl. 1, fig. 3). In *P. venator*, a much deeper emargination is present, creating a subtle transition from
mesosoma to metasoma. Typically, the metasoma (not including the telson) is at least the length of the mesosoma. However, *P. venator* has a mesosoma that is larger than the metasoma. Individual metasomal segments are short, wide and bilobed (Fig. 4.3). A similar pattern has been documented from the early embryology of some extant scorpions (compare to Farley, 2001a, fig. 15).

**Age**—*Parioscorpio venator* is among the oldest scorpions known at present (Fig. 4.5). It co-occurs with graptolites indicative of the Oktavites spiralis Zone (Llandovery, Telychian; Mikulic et al., 1985a, b; Saunders et al., 2009). *Dolichophonus loudonensis* from the Deerhope Formation of the Pentland Hills, Scotland is roughly coeval (see Anderson et al., 2007). The Deerhope Formation spans the *O. spiralis* to *Cyrtograptus lapworthi* Zones (Loydell, 2005; Molyneux et al., 2008; Loydell, 2012).

**Systematics and Phylogeny**—Stockwell (1989) and Jeram (1994a, b; 1998) attempted to resolve phylogenetic relationships among early scorpions. Subsequent to the time of Jeram’s publications, some taxa have been re-evaluated (Dunlop et al., 2008; Poschmann et al., 2008; Kühl et al., 2012). Some taxa erected by Kjellesvig-Waering (1986) have been suppressed (see Dunlop et al., 2008; Legg et al., 2012).

Evolutionary relationships between extinct and extant scorpions are poorly resolved. Attempts to include fossil taxa in phylogenetic analyses along with extant taxa (Soleglad and Fet 2001, 2003) have been criticised (Prendini and Wheeler, 2005). A disconnect exists between extant and fossil scorpion systematics because Holocene taxa
are commonly described using very different terminology and character traits (Dunlop et al., 2008). Disagreement over preserved anatomical structures has led to mistaken relationships, taxonomic splitting, and poor understanding of scorpion evolutionary history (Jeram, 1998; Prendini and Wheeler, 2005; Dunlop et al., 2008; Kühl et al., 2012; Legg et al., 2012). Extant scorpions are classified primarily on anatomical features that may be absent in primitive members (e.g., pectines, book lungs, and spiracles) or may not preserve (e.g., three-dimensional features, soft-tissue features, sensory hairs, colouration, and behavior; Prendini and Wheeler, 2005). Relationships among extant scorpion families are inferred largely from the morphology of the hemispermatophore, pigmentation pattern, and the position and number of trichobothria and carinae (e.g., Mattoni et al., 2012; Ojanguren-Affilastro et al., 2012; Santibanez-Lopez et al., 2014). These features do not preserve or are taphonomically distorted in fossils, rendering their phylogenetic utility questionable in many extinct taxa. Fossil scorpions preserved in amber and copal are notable exceptions to these preservational biases; they commonly preserve many features upon which extant scorpions are diagnosed (e.g., Lourenço and Weitschat, 2009; Lourenço, 2009; Riquelme et al., 2015).

There is no consensus about the higher systematics of fossil scorpions. Kjellesvig-Waering (1986) recognised two suborders and numerous families, most of which were monogeneric. Stockwell (1989), in an unpublished dissertation, proposed a substantially revised classification. Jeram (1994a, b) and Dunlop et al. (2007) published phylogenies that incorporated some of Stockwell’s argumentation. New information presented here modifies our understanding of the morphology of the earliest scorpions, which will have
an impact on phylogenetic interpretation. Table 4.1 briefly summarises characters that often are used to indicate primitive or derived status in some of the better preserved Palaeozoic scorpions, and Figure 4.7 is a tentative hypothesis of evolutionary relationships among these forms.

**Ecology**—Whether early scorpions were terrestrial or aquatic has been subject to differing interpretation (e.g., Whitfield, 1885; Thorell, 1866; Pocock, 1901; Clark and Ruedemann, 1912; Petrunkevitch, 1949; Petrunkevitch, 1953; Kjellesvig-Waering, 1986; Selden and Jeram, 1989; Jeram, 1990; Dunlop, 1998; Jeram, 1998; Weygoldt, 1998; Dunlop and Webster, 1999; Dunlop and Braddy, 2001; Scholtz and Kamenz, 2006; Dunlop et al., 2008; Poschmann et al., 2008; Kühl et al., 2012; Waddington et al., 2015; see table 4.2 summarising arguments). It has been argued that the Arachnida represents a grade of terrestrial chelicerate supported by ecologic adaptation or convergence (Selden and Jeram, 1989; Dunlop, 1997; Dunlop 1998; Kraus, 1998; Dunlop and Webster, 1999). If true, arachnids underwent more than one terrestrialisation event. Most arguments have focused on the presence or absence of respiratory structures, although these are rarely preserved in fossils. Indirect evidence for habitat such as feeding mechanisms, sensory structures, locomotion, and lithofacies commonly have been used to support ecologic arguments.

Aquatic and terrestrial chelicerates (arachnids) tend to have different feeding methods. Terrestrial chelicerates normally use external pre-digestion and liquification, whereas aquatic chelicerates commonly tear and shred food. Extant scorpions use a
preoral tube, composed of coxapophyses, for external liquid feeding. This technique has been described as being unfeasible under water (Farley, 2001b; Poschmann et al., 2008; Legg et al., 2012; Waddington et al., 2015). The first unequivocal coxapophyses did not appear until the Early Devonian (Praearcturus; see Jeram, 1998). Shultz (2007) suggested that primitive scorpions could have had coxapophyses composed of soft-tissue similar to the feeding apparatus (stomothecae) of harvestmen (Opiliones). Such feeding structures have been interpreted as convergent (Weygoldt, 1998; Dunlop and Braddy, 2001; Poschmann et al., 2008). Some early scorpions may have macerated their food (Kjellesvig-Waering, 1986). To date, unambiguous evidence of feeding method has not been reported in any Silurian scorpion (see Dunlop et al., 2008).

Sensory structures are an indicator of how an organism interacts with its environment. Sensory function differs between the air and water as discussed by Selden and Jeram (1989), and the structure of sensory structures may differ as well. Scorpions use a variety of sensory structures including lateral and median eyes, trichobothria, and pectines. Extant scorpions have lateral ocelli, used for light detection, and median ocelli, used for acute and spatial vision (Loria and Prendini, 2014). Early scorpions have large lateral compound eyes and anteromedian ocelli. Vision must have played an important role in the lifestyle of primitive scorpions (Jeram, 1998; Legg et al., 2012).

Trichobothria are mechano-sensory structures consisting of a pore and a setal hair capable of detecting air movement and vibration (Hjelle, 1990). Unfortunately, setal hairs have a poor preservation record. The pores are the most likely structures to preserve, although they are small (Hjelle, 1990, fig. 2.16) and difficult to see in most fossils. The
earliest known trichobothria (pores) are from fragmentary cuticular specimens of Carboniferous age (Jeram, 1994a). Whereas trichobothria may be an adaptation to a terrestrial habitat, their apparent absence on *Pulmonoscorpius*, which has long been considered a terrestrial scorpion, may indicate that this feature evolved after terrestrialisation.

Pectines, which are unique chemosensory structures on the ventral surface of a scorpion, are not known in most Silurian and Devonian scorpions. They may have been absent or not preserved. Kjellsvig-Waering (1986) incorrectly reported the presence of pectines in most early scorpions. He speculated that they had a role in reproduction, rather than chemosensory and presumed that chemosensory structures could not have functioned under water. Structures interpreted as pectines are known from *Eramoscorpius* (Silurian) are small and abut directly against the sternum instead of against the genital operculum as expected. It is possible that the pectines are overlapping the genital operculum or that these structures were erroneously interpreted. Their shape is similar to the genital operculum of *Pulmonoscorpius* (see Jeram, 1994b, fig. 6a; Dunlop and Penney, 2012, fig. 13). The scarcity of preserved pectines in early scorpions makes it difficult to elaborate on their possible function and ecological implications. The function of the earliest pectines remains unknown and are thought to have functioned similarly in extant scorpions.

Arthropods transitioning from an aquatic to terrestrial lifestyle need to contend with the loss of buoyancy and increased forces on their body during locomotion (Selden and Jeram, 1989). It has been argued that because many Silurian scorpions retained a
digitigrade or ‘crab-like’ stance used by eurypterids they must also be aquatic organisms (Störmer, 1976; Kjellesvig-Waering, 1986; Selden and Jeram, 1989; Dunlop et al., 2008; Waddington et al., 2015). They argued that by walking on the tips of the tarsus, weight is not distributed and buoyancy provided by water is needed to enable movement across the substrate. Extant and many fossil scorpions have a plantigrade stance in which the tarsus is used as a ‘foot’ equally distributing weight over a greater surface area thereby facilitating locomotion outside of the water (Selden and Jeram, 1989; Dunlop et al., 2008; Waddington et al., 2015). *Eramoscorpius* (Silurian) was described as a transitional form between aquatic and terrestrial lifestyles due to the elongation of the basitarsus and shortening of the tarsus allowing for the earliest plantigrade or plantigrade-like locomotion presumably for forays onto land (Waddington et al., 2015, fig. 1j). The shift in scorpion limb stance denotes a change in locomotion, but the two stances may not be exclusive of a particular environment. The extant whip scorpion, *Mastigoproctus giganteus*, is a large (>5 cm excluding the whip) terrestrial arachnid that successfully utilises a digitigrade stance across a soft substrate using only three pairs of limbs (Schmerge et al., 2013). In consideration of this evidence, habitat, whether aquatic or terrestrial, cannot be deduced from locomotory stance alone.

The most commonly used argument for an aquatic habitat in early scorpions is that they are all found in marine sediments (Whitfield, 1885; Dunlop et al., 2008; Kühl et al., 2012; Waddington, 2015) and, therefore, must be aquatic organisms. For example, specimens of *Eramoscorpius* (Eramosa Formation), *Proscorpius* (Bertie Formation), and *Parioscorpio* (Brandon Bridge Formation) are all preserved in dolostone deposits.
indicating warm, shallow marine deposits. However, the Brandon Bridge and Bertie formations have sedimentary features such as microbial mats, mud cracks, salt hoppers and vascular plants (the latter two only present in Bertie) that indicate a shallow, nearshore, possibly hostile, marine environment that periodically was subaerially exposed (Dunlop et al., 2008), such as an intertidal salt flat.

Reported specimens of *Eramoscorpius* were described as moults preserved in situ after ecdysis (due to their completeness) in a nearshore environment, following rapid microbial overgrowth that allowed for exceptional preservation (Waddington et al., 2015). Waddington et al. (2015) theorised that *Eramoscorpius* traveled to shallow intertidal waters to safely moult free of predators like eurypterids. However, evidence of microbial overgrowth is indicative of a hostile environment (e.g., hypersalinity or anoxia) devoid of grazing and burrowing organisms that would have prevented mat build up (Hagadorn and Bottjer, 1999; McIlroy and Logan, 1999; Tarhan et al., 2013). Furthermore, the presence of articulated arthropods does not necessarily indicate little to no transportation. Taphonomic experiments using extant aquatic chelicerates such as *Limulus* indicate that corpses can travel great distances within the first 10 days prior to losing any their limbs (Babcock and Chang, 1997; Babcock et al., 2000). Extant scorpion moults and carcasses can undergo several days (2-8) of transport prior to the start of disarticulation (McCoy and Brandt, 2009).

*Eramoscorpius*, *Proscorpius* and *Parioscorpio* represent some of the better known Silurian scorpions. Sedimentary and microbial features indicate that they were preserved in hostile, microbially rich environments. This suggests that they were transported
allochthonous), from adjacent environments, either terrestrial or marine, prior to burial.

Extant scorpions are common inhabitants that hunt and scavenge along the shoreline of salt flats (hostile environment) around the Arabian Peninsula (Hogarth and Tigar, 2002).

Aquatic (xiphosuran) and terrestrial (arachnid) chelicerates use structurally similar, but functionally distinct respiratory organs (Wirkner et al., 2013; Göpel and Wirkner, 2015). Extant xiphosurans use book gills to extract oxygen from water, whereas scorpions use book lungs to process oxygen from air allowing for terrestrial life. Book lungs have also been noted in several other extinct and extant arachnid groups including the Uropygi, Amblypygi, Aranea, and Trigonotarbida. Scholtz and Kamenz (2006) analysed book lungs in these groups and concluded that they were homologous, indicating a single terrestrialisation event and a monophyletic Arachnida (see Sharma et al., 2014 for discussion of multiple terrestrialisation events in a monophyletic Arachnida). This does not mean that scorpions were not originally aquatic, just that all arachnids descended from a single terrestrial common ancestor.

Determination of habitat from respiratory structures is difficult in fossil scorpions as such internal structures tend to preserve poorly, if at all. Book lungs uncommonly preserve in arachnids (Selden and Jeram, 1989), and their first unequivocal appearance in scorpions is in the Carboniferous Pulmonoscorpius (Jeram, 1990, 1994b). Earlier structures have been interpreted as book lungs in two Devonian scorpions, although their identity remains equivocal (Shear et al., 1996; Kühl et al., 2012). The earliest undisputed arachnid book lungs were described in an Early Devonian trigonotarbid (Kamenz et al., 2008) suggesting that the apparent lack of book lungs in early scorpions may be due to
preservational bias rather than an indication of aquatic lifestyle.

Intrasternite spiracles, which are external openings in the sternites that aerate the book lungs, are more likely to preserve and would denote the presence of book lungs. Conversely, their absence has been used as evidence of an aquatic lifestyle. Unfortunately, their first appearance in scorpions is in the Carboniferous, following the earliest appearance of book lungs in scorpions (Legg et al., 2012). Spiracles have not been observed on *Pulmonoscorpius*, but Jeram (1994b) suggested that they may have been obscured between overlapping sternites, a condition similar to that known in whip scorpions (Uropygi; Kamenz, 2009) and whip spiders (Amblypygi; Kamenz, 2009). Spiracles currently are the only known external respiratory structure that would indicate the presence of book lungs and terrestriality. Unfortunately, they may not discernible on early scorpions; therefore the absence of spiracles is not evidence of an aquatic lifestyle.

The presence of gills, on the contrary, would be indisputable evidence of an aquatic origin. Several early scorpions were described as having gill-like openings (Kjellesvig-Waering, 1986), these observations have since been refuted (Dunlop et al., 2008; Kühl et al., 2012). The Devonian scorpion *Waeringoscorpio* has been described as having long filamentous external ‘gills’ (Poschmann et al., 2008). If these structures are indeed gills, they likely represent a secondarily aquatic adaptation and are not informative of the original scorpion bauplan.

The holotype of *P. venator* preserves anatomical structures inferred to represent the pulmo-pericardial sinuses and the pericardium (Figs. 4.2D, E; compare Wirkner and Prendini, 2007, fig. 1f; Wirkner et al., 2013; Chapter 3). In extant scorpions, the pulmo-
pericardial sinuses connect the circulatory system with the respiratory system (book lungs). The book lungs oxygenate the haemalymph (‘blood’) and deliver it to the pericardium (Wirkner and Prendini, 2007; Wirkner et al., 2013). Aquatic chelicerates such as present-day *Limulus* extract oxygen from water through morphologically indistinguishable book gills (compare Göpel and Wirkner, 2015, figs. 7a, 10a, c). However, despite the major physiological differences between living aquatic (xiphosurines) and terrestrial chelicerates (arachnids), the structures of the circulatory and respiratory systems are fundamentally similar. This change is also indistinct between the cardiovascular and respiratory systems of Silurian and present-day scorpions suggesting that the fundamental architecture of the respiratory and cardiovascular systems was evolutionarily conservative. With so little change apparent in the structures of these systems between extant aquatic chelicerates and both extinct and extant arachnids, it is likely that early arachnids already possessed the structures and mechanisms (exaptation) for life on land.

were structurally ‘preadapted’ to life on land. Accordingly, any ‘expected’ morphological change that might have accompanied the transition from water-to-land would have been undetectable at the time of terrestrialisation.

**References**

ANDERSON, L. I., CLARKSON, E. N. K., STEWARD, S. E. and MITCHELL, D. 2007. An Upper Llandovery Konzervat-Lagerstätte in a depositional context: the


— 2001b. Structure, reproduction, and development. 13–78. In BROWNELL, P. and


LORIA, S. F. and PRENDINI, L. 2014. Homology of the Lateral Eyes of Scorpionidae: A


MCLAUGHLIN, P. I., MIKULIC, D. G., and KLUESSENDORF, J. 2013. Age and correlation of Silurian rocks in Sheboygan, Wisconsin, using integrated stable


POCOCK, R. I. 1901. The Scottish Silurian scorpion. *Quarterly Journal of


SPENGLER, A. E. and READ, J. F. 2010. Sequence development on a sediment-starved, low accommodation epeiric carbonate ramp: Silurian Wabash Platform, USA mid-


TABLE 4.1: Characters and character states present in some of the most completely known Paleozoic scorpions.
<table>
<thead>
<tr>
<th>Species</th>
<th>Geologic Age</th>
<th>Compound lateral eyes or ocelli</th>
<th>Anterior or posterior median eyes</th>
<th>Coxapophyses</th>
<th>Sternites</th>
<th>Intrasternite spiracles</th>
<th>Metasoma Length</th>
<th>Limb Stance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parascorpio</td>
<td>Silurian</td>
<td>Compound</td>
<td>anterior</td>
<td>absent</td>
<td>7</td>
<td>absent</td>
<td>short</td>
<td>unknown</td>
</tr>
<tr>
<td>Proscorpius</td>
<td>Silurian</td>
<td>Compound</td>
<td>anterior</td>
<td>absent</td>
<td>6</td>
<td>absent</td>
<td>long</td>
<td>digitigrade</td>
</tr>
<tr>
<td>Eramoscorpius</td>
<td>Silurian</td>
<td>Unknown</td>
<td>unknown</td>
<td>absent</td>
<td>6</td>
<td>absent</td>
<td>long</td>
<td>transitional</td>
</tr>
<tr>
<td>Waeringoscorpio</td>
<td>Devonian</td>
<td>Unknown</td>
<td>posterior</td>
<td>absent</td>
<td>5</td>
<td>unknown</td>
<td>long</td>
<td>unknown</td>
</tr>
<tr>
<td>Pulmonoscorpius</td>
<td>Carboniferous</td>
<td>Unknown</td>
<td>unknown</td>
<td>present</td>
<td>5</td>
<td>absent</td>
<td>long</td>
<td>plantigrade</td>
</tr>
</tbody>
</table>

**Table 4.1**
TABLE 4.2: Comparison of data used to infer habitats of some Paleozoic scorpions.
<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Lithology</th>
<th>Associated Biota</th>
<th>Intrastenite Spicules</th>
<th>Book lungs/ base gills</th>
<th>Sensory</th>
<th>Limb Stance</th>
<th>feeding method</th>
<th>Other argument</th>
<th>Reference about habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proacorylalım</td>
<td>Sil.</td>
<td>dolostone</td>
<td>vascular plants, eurypterids</td>
<td>absent</td>
<td>gill slits reported</td>
<td>unknown</td>
<td>digitigrade</td>
<td>lacks osseoprocesses</td>
<td></td>
<td>Kjellesvig-Waering, 1986 = aquatic</td>
</tr>
<tr>
<td>Eoacorylalım</td>
<td>Sil.</td>
<td>dolostone</td>
<td>Echinoderms, tribolites, brachiopods, ophiactins, eurypterids</td>
<td>absent</td>
<td>unknown</td>
<td>possible</td>
<td>pectines</td>
<td>transitional</td>
<td>lacks osseoprocesses</td>
<td>Kjellesvig-Waering., 1986 = ambiguous</td>
</tr>
<tr>
<td>Waeringacoryl álím</td>
<td>Dev.</td>
<td>organic-rich</td>
<td>eurypterids, brachiopods, hiracanthids, cheermatae, vascular plants</td>
<td>unknown</td>
<td>unknown</td>
<td>possible</td>
<td>pectines</td>
<td>unknown feeding method</td>
<td></td>
<td>Waddington et al., 2015 = aquatic with possible terrestrial forays</td>
</tr>
<tr>
<td>Palaeacoryl álím</td>
<td>Dev.</td>
<td>black shale</td>
<td>echinoderms, sponges, brachiopods, polychaete worms, trilobites, horseshoe crabs, ammonoids, fish, ~</td>
<td>unknown</td>
<td>unknown</td>
<td>unknown</td>
<td>digitigrade</td>
<td>unknown</td>
<td></td>
<td>Kjellesvig-Waering, 1986 = secondary/ aquatic</td>
</tr>
<tr>
<td>Pliomisacoryl álím</td>
<td>Carb.</td>
<td>plant-rich</td>
<td>amphibians, reptiles, other arachnids, lycopsids, gymnosperms, myriapods, plantaepermis, rare eurypterids, ~</td>
<td>absent</td>
<td>book lungs</td>
<td>pectines</td>
<td>plantigrade</td>
<td>coxoprocesses</td>
<td></td>
<td>Kjellesvig-Waering, 1986 = aquatic</td>
</tr>
<tr>
<td>Compacoryl álím</td>
<td>Carb.</td>
<td>silicic</td>
<td>arachnids, myriapods, plantaepermis, comparable to Mason Creek fauna</td>
<td>present</td>
<td>asssumed presence due to sprinacies</td>
<td>tentative</td>
<td>plantigrade</td>
<td>coxoprocesses</td>
<td></td>
<td>Legg et al., 2012 = terrestrial</td>
</tr>
</tbody>
</table>

Table 4.2
FIGURE 4.1: Par ioscorpio venator, n. gen., n. sp., holotype, part, UWGM 2162, Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin preserved in dolomudstone. A, photograph under low-angle lighting; B, interpretive drawing; C, photograph under high-angle lighting. Abbreviations: fe, femur; fr, free finger; fx, fixed finger; le, lateral eye; me, median eyes; mpr, median prosomal ridge; mt #, metasomal segment; pa, patella; pc, pericardium; pfm, pedipalp femur; pm, pedipalp manus; pm.c, pedipalp manus charinae; ppt, pedipalp patella; pr, pedipalp rami; ps, pulmo-pericardial sinus; ptr, pedipalp trochanter; tr, trochanter; t, telson vesicle; wl, walking leg. Scale bar equals 5 mm.
Fig. 4.1
FIGURE 4.2: *Parioscorpio venator*, n. gen., n. sp., holotype, UWGM 2162, Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin. A, photograph used as a map for magnified portions of exoskeleton (B–F); B, left pedipalp and charinae; C, prosoma; D, inferred pulmono-pericardial sinuses; E, inferred pedicardium; F, metasomal segment 5 with bulbous area, inferred to be telson vesicle; G, counterpart overlain with secondary authigenic phosphate. Scale bars equal 5 mm (A, G) and 1 mm (B–F).
FIGURE 4.3: *Parioscorpio venator*, n. gen., n. sp., paratype, UWGM 2163, a specimen preserving some ventral anatomy but split through the body, Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin. A, photograph taken under low angle lighting and emphasising inferred gut tract; B, interpretive drawing.

**Abbreviations:** cx #, coxae; gt, gut tract; mr, midline ridge; mt #, metasomal segment; pp, partial pedipalp; st, sternum; stn #, sternite. Scale bar equals 5 mm.
Fig. 4.3
FIGURE 4.4. Circulatory and respiratory system of a Holocene scorpion. A, Male *Hadogenes troglodytes* dorsal surface, showing medial structure reflecting the position of the internal pericardium; B, SEM micrograph of the pericardium and pulmo-pericardial sinuses of *Centruroides exilicauda*. Abbreviations: bl, book lungs; pc, pericardium; ps, pulmo-pericardial sinus. Scale bar is 2 mm.
Fig. 4.4
FIGURE 4.5: Chronostratigraphic positions of Silurian to Carboniferous (Mississippian) scorpions. Grey dots indicate uncertain stratigraphic position. Asterisk indicates fragmentary specimen.
Fig. 4.5

- Parinoscorpio venator
- Dolichophonous loudonensis
- Allopalaeophonous caledonicus
- Palaeophonous nuncius
- Eramoscorpio brucensis

- Palaeoscorpius devonicus
- Waeringoscorpio hefteri
- Waeringoscorpio westwaldensis

undetermined scorpion* sensu Dunlop & Selden, 2013

Gondwanascorpio emzantsiensis* •

- Proscorpio osborni

- ?Palaeophonous lightbodyi* •
- Brontoscorpio anglicus •
- Praearcturus gigas •

- Gigantoscorpio willsi •
- Archaeoctonus glaber •
- Pulmonoscorpius kirktonensis •
- Labioscorpio alliedensis •
FIGURE 4.6: Reconstruction of *Parioscorpio venator* n. gen., n. sp. Structures outlined in grey are inferred from *Proscorpius* and other Silurian scorpions. Structures infilled in grey denote circulatory and respiratory anatomy.
FIGURE 4.7: Hypothesis of relationship among some of the more completely known Paleozoic scorpions, with geologic time scale at left. Character states are indicated by bars on the cladogram. Bar 1 = presence of seven sternites (plesiomorphic condition); bar 2 = presence of six sternites; bar 3 = presence of five sternites; bar 4 = presence of coxapophyses.
Fig. 4.7
Chapter 5: New cheloniellid arthropod from the Silurian of Wisconsin, USA

Introduction

Non-biomineralised or lightly skeletonised arthropods are common in Paleozoic Konservat-lagerstätten (e.g., Van Roy et al., 2010; Caron et al., 2014; Patterson et al., 2015; Rust et al., 2016). However, owing to preservational biases and a high degree of morphological diversity, their affinities are commonly difficult to interpret. Non-biomineralised arthropods with raptorial or grasping appendages are often referred to as ‘great appendage arthropods’ until their affinities are resolved (e.g., Chen et al., 2004; Kühl et al., 2009). The ‘great appendage arthropods’ comprise a morphologically diverse assortment of species. The term probably refers to a taxonomic wastebasket, and relationships to each other and within the Arthropoda are ambiguous (e.g., Chen et al., 2004; Waloszek et al., 2005; Scholtz & Edgecombe, 2006; Briggs et al., 2008; Hendricks & Lieberman, 2008; Budd & Telford, 2009; Kühl et al., 2009; Vannier et al., 2009; Daley & Budd, 2010; Edgecombe, 2010; Edgecombe et al., 2011; Van Roy & Briggs, 2011; Babcock et al., 2012; Edgecombe & Legg, 2014; Ortega-Hernández & Budd, 2016).

Here we report a new arthropod with large appendages that suggests inclusion as a ‘great appendage arthropod’ in the broad sense, but which is also referable to the order
Cheloniellida. A large number of specimens from the Waukesha Lagerstätte in the Brandon Bridge Formation (Silurian) of southeastern Wisconsin offer the opportunity to describe previously unknown or little known features in the group. Cheloniellids are a group of non-biomineralised or lightly skeletonised Paleozoic arthropods characterised by a wide, ovoidal carapace, forward curved or angled posterior cephalic margin and pleural tips that are anterolaterally directed at the front and become increasingly posterolaterally directed toward the rear (e.g., Dunlop and Selden, 1998; Dunlop, 2002). This new form is among the best preserved cheloniellids and allows for a rediagnosis of the group.

Material and Methods

This study is based on five of the better preserved specimens collected from the Waukesha Lagerstätte at the Waukesha Lime and Stone Company quarry near Waukesha, Wisconsin. Specimens are deposited in the University of Wisconsin Geology Museum, Madison, Wisconsin, USA (UWGM).

Specimens were photographed with a Canon EOS Rebel T3i Digital SLR with a Canon MP-E 65 mm macro lens and full spectrum lighting. Specimens, where noted, were whitened with ammonium chloride to enhance contrast. Images were z-stacked using Adobe Photoshop CC and measurements were made using ImageJ.

Geological Setting
Exceptionally preserved fossils occur in a 12 cm layer of finely laminated dolomitised plattenkalk at the base of the Brandon Bridge Formation (Mikulic et al., 1985 a, b; Kluessendorf & Mikulic, 1996). The Brandon Bridge Formation (Silurian) in southeastern Wisconsin contains graptolites of the *Oktavites spiralis* Zone, which suggests correlation with the Llandovery Series, Telychian Stage (Mikulic et al., 1985 a, b; Chapter 2). Fossils occur either in thinly laminated, fissile, organic-rich, argillaceous dolomudstone (termed flinz) or thinly laminated, non-fissile, dolomudstone (termed fäule; see Chapter 2). All but one specimen reported here is preserved in flinz. Specimens from flinz layers are preserved by a coating of authigenic phosphate overlying a thin dark organic film and are generally more detailed (see Chapter 2). UWGM 2345 is in a fäule layer and is preserved by a thin coating of organic film.

Sedimentary and microbial structures in the Brandon Bridge Formation indicate that organisms are allochthonous, having been washed in from nearby areas and accumulated in small sedimentary traps along a tidally influenced shoreline (see Chapter 2). Organisms were neither consumed nor readily decayed, thus increasing their chances of preservation. High salinity or other environmental factors were evidently limiting to most macroscopic organisms. Limited bioturbation indicates that this environment was devoid of most burrowers and grazers that allowed a diverse microbial biota, including microbial mats, to develop and flourish. Microbial-mediated processes, such as authigenic mineralisation, facilitated the preservation of much of the Waukesha Biota including non-biomineralised and lightly skeletonised organisms (see Allison, 1988;
SYSTEMATIC PALAEOONTOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank:

Phylum ARTHROPODA von Siebold, 1848
Class Uncertain
Order CHELONIELLIDA Broili, 1932

Emended diagnosis. Small to medium-size, biramous?, arthropods having wide, ovoidal, non-biomineralised or lightly skeletonised dorsal exoskeleton. Cephalon short, with suture separating procephalon from gnathocephalon; eyes present; trunk wider than cephalon, with 8 to 13 tergites; trunk normally with narrow, convex medial area and nearly flat plural areas; distal ends of first few tergites directed anterolaterally, becoming increasingly posterolaterally directed rearward. Terminal tergite cylindrical or round, bears anus, and encompassed by previous tergite. Caudal assembly consists of an elongate, forked, posteriormost segment bearing anus; elongate medial spine may articulate with it. Cephalic appendages uniramous, consisting of long paired antennae and five pairs of endopods, all except the first endopod bear ganthobases; brush-like
structures on endopods do not appear to be exopods. Trunk appendages biramous, with one pair per segment, consisting of an endopod and shorter exopod, not present on terminal tergite.

Discussion. Cheloniellids, as reviewed by Dunlop (2002), range from the Early Ordovician (Tremadoc) to the Early Devonian (Emsian). Prior to this paper, six monospecific genera were described and referred to the group: *Triopus drabowiensis* Barrande, 1872 (Ordovician of the Czech Republic), *Duslia insignis* Jahn, 1893 (Ordovician of the Czech Republic and Morocco), *Cheloniellon calmani* Broili, 1932 (Devonian of Germany), *Neostrabops martini* Caster & Macke, 1952 (Ordovician of the USA), *Pseudarthron whittingtoni* Selden & White, 1984 (Silurian of Scotland), and *Paraduslia talimaeae* Dunlop, 2002 (Devonian of Russia). In addition, an undescribed cheloniellid, has been illustrated from the Ordovician of Morocco (Van Roy et al., 2010, fig. 2b; Van Roy, 2011, fig. 2a, b). Two arthropods left in open nomenclature, both from the Silurian, are here referred to the Chelonieliida. One species is from Ontario (von Bitter et al., 2007, fig. 2j), and the other, which is described from articulated material below, is from Wisconsin (previously illustrated by Mikulic et al., 1985b, fig. 16, 21). A head shield described as *Drabovaspis complexa* (Barrande, 1872; see Chlupač, 1963; Ortega-Hernández et al., 2010a) from the Ordovician of the Czech Republic may also be a cheloniellid.

Affinities of the Cheloniellida within the Arthropoda are uncertain. By various authors they have been interpreted as Crustacea (Barrande, 1872; Delle Cave &
Simonetta, 1991), Trilobita (Broili, 1933), Arachnomorpha (Størmer, 1944, 1959), Aglaspida (Chlupáč, 1965), Xiphosura (Bergström, 1968; Ortega-Hernández et al., 2010b), and as a sister group to Chelicerata (Cotton & Braddy, 2004). Jahn (1893) referred the cheloniellids to the phylum Mollusca.

Cheloniellids are characterised by a wide, ovoidal carapace; a procurved or forward angled posterior cephalic margin; and a thickened or lobed medial region, except in Neostrabops. A doublure is often present around the anterior cephalic margin (e.g., Stürmer & Bergström, 1978, fig. 4; Van Roy, 2011, fig. 2a, b). With the exception of Cheloniellon, cheloniellids were reported to lack eyes, however eyes may have been present and may be evident in published figures (e.g., Selden & White, 1984: fig. 4b; Chlupáč, 1988: plate 56, fig. 5, on either side of the axial lobe; Van Roy, 2006: figs., 6.2, 6.4, 6.10, 6.11, 6.12). Cephalic sutures were reported in some cheloniellids (e.g., Chlupáč, 1988: text-fig. 1). Cheloniellon has a reduced head segment, which we regard as a procephalon, with a larger segment (gnathocephalon) baring gnathobases.

Cheloniellids have a wide, ovoid trunk with between 8 (Pseudarthron) and 13 (Waukesha form) tergites. Tergites are narrow medially and wider laterally. Anterior 2-3 pleural tips directed forward, the rest become increasingly posterolaterally directed toward the rear. Cheloniellon uniquely has an expanded second to last tergite (Stürmer & Bergström, 1978, fig. 11a). Some forms have a marginal spiny fringe around the entire organism (Duslia, Moroccan and Waukesha forms).

The terminal tergite is either cylindrical or round and encompassed by the previous tergite. Both Stürmer & Bergström (1978) and Cotton & Braddy (2004) reported a
segment behind the terminal tergite that they referred to as a telson in cheloniellids. Cotton & Braddy (2004) described a ‘faint tergite boundary’ on the terminal tergite indicating the presence of a small telson in *Duslia* (Chlupáč, 1988: plate 57, fig. 4). We consider this to likely be taphonomic, though it could be construed as evidence of a median spine. Similarly, *Cheloniellon* was reconstructed with a large telsonic segment, behind the insertion of the furcae (Stürmer & Bergström, 1978, figs. 1, 2). However, figured specimens do not appear to reflect this reconstructed morphology (compare Stürmer & Bergström, 1978, figs. 10, 11). Contra Stürmer & Bergström (1978) and Cotton & Braddy (2004), we find no evidence of a telson behind the terminal tergite in cheloniellids.

Cheloniellids display a wide range of morphological variation in the post-abdomen. Cheloniellid species with preserved posterior regions have caudal furcae attached to the terminal tergite. *Cheloniellon* possesses long, flexible furcae, whereas *Paraduslia*, *Duslia*, the Moroccan and Waukesha forms possess short furcae. Species with short furcae are further differentiated by the structure and shape of the furcae, seemingly being either flexible tassels (*Paraduslia*) or inflexible spines (*Duslia*, Moroccan and Waukesha forms). The Waukesha form is further differentiated by the presence of a separate, longer medial spine.

Appendages are poorly known in cheloniellids. Prior to this description, *Cheloniellon* was the only described species with preserved appendages. *Cheloniellon* has six uniramous paired cephalic appendages, including narrow long antennae and five endopods, the posterior four endopods bear gnathobases (Stürmer & Bergström, 1978:
An unusual brush-like structure was also noted by Stürmer & Bergström (1978) on the second cephalic appendage but it was not included in the reconstruction or diagnosis. The undescribed Moroccan cheloniellid preserves long antennae; no other appendages are apparent (Van Roy et al., 2010, fig. 2b; Van Roy et al., 2011, fig. 2a, b). Trunk appendages are biramous, based on several frilled, ovoid elements on one specimen of Cheloniellon that are interpreted to be gilled exopods (Stürmer & Bergström, 1978: fig. 8).

Genus *LATROMIRUS* nov.

*Etymology.* From Latin, *latro*, hunter, and *mirus*, extraordinary (masculine), in reference to the raptorial appendages.

*Diagnosis.* As for the species.

*Type species.* *Latromirus tridens* sp. nov.

*Diagnosis.* Exoskeleton small, wide and oval with spiny marginal fringe. Cephalic shield short and wide; anterior margin rounded with doublure; posterior margin angled forward. Lateral eyes, large, compound?, located midway from anterior margin; paired sutures extending anteromedial area to at least medial area; trunk with 11-13 tergites; first two tergites directed anterolaterally, third tergite directed laterally, remaining tergites become
increasingly posterolaterally directed; terminal tergite round with centrally located anus; caudal apparatus articulates to terminal tergite and is composed of paired lateral spines and separate longer medial spine; cephalic appendages consisting of small paired setal appendages and large paired, laterally oriented raptorial appendages; trunk appendages biramous?, hooked endopod and possible brush-like exopod; appendages present on all but last tergite.

**Discussion.** *Latromirus tridens* is most similar to two other cheloniellids, *Duslia* and the undescribed cheloniellid from the Ordovician of Morocco. All three forms have spiny marginal fringes and forked spines (furcae). Neither *Duslia* nor the Moroccan form preserve evidence of raptorial appendages, which is at this point either a structure that is novel to *L. tridens* or one that does not readily preserve.

An unnamed arthropod, ROM 57980, in Von Bitter et al., 2007 (fig. 2J) may be congeneric based on the presence of putative raptorial appendages, a thickened medial region and a poorly preserved laterally expansive pleural region.

*Latromirus tridens* sp. nov.

Figure 5.1–5.13

1985a ?branchiopod crustacean Mikulic et al., p. 716, fig. 2d.

1985b branchiopod or remipede crustacean Mikulic et al., p. 80, fig. 16.

**Etymology.** From Latin, *tridens*, a three-pronged spear, in reference to the caudal
assembly.

*Holotype.* UWGM 2439 (Figs. 5.1.1, 5.1.2, 5.1.8, 5.1.11, 5.1.12).

*Paratypes.* UWGM 2345 (Fig. 5.1.3), UWGM 2575 (Figs. 5.1.4, 5.1.9), UWGM 2436 (Figs. 5.1.5, 5.1.6, 5.1.10, 5.1.13), UWGM 2437 (Figs. 5.1.7).

Additional material. 14 specimens.

*Occurrence.* Silurian (Llandovery, Telychian), occurring in a 12 cm layer approximately in the lower Brandon Bridge Formation, Waukesha Lime and Stone Company quarry, north of State Highway 164, Waukesha, Wisconsin, USA.

*Diagnosis.* As for genus.

*Description.* Exoskeletal length ranging to at least 45 mm and likely weakly mineralised. Body width approximately 70% of the body length excluding furcae. Cephalic shield with anterior margin rounded; short, wide with doublure; posterior margin angled forward. Lateral eyes large, ovoid located midway between anterior and posterior margins, directed anteromedially. Cephalic shield raised medially between eyes extending posteriorly through trunk. Sutures originate directly posterior to eye and extend anterolaterally, separating the procephalon from the gnathocephalon. 'Lobes’ large,
paired, present posteromedially from the eyes.

Abdomen ovoid, wider than cephalon with 11-13 tergites present. Trunk widest at tergites 5 and 6. Medial region moderately wide with thickened cuticle. Pleural region cuticle thin, commonly poorly preserved. Tergites appear wider laterally and thinner medially. Anterior two pleural tips directed forward, third tergite is directed laterally and the rest become increasingly posterolaterally directed toward the rear. Terminal tergite is circular and bears anus medially.

Caudal apparatus composed of two parts, a forked sclerite with stout, bowed posteriorly directed spines and a moderately long, stout median spine. Forked sclerite abuts and wraps around edges of the terminal segment. Lateral spines situated ventrally, whereas the median spine is dorsally situated.

Two pairs of appendages observed on the cephalic shield. Small paired setae bearing appendages and raptorial appendages extending anterolaterally, consisting of approximately five elongate podomeres. Base of the raptorial appendage attaches adjacent to inferred position of the mouth. Distal podomere articulates at 90° to preceding podomere; terminates in a sharp, stout, tip. Trunk limbs extend just beyond the medial region and consist of sharply hooked endopod. Brush-like structures may represent exopods.

Discussion. Latromirus tridens is one of the more common organisms reported by Mikulic et al., (1985a, b) from the Waukesha Lagerstätte. It is known from more than 20 specimens. UWGM 2439 and UWGM 2345 are preserved in dorsal view, and all others
in ventral view. Some specimens are partly split through the exoskeleton. Studied specimens are predominately incomplete, and show varied preservational conditions including the loss of cephalic appendages, differential preservation of medial and pleural regions of the abdomen, and secondary authigenic early mineralisation. Often specimens do not preserve the pleural regions well, giving the appearance of a more slender organism. This condition entered into the original interpretation of this unusual arthropod (Mikulic et al., 1985b, fig. 21). The positions of the pleural margins in some specimens can be approximated by the more easily identifiable microbial decay halo (see Borkow & Babcock, 2003), which lies just beyond the ends of the tergites (Fig. 5.1.7). The cuticle of the pleural regions may have been quite thin in life, which leads to some difficulty in interpretation. Sufficiently well preserved material is necessary for correct interpretation of morphology and affinities. Without the thin lateral areas of the carapace, this animal resembles a branchiopod crustacean (as noted by Mikulic et al., 1985a, b).

Non-biominalised arthropod cuticle, primarily composed of chitin, is relatively rare in the fossil record (Potnick, 1986). In most environments, it is readily digested by microorganisms and macroorganisms (Borkow and Babcock, 2003.). Specific environments have been shown to limit biodegraders and the biodegradation of chitin, allowing the chitin to survive long enough to fossilise (see Chapter 2). Mikulic et al. (1985a, b) and Chapter 2 discussed paleoenvironmental and depositional conditions leading to exceptional preservation in the Waukesha Lagerstätte. The Waukesha Biota was deposited in a microbially-rich environment that facilitated exceptional preservation (Chapter 2). Macroorganisms including *Latromirus tridens* were transported into a
nearshore environment where breakdown of chitin was inhibited. Non-biomineralised and lightly skeletonised arthropods in the Waukesha Lagerstätte tend to be compressed and have secondary phosphatic overgrowths (Moore et al., 2005; Chapters 2). Overgrowths are commonly crinkled and tend to distort or obscure morphologic features (Moore et al., 2005; Chapters 2).

All observed specimens of *Latromirus tridens* are articulated. Taphonomic experiments demonstrate that arthropods can remain at the sediment surface for weeks before complete disarticulation (Babcock & Chang, 1997; Babcock et al., 2000). Limbs and gills are among the first structures to be lost in arthropods. They begin to separate from the exoskeleton in about one week (Babcock & Chang, 1997; Babcock et al., 2000; McCoy & Brandt, 2009). Endopods are commonly present, whereas the gilled exopods are commonly lost. Babcock & Chang (1997) and Babcock et al. (2000) found that the first structures to disarticulate in extant arthropods are gills, followed by limbs. Most specimens retain some walking legs. All but one specimen of *L. tridens* has lost the brush-like structures (compare Stürmer & Bergström, 1978). If these structures are gills, then the gills were the first body parts lost in *L. tridens* (compare Babcock et al., 2000), which would suggest burial within about two weeks of death.

Ambiguity in the limb structure of cheloniellids should be noted. Within the cephalon of *Cheloniellon*, unusual brush-like structures were noted on ‘uniramous’ appendages by Stürmer & Bergström (1978, fig. 5). Similar structures are preserved on a ventrally preserved specimen of *Latromirus tridens* (Fig. 5.1.4) across the head and trunk. These brush-like elements may represent gilled exopods or possibly structures that
supported the marginal frill. We infer that these structures were lost quite readily, whether they functioned as gills or not, and we do not suggest homology or function.

The general morphology of *Latromirus tridens* indicates affinity with cheloniellids supported by the posterior margin of the head, widely ovoid body, posterolaterally trending tergites and caudal furcae among other features. However, it possesses some unusual morphology that is unique within the cheloniellids including raptorial appendages and a medial spine. Originally, *L. tridens* was interpreted by Mikulic et al. (1985a, b) as bearing affinities to either branchiopod or remipedian crustaceans on the basis of large, specialised cephalic appendages. Without a large number of differentially preserved specimens, the inferred affinities of *L. tridens* would be different.

In general, cheloniellids could easily be confused with a number of other Paleozoic arthropods that have grossly similar body forms including the trilobite *Burlingia* (Walcott, 1908; Whittington, 1994; Robison & Babcock, 2011; Robison et al., 2015) and non-biomineralised arthropods, such as *Arthroaspis* (Stein et al., 2013) and aglaspid-like arthropods (see Ortega-Hernández et al., 2010b). Even some extant arthropods share similar morphology including serolid isopods (Wägle, 1986) and larval water penny beetles (Murvosh, 1971). Cheloniellids such as *Latromirus tridens* could also be confused with great appendage arthropods. Without a preserved pleural region, the raptorial appendages appear as more prominent structures.

Raptorial appendages within arthropods greatly vary in function and form. Anomlocaridid-type grasping appendages (e.g., Daley & Budd, 2010; Lerosey-Aubrill et al., 2014) and mantis-shrimp-like raptorial appendages (Chen et al., 2004; Haug et al.,
are common in Paleozoic arthropods and functioned dorso-ventrally. The raptorial appendages of *Latromirus tridens* appear to have functioned laterally with the appendage tips meeting at the midline, possibly to pierce and immobilise prey. Dorso-ventral oriented appendages were more likely used for crushing, slicing or capturing prey. In this respect, the appendages of *Latromirus tridens* are apparently unique among known raptorial appendage-bearing Paleozoic arthropods.

References Cited


Broili, F. 1933. Ein zweites Exemplar von *Cheloniellon*. *Sitzungsberichte*
Bayerische Akademie der Wissenschaften, **1933**, 11–32.


Stürmer, W. and Bergström, J. 1978. The arthropod *Cheloniellon* from the Devonian


Van Roy, P. 2006. *Non-trilobite arthropods from the Ordovician of Morocco.*


Wägle, J. W. 1986. Polymorphism and distribution of *Ceratoserolis trilobitoides* (Eights,
1833) (Crustacea, Isopoda) in the Weddell Sea and Synonymy with *C. cornuta* (Struder, 1879). *Polar Biology*, 6, 127–137.


Figure 5.1. *Latromirus tridens*, n. gen. sp. from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin preserved in dolomudstone. UWGM 2439, holotype, counterpart (1) photographed dry and part (2) photographed wet; (3) UWGM 2345 preserving dorsal anatomy; (4) UWGM 2575 preserving ventral anatomy and brisk-like structures; (5) UGWM 2436 preserving ventral anatomy and limbs; (6) UWGM 2436 whitened with ammonium chloride and photographed under low-angle lighting, arrows indicate pleural segments; (7) UWGM 2437 preserving ventral anatomy with limbs and partially preserved pleural region, arrow indicates decay halo; (8) closeup of the spiny marginal fringe of UWGM 2439; (9) closeup of brush-like (gills?) elements of UWGM 2575; (10) closeup of caudal apparatus of UWGM 2436; (11) closeup and whitened raptorial appendages of UWGM 2436; (12) left side of part superimposed next to right side of part of UWGM 2439 (13). Scale bar equals 5 mm for 1–7, 13; 2 mm for 8–10. Abbreviations: 1-11, numbered tergites; an, anus; bs, basal lobe; db, doublure; e, eyes; fs, facial suture; la, labrum; lg, leg; ls, lateral spines; ms, median spines; pcm, posterior cephalic margin; ra, raptorial appendage; rs, round sclerite; sa, setal appendage.
Fig. 5.1
Chapter 6: Silurian lobopodians from the Waukesha Lagerstätte of Wisconsin

Introduction

Lobopodians are a morphologically diverse group of Paleozoic non-biomineralised organisms with unsegmented limbs and thin sclerotized cuticle (Ortega-Hernádez, 2015). Like most non-biomineralized organisms, they are relatively poorly represented in the fossil record and articulated specimens are primarily known from Konservat-lagerstätten such as Chengjiang, Burgess Shale, and Mazon Creek. The vast majority of known lobopodians are Cambrian in age, and nearly half of these taxa occur in the Chengjiang Biota (see Table 6.1). More recently, younger Paleozoic lobopodians have been reported (e.g., von Bitter et al., 2007; Whittle et al., 2009; Van Roy et al., 2010; Haug et al., 2012; Murdock et al., 2016) and fill in gaps in their fossil record, which currently extends into the Carboniferous.

Conventionally lobopodians were thought to be ancestral onychophorans based on seemingly similar morphology (e.g., Hou and Bergström, 1995; Ramsköld and Chen, 1998). This interpretation is now controversial (e.g., Ou et al., 2012; Edgecombe and Legg, 2014). Currently, some workers consider lobopodians to represent a morphological grade comprising stem members of three groups: Tardigrada (e.g., Budd, 2001),
Onychophora (e.g., Ou et al., 2011) and Euarthropoda (e.g., Liu et al., 2011).

Here, we report two new lobopodians from the Silurian (Llandovery, Telychian) Waukesha Lagerstätte of Wisconsin. Several specimens yield two distinct forms, a small lobopodian with narrow limbs, curved claws, and rounded plates and a large lobopodian with stout annulate limbs. Both forms are distinct; however they lack preserved diagnostic head regions and, therefore, are left in open nomenclature. The addition of these forms represents the first described Silurian lobopodians, and although these specimens may not add to the discussion of lobopod affinity, they add to their sparse post-Cambrian record.

Material and Methods

This study is based on three specimens collected from the dolostone of the Brandon Bridge Formation (Silurian), Waukesha Lime and Stone Company Quarry, near Waukesha, Wisconsin. Specimens are deposited in the University of Wisconsin Geology Museum in Madison, Wisconsin, USA (UWGM 2427, 2428, 2429).

Geological Setting and Fauna

The Waukesha Lagerstätte occurs at the base of the Brandon Bridge Formation in 12 cm layer of finely laminated dolomitized plattenkalk (Mikulic et al., 1985a, b; Kluessendorf and Mikulic, 1996, Chapter 2) deposited during a transgressive episode.
over the Schoolcraft and Burnbluff Dolomites (Mikulic and Kluessendorf, 1998; Chapter 2). Subaerial exposure of the Schoolcraft and Burn Bluff dolomites prior to Brandon Bridge deposition generated an 8-m scarp with a gentle slope and epikarstic features (Kluessendorf and Mikulic, 1996; Mikulic and Kluessendorf, 1998; Chapter 2). Sedimentary traps, which formed along the base of the scarp in the intertidal or supratidal zones, received remains of both marine and terrestrial organisms washed in from nearby areas. Microbial mats coated and cemented bodily remains in place. Microbial processes are implicated in the exceptional preservation through the precipitation of thin phosphatic coatings on to remains (see Chapter 2, 4, 5).

The Waukesha Biota is diverse and primarily composed of non-biomineralized and lightly skeletonized organisms including scorpions, great appendage arthropods, lobopodians, ‘worms’, and jellyfish (see Chapter 2). Common biomineralized organisms include trilobites and conulariids. Brachiopods, corals, cephalopods and echinoderms are rare, whereas gastropods, bryozoans and bivalves are unknown. Microbial-influenced dissolution was implicated in the loss of the calcium carbonate shelly organisms (Chapter 2) that would have been more typical of a Laurentian shelf in the Silurian (compare Taylor and Brett, 1996; Peters and Bork, 1999).

**Systematic Paleontology**

Lobopodia Snodgrass, 1938

Xenusia Dzik and Krumbiegel, 1989
Undetermined lobopod 1

Figures 6.1.1–6.1.3

**Material.**—One incomplete specimen, part and counterpart, UWGM 2427. Both part and counterpart are backed with epoxy (visible in the counterpart) due to the fragility of the host rock.

**Discussion.**—The specimen is compressed dorsally, and the limbs are splayed out on one side and split through on the other (Figs. 6.1.1, 6.1.2). The anterior end is missing, and the posterior end is preserved but becomes increasingly indistinct toward the rear. The cuticle is unornamented and wrinkled and was likely thin in life. Few structures are raised other than a gut and annulations on the limbs. The exposed portion of the body is 56 mm long and has a maximum width, excluding limbs, of 5.4 mm. Body tapers posteriorly and as preserved has 16 pairs of stout limbs. The limbs are longest at ‘mid-section’ and shorten posteriorly but are equidistant apart throughout the entire animal. The largest limbs are 8.5 mm long and 3.8 mm wide; smallest limbs too indistinguishable for measurements. Limb annulations are more prominent on the proximal half of the limb with 3-4 annulations/mm (Fig. 6.1.3). A pronounced central canal is present medially through each limb. No claws were observed on the limbs. A putative gut is preserved. The trunk extended beyond the observed limbs.

This form exhibits similarly to several xenusiid lobopodians with stout limbs such as *Jianshanopodia* (Cambrian, China; Liu et al., 2006), *Xenusion* (Cambrian, Germany;
Dzik and Krumbiegel, 1989), *Hadranax* (Cambrian, Greenland; Budd and Peel, 1998) and an unnamed lobopodian from the Soom Shale (Ordovician, South Africa; Whittle et al., 2009). This form is morphologically most similar to an unnamed Soom Shale lobopodian (Whittle et al., 2009), both of which have simple, unornamented stout limbs that shorten posteriorly. However, the limbs remains equidistant, rather than becoming closer together in this first form. Comparisons are difficult as the comparable forms are also known from incomplete material, often from one or two specimens.

**Systematic Paleontology**

Lobopodia Snodgrass, 1938

Xenusia Dzik and Krumbiegel, 1989

Undetermined lobopod 2

Figures 6.1.4–6.1.7

**Material.**—Two specimens known, both incomplete and preserved in lateral view. UWGM 2428, part and counterpart, is best preserved but lacks a preserved head. UWGM 2429 may preserve the head but is more poorly preserved.

**Discussion.**—Much of this discussion is based on the better preserved specimen, UWGM 2428 (Figs 6.1.4–6.1.6). The specimens are compressed laterally. The anterior end is incompletely known. A large indistinct structure that may represent the anterior end is
present on UWGM 2429 (Fig. 6.1.7). The posterior end is also incompletely known. Specimens range in length from 24 mm to 26 mm. The body tapers slightly posteriorly. At least 19 pairs of limbs present. Limbs are narrow and flexible and lack observed annulations. At least one limb preserved a large curved claw (Fig. 6.1.6). Limbs shorten and become more closely spaced posteriorly. A central canal is present but faint. The longest limbs are nearly 4 mm long, the shortest are 2 mm. Small rounded ‘plates’ are present on the dorsal margin of each segment.

This animal bears some similarity to the armored lobopodian *Hallucigenia* in possessing narrow limbs with hooked claws (compare Smith and Ortega-Hernández, 2014, fig. 1a). Additionally, the presence of rounded, possibly armored, plates is also known from *Hallucigenia*, which has rounded plates at the base of each of its characteristic spines (Liu and Dunlop, 2014, figs 1e, 2). We considered the possibility that these plates might have a digestive origin (see Vannier et al., 2014), however these structures occur directly above the limbs rather then between successive limbs.

References


Budd, G. E. 2001. Tardigrades as ‘stem-group arthropods’: the evidence from the


lobopod-bearing animal (Murero, Spain) and the problem of the Ecdysozoan early
diversification. In: Pintarotti, P. (Ed.), *Evolutionary Biology—Concepts,

monster’-type lobopodian from the Emu Bay Shale Konservat-Lagerstätte
(Cambrian), South Australia. *Alcheringa: An Australasian Journal of

Haug, J. T., Mayer, G., Haug, C. and Briggs, D. E. G. 2012. A Carboniferous non-
onychophoran lobopodian reveals long-term survival of a Cambrian morphotype.
*Current Biology*, **22**, 1673–1675.

animal, *Luolishania* gen. nov. from Chengjiang, Yunnan. *Acta Palaeontologica

Hou, X.-G., Ramsköld, L. and Bergström, J. 1991. Composition and preservation of the
395–411.


Liu, J., Shu, D., Han, J. and Zhang, Z. 2004. A rare lobopod with well-preserved eyes


Peters, S. E. and Bork, K. B. 1999. Species-Abundance Models: An Ecological Approach to Inferring Paleoenvironment and Resolving Paleoeological Change in the


Thompson, I. and Jones, D. S. 1980. A possible onychophoran from the Middle


Table 6.1. Paleozoic lobopodians known from articulated material. Asterisk (*) indicates that affinities with Lobopodia are uncertain (see Edgecombe, 2009 for review). Double asterisk (**) indicates nomina dubia (according to Murdock et al., 2016).
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Description</th>
<th>Age</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actinoecus stichus</td>
<td>Conway Morris &amp; Robison, 1988</td>
<td>Cambrian</td>
<td>USA</td>
</tr>
<tr>
<td>Antennamanthopodia gracilis</td>
<td>Ou et al., 2011</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Asheaita pedunculata</td>
<td>Walcott, 1911</td>
<td>Cambrian</td>
<td>Canada</td>
</tr>
<tr>
<td>Asheaita? prolata</td>
<td>Robison, 1985</td>
<td>Cambrian</td>
<td>USA</td>
</tr>
<tr>
<td>Cardiodictyon catusulum</td>
<td>Hou et al., 1991</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Collinsium ciliatum</td>
<td>Yang et al., 2015</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Diania cactiformis</td>
<td>Liu et al., 2011</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Hadronas augustus</td>
<td>Budd &amp; Peel, 1998</td>
<td>Cambrian</td>
<td>Greenland</td>
</tr>
<tr>
<td>Hallucigenia fortis</td>
<td>Hou &amp; Bergström, 1995</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Hallucigenia mongeia</td>
<td>Steiner et al., 2012</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Hallucinognic sparsa</td>
<td>Walcott, 1911</td>
<td>Cambrian</td>
<td>Canada</td>
</tr>
<tr>
<td>Indet. huolishanii (&quot;Collins’ Monster&quot;)</td>
<td>Collins, 1986</td>
<td>Cambrian</td>
<td>Canada</td>
</tr>
<tr>
<td>Indet. huolishanii</td>
<td>García-Bellido et al., 2013</td>
<td>Cambrian</td>
<td>Australia</td>
</tr>
<tr>
<td>Jianhuangopodia decoria</td>
<td>Liu et al., 2006b</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Kerystomachela kierkegaardi*</td>
<td>Budd, 1993</td>
<td>Cambrian</td>
<td>Greenland</td>
</tr>
<tr>
<td>Lusolithania longicruris</td>
<td>Hou and Chen, 1989a</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Megadictyon haikuensis</td>
<td>Luo et al., 1999</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Microdictyon zinicum</td>
<td>Chen et al., 1989</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Mitrailolithania haikuensis</td>
<td>Liu et al., 2004</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Murenopodia apae</td>
<td>Gámez Vintaned et al., 2011</td>
<td>Cambrian</td>
<td>Spain</td>
</tr>
<tr>
<td>Onychodictyon ferox</td>
<td>Hou et al., 1991</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Onychodictyon gracilis</td>
<td>Liu et al., 2008</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Orstenolutus evanuellerae</td>
<td>Maas et al., 2007</td>
<td>Cambrian</td>
<td>Sweden</td>
</tr>
<tr>
<td>Pambdelurion whitington*</td>
<td>Budd, 1997</td>
<td>Cambrian</td>
<td>Greenland</td>
</tr>
<tr>
<td>Pacipodina haikuensis</td>
<td>Luo et al., 1999</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Pacipodina inermis</td>
<td>Chen et al., 1995</td>
<td>Cambrian</td>
<td>China</td>
</tr>
<tr>
<td>Silerton lenaicus</td>
<td>Drzik, 2011</td>
<td>Cambrian</td>
<td>Russia</td>
</tr>
<tr>
<td>Xenusion auerwaldae</td>
<td>PompeykJ, 1927</td>
<td>Cambrian</td>
<td>Germany</td>
</tr>
<tr>
<td>Indet. Xenusid</td>
<td>Whittle et al., 2009</td>
<td>Ordovician</td>
<td>South Africa</td>
</tr>
<tr>
<td>Undescribed armored lobopodian</td>
<td>Van Roy et al., 2010</td>
<td>Ordovician</td>
<td>Morocco</td>
</tr>
<tr>
<td>Undescribed lobopodian</td>
<td>von Bitter et al., 2007</td>
<td>Silurian</td>
<td>Canada</td>
</tr>
<tr>
<td>Undescribed lobopodian 1</td>
<td>This publication</td>
<td>Silurian</td>
<td>USA</td>
</tr>
<tr>
<td>Undescribed lobopodian 2</td>
<td>This publication</td>
<td>Silurian</td>
<td>USA</td>
</tr>
<tr>
<td>Carbotubulus waloszei</td>
<td>Haug et al., 2012</td>
<td>Carboniferous</td>
<td>USA</td>
</tr>
<tr>
<td>Helmsdorina inquinata</td>
<td>Thompson and Jones, 1980</td>
<td>Carboniferous</td>
<td>USA</td>
</tr>
<tr>
<td>Ilyodes divisa**</td>
<td>Scudder, 1890</td>
<td>Carboniferous</td>
<td>USA</td>
</tr>
<tr>
<td>Ilyodes elongata**</td>
<td>Scudder, 1890</td>
<td>Carboniferous</td>
<td>USA</td>
</tr>
</tbody>
</table>
Figure 6.1. Undetermined lobopodians from the Brandon Bridge Formation, Silurian (Llandovery, Telychian), Wisconsin. Lobopodian form 1, UWGM 2427, part (1) and counterpart (2) with a closeup of the legs of part (3). Lobopodian form 2, UWGM 2428, part (4) and counterpart (5) with closeup of the legs of part photographed wet (6). Second specimen of Unidentified lobopodian form 2, UWGM 2429 (7). 1-16, limbs; ann, annulations; cc, central canal; cl, claw; gt, gut. Arrows indicate rounded plates. Scale bar equals 20 mm (1–2), 5 mm (3, 6), 10 mm (4, 5, 7)
Chapter 7: A non-biomineralized chordate with caudal anatomy from the Waukesha Lagerstätte (Silurian), Wisconsin, USA

Introduction

The origin and early evolution of chordates is fascinating and contentious. Many recent papers (e.g., Hou et al., 2002; Rowe, 2004; Aldridge et al., 2007; Donoghue and Purnell, 2009; Turner et al., 2010; Friedman and Sallan, 2012; Mallet and Holland, 2013; Conway Morris and Caron, 2014; Donoghue and Keating, 2014; Janvier, 2015) have addressed the topic, but a number of fundamental issues remain unresolved. Recent papers (e.g., Conway Morris and Caron, 2014; McCoy et al., 2016) suggest that there was considerable disparity among Paleozoic chordates (including vertebrates). Some early Paleozoic (Cambrian to Ordovician) animals interpreted as vertebrates were biomineralizers (e.g., Anatolepis, Smith et al., 1996; Sacabambaspis, Gagnier, 1987), whereas others did not biomineralize (e.g., Metaspriggina, see Conway Morris, 2008; Haikouichthys, Shu et al., 1999). Non-biomineralized vertebrates or ‘un-skeletonized jawless vertebrates’ (e.g., Metaspriggina, Conway Morris and Caron, 2014) differ from non-biomineralized chordates (e.g., extant Branchiostoma) by possessing a cranium and developed sensory structures. Early chordates include an assortment of crown taxa.
(Friedman and Sallon, 2012; Janvier, 2015) many of which are biomineralizers and some of which are non-biomineralizers (e.g., lampreys and hagfishes; Friedman and Sallon, 2012).

Early Paleozoic chordates that were capable of biomineralizing have mineral (calcium phosphate) reinforcement of either the dermal or axial skeleton or both (Reif, 1982; Donoghue and Sansom, 2002). Taphonomic filtering has biased the record of early chordates with preservational factors favoring biomineralizers. The known fossil record of non-biomineralizing chordates is meager (Samson et al., 2010, 2011; Janvier, 2015). Fossils of early non-biomineralized chordates are known primarily from Konservat-Lagerstätten (Chen et al., 1995; Shu et al., 1996; Chen and Li, 1999; Shu et al., 1999; Luo et al., 2001; Conway Morris and Caron, 2012, 2014).

Here we report the remains of new non-biomineralizing chordates from the Silurian of Wisconsin. Numerous incomplete specimens are known. None of the examined specimens retains the cranial region, and therefore identification is uncertain. We are also uncertain about how many taxa are represented. Apart from the absence of the cranial region, the examined specimens are well-preserved. Most have a laterally compressed trunk and tail region, well-defined, v-shaped myomeres, and a notochord. One specimen has a differentiated caudal region with a caudal peduncle and symmetrical caudal fin having ray-like elements.
Material and Methods

This study is based on numerous specimens from dolostone of the Brandon Bridge Formation collected in the Franklin Aggregate Quarry in Franklin, Wisconsin (Fig. 7.1). Two specimens are illustrated (Figs 7.2, 7.3). Specimens are deposited in the Field Museum of Natural History in Chicago, Illinois, USA (FMNH).

Specimens were photographed using a Canon EOS Rebel T3i Digital SLR with a Canon MP-E 65 mm macro lens and full spectrum lighting. Images were z-stacked and stitched using Adobe Photoshop CC. Specimens, where noted, were photographed wet to increase contrast. Measurements were obtained using ImageJ (Schneider et al., 2012).

Geological Setting and Fauna

The Brandon Bridge Formation is known for hosting a diverse Silurian biota exposed in the Waukesha Lime and Stone Company quarry (referred to simply as Waukesha quarry herein) in Waukesha, Wisconsin (Mikulic et al., 1985a, b; Chapter 2). The Franklin Aggregate Incorporated quarry (referred to simply as Franklin quarry herein) is located approximately 32 kilometers southeast of the Waukesha Quarry in Franklin, Wisconsin (Fig. 7.1). Based on lithology, preservation and overlapping biota, it appears to expose the same beds as the Waukesha Quarry. Specimens were not collected in situ; collection of material was only briefly available from spoil piles.

The Brandon Bridge Formation in the Franklin quarry comprises finely laminated
dolomitized plattenkalk. Plattenkalk terminology follows Barthel et al. (1990). Specimens are preserved either in thinly laminated (mm scale), non-fissile, silt-sized dolomudstone (flinz) or thinly laminated (< 1 mm thick), fissile, organic-rich, clay-sized argillaceous dolomudstone (fäule). The depositional conditions of the Brandon Bridge Formation in southeastern Wisconsin were interpreted as having microbially influenced sedimentation and preservation (see Chapter 2). Much of the study was based on material from the Waukesha quarry but similar conditions were present in the Franklin quarry area. The Franklin quarry biota is primarily composed of non-biomineralized and lightly skeletonized organisms including synxiphosurines, lobopodians, and ‘worms.’ Differences in the Franklin quarry material includes a much higher concentration of organisms and wavy or hummocky plattenkalk layers (see Chapter 2; Fig 7.3).

Systematic Paleontology

Chordata Haeckel, 1874

Cephalochordata? Haeckel, 1866

Figures 7.2 7.3

Illustrated Material.—Two incomplete specimens without counterparts, collected by D.G. Mikulic and J. Kluessendorf. FMNH #A represents the caudal region and a portion of the trunk. FMNH #B is an isolated mid-section.
**Discussion.**—Numerous fragmentary specimens of chordates, primarily sections of trunk, are present on dolostone slabs from the Franklin quarry, together with fragmentary material of other animals, especially arthropods and ‘worms’ (Figure 7.3). None of the examined chordates preserves the head, and most are missing the tail. It is possible that these remains are preserved in such condition because of the action of predators. Few specimens are sufficiently complete to describe in detail, and the discussion that follows is based primarily on two specimens (Figures 7.2, 7.3).

Specimens are compressed with little relief and are incompletely preserved. FMNH #A is the most complete specimen observed and preserves the trunk and caudal fin. Unless otherwise noted, the description will be based on this specimen. As preserved the body is 29 mm long and 3 mm at maximum width. It is preserved in lateral view suggesting that this animal was, at least in part, laterally compressed in life. V-shaped muscle blocks, or myomeres, are evenly spaced (2-3/mm) throughout the ‘trunk’ becoming less apparent towards the caudal region, though this is likely a preservational artifact rather than their absence. FMNH #B has wavy myomeres, likely the result of decay (compare Briggs and Kear, 1993; Sansom et al., 2010, 2011, 2013; Fig. 7.3). A notochord runs the length of the body into the tail. Anterior of the caudal fin, the trunk narrows. This is inferred to be the start of a caudal peduncle, indicating that propulsion was beginning to be driven by this animal’s tail. The caudal fin is symmetrical with a distinct thickening on the dorsal and ventral margins. Single, segmented structures occur along this thickening and are interpreted to be ray-like elements. The tail terminates in a rounded ‘lobe.’
These specimens are interpreted as chordates. Chordates are defined by the presence of a notochord, pharyngeal gill slits, dorsal nerve cord, postanal tail and myomeres. While not all of these features are present in available material, the illustrated specimens preserve a notochord and myomeres. In general body form, the Franklin quarry chordate bears similarities with the conodont *Clydagnosthus* (Briggs et al., 1993; Aldridge et al., 1996; Sweet and Donoghue, 2001) and the extant cephalochordate *Branchiostoma* (compare Briggs and Kear, 1993).

Similarities between the Franklin quarry chordate and articulated conodonts (*Clydagnosthus* and *Promissum*; see Sweet and Donoghue, 2001) include well developed \(v\)-shaped myomeres, a notochord and a distinct caudal region (compare Donoghue and Keating, 2014, figs. 2l, 2o, 2p). *Clydagnosthus* has a phosphatic postcranium indicating it was at least partially biomineralized. The Franklin quarry chordate lacks any preserved biomineralized elements. Phosphatic preservation is common in the Franklin deposit and arthropods preserved around the chordate are coated in phosphate that overlies organic film (Fig. 7.2). *Clydagnosthus* differs in having an asymmetrical caudal fin with long fin rays (Donoghue and Keating, 2014, fig. 2o), distinct from the symmetrical tail with short rays in FMNH #A. Both *Clydagnosthus* and *Promissum* (Aldridge and Theron, 1993; Sweet and Donoghue, 2001, fig. 3) have thick notochords. The notochord of *Clydagnosthus* takes up to 40% of the trunk width, compared to 12-20% in extant chordates such as *Branchiostoma* (Aldridge et al., 1993). The notochord of FMNH #A ranges from 12-16% of the trunk width.

A conodont with ‘soft tissue’ and elements has been described from the Waukesha
Lagerstätte, but preservation of the postcranial region is too poor for description (Smith et al., 1987). No comparable features exist between the Waukesha conodont and Franklin quarry chordate because conodont elements have not been found near or in direct association with the observed Franklin quarry chordate specimens. Comparisons between these fossils are not possible because they preserve dissimilar anatomy.

Greater similarities exist between the Franklin quarry chordate and cephalochordates (e.g., *Branchiostoma*). Both forms share non-biomineralized tissue, a laterally compressed body, similarly angled v-shaped myomeres, more narrow notochord than conodonts and a distinct caudal region. Additionally, FMNH #B has distorted myomeres having lost their distinct v-shape. This is comparable to decayed myomeres in *Branchiostoma* (compare Samson et al. 2010, 2011, 2013, figs 2e, 3f). Differences between these forms include the development of a caudal peduncle and thickened caudal margin with ray-like elements, which suggests a more active swimming role in the Franklin quarry chordate. *Branchiostoma* larvae are active swimmers, whereas adult forms, though capable of active swimming, are large sedentary organisms (Briggs and Kear, 1993).

This form is placed within Chordata based on the possession of a notochord and myomeres. However, without knowledge of the head, the affinities of this specimen are uncertain. The presence or absence of a cranium would greatly affect the systematic position of this animal. Pending more complete material, this form is left unassigned at the generic and tentatively placed in Cephalochordata based on myomere shape, notochord width and taphonomic comparison with *Branchiostoma*.
References


Figure 7.1. Location of Franklin Aggregate Inc. quarry. (1) map of the United States showing the location of Wisconsin (2). (2) Map of Wisconsin showing the location the Franklin Aggregate Inc. quarry (FQ) in relation to the Waukesha Lime and Stone Co. quarry (WQ). (3) Part of Greendale 7.5’ topographic quadrangle map, Wisconsin (U.S. Geological Survey, 2013, 1:24,000) showing position of Franklin Aggregate Inc. quarry (FQ).
Fig. 7.1
Figure 7.2. Incomplete chordate from the Brandon Bridge Formation (Silurian, Llandovery, Telychian), Franklin Aggregate Inc. quarry, Franklin, Wisconsin, showing trunk and caudal regions, FMNH #A (1) Specimen photographed under high-angle lighting. (2) Specimen photographed under water. cl, caudal lobe; cp, caudal peduncle; frs, fin ray-like structures; my, myomeres; no, notochord; p.arth, phosphatized arthropod; tcm, thickened caudal margin.
Fig. 7.2
Figure 7.3. Slab with incomplete chordate, unidentified arthropods and ‘worms’ from the Brandon Bridge Formation (Silurian, Llandovery, Telychian), Franklin Aggregate Inc. quarry, Franklin, Wisconsin, FMNH #B. (1) Slab photographed under high-angle lighting. (2) Closeup of incomplete chordate photographed under high-angle lighting. my, myomeres; no, notochord.
References


phyllodop bed-like assemblage from the Burgess Shale of the Canadian Rockies.

*Nature Communications*, 5, 3210.


Conway Morris, S., and Caron, J.-B. 2012. *Pikaia gracilens* Walcott, a stem-group
chordate from the Middle Cambrian of British Columbia. Biological Reviews, v. 87, p. 480–512.


Dick, V.B. & Brett, C.E. 1986: Petrology, taphonomy, and sedimentary environments of pyritic fossil beds from the Hamilton Group (Middle Devonian) of western New


Dunlop, J. A. and Selden, P. A. 1998. The early history and phylogeny of the


Farley, R.D. 2001b. Structure, reproduction, and development. 13–78. *In BROWNELL*,...


Hou, X.-G., Ramsköld, L. and Bergström, J. 1991. Composition and preservation of the


Jeram, A.J. Carboniferous Orthosterni and their relationships to living scorpions.


Leinfeldter, R.R., Werner, W., Nose, M., Schmid, D.U., Krautter, M., Laternser, R.,


Liu, J., Steiner, M., Dunlop, J. A., Keupp, H., Shu, D., Ou, Q., Han, J., Zhang, Z. and


McIlroy, D. and Logan, G. A. 1999. The Impact of Bioturbation on Infaunal Ecology and


Ortega-Hernández, J. Braddy, S. J. and Rak, S. 2010a. Trilobite and xiphosuran affinities
for putative arthropods *Caryon* and *Drabovaspis*, Upper Ordovician, Czech Republic. *Lethaia*, 43, 427–431.


Peters, S. E. and Bork, K. B. 1999. Species-Abundance Models: An Ecological Approach to Inferring Paleoenvironment and Resolving Paleoeoecological Change in the


Puckett, M.K., McNeal, K.S., Kirkland, B.L., Corley, M.E. & Ezell, J.E. 2011: Biogeochemical stratification and carbonate dissolution-precipitation in hypersaline microbial mats (Salt Pond, San Salvador, The Bahamas). Aquatic Geochemistry 17,


Schmerge, J. D., riese, D. J. and Hasiotis, S. T. 2013. Vinegaroon (Arachnida:
The text on the page is a list of references, formatted in APA style. Here is the plain text representation:


233


Van Roy, P. 2006. *Non-trilobite arthropods from the Ordovician of Morocco.*


Weller, S. 1900: The paleontology of the Niagaran Limestone in the Chicago area; the Crinoidea. *Chicago Academy of Sciences* 4, 1–152.


