EURYPTERID PALEOECOLOGY: CHARACTERIZATION AND ANALYSIS OF A LATE SILURIAN SHALLOW MARINE FOSSIL ASSEMBLAGE FROM SOUTHERN ONTARIO, CANADA

by

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Eurypterids were giant chelicerate arthropods that have been extinct since the Permian Period. Eurypterids are rare as fossils, and many eurypterid fossils are likely skeletons shed during life (mols), which make it problematic when seeking to determine the types of environments in which they lived. Analysis of functional morphology in conjunction with investigations of their paleobiogeography often are employed to study eurypterid paleoecology and paleoenvironments.

A selection of specimens from the Ciurca Collection in Yale University’s Peabody Museum of Natural History was examined to determine the composition of the fossil assemblage, state of preservation, implications for environmental interpretation and potential community relationships, and the utility of faunal associations for paleoenvironmental interpretation in this case. Specimens are from the Williamsville Formation (Silurian) in Fort Erie, Ontario, Canada. Due to the predominance of microenvironments represented in the Williamsville Formation, a localized environment in a narrow time range was selected to focus the evaluation.

Eurypterids in this important collection include the genera *Eurypterus*, *Pterygotus*, *Dolichopterus*, *Buffalopterus*, and *Paracarcinosoma*. Fossil fragments are most common, but nearly complete specimens also are present. Orthocone nautiloids, brachiopods, hydrozoans, synxiphosurans, phyllocarid crustaceans, unidentified gastropods, and the terrestrial plant *Cooksonia* are also known from this locality, although many of these other organisms are neither abundant nor well preserved.
The presence of orthocone nautiloids, articulate brachiopods and prosobranch gastropods indicates a marine environment, which is inconsistent with the previously published interpretation of the Williamsville Formation as representing shallow, nearshore brackish to hypersaline environments, such as lagoons. This fossil assemblage may indicate less restricted, more open marine salinity, though this remains uncertain based on this analysis, and the lack of trace fossils in these specimens suggests little or no bottom-dwelling life as a result of low oxygen availability as opposed to hypersalinity. This evidence may represent unusual conditions in a localized environment, and it cannot be generalized to describe the entire Williamsville Formation.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>ii</td>
</tr>
<tr>
<td>1. INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>2. BACKGROUND</td>
<td></td>
</tr>
<tr>
<td>2.1 THE EURYPTERIDA</td>
<td>2</td>
</tr>
<tr>
<td>2.2 THE WILLIAMSVILLE FORMATION</td>
<td>8</td>
</tr>
<tr>
<td>2.3 EURYPTERID PALEOECOLOGY, PALEOENVIRONMENTS, AND POSSIBLE ANOXIA</td>
<td>10</td>
</tr>
<tr>
<td>3. MATERIALS AND METHODS</td>
<td></td>
</tr>
<tr>
<td>3.1 LITERATURE REVIEW</td>
<td>12</td>
</tr>
<tr>
<td>3.2 COLLECTION EXAMINATION</td>
<td>12</td>
</tr>
<tr>
<td>4. RESULTS</td>
<td></td>
</tr>
<tr>
<td>4.1 EURYPTERIDS</td>
<td>16</td>
</tr>
<tr>
<td>4.2 NON-EURYPTERIDS</td>
<td>19</td>
</tr>
<tr>
<td>4.3 TRACE FOSSILS AND SEDIMENTARY STRUCTURES</td>
<td>20</td>
</tr>
<tr>
<td>5. DISCUSSION</td>
<td></td>
</tr>
<tr>
<td>5.1 UTILITY OF FAUNAL ASSOCIATIONS FOR PALEOENVIRONMENTAL INTERPRETATION</td>
<td>20</td>
</tr>
<tr>
<td>5.2 TRACE FOSSILS, PALEOENVIRONMENT, AND PRESERVATION</td>
<td>25</td>
</tr>
<tr>
<td>6. CONCLUSIONS</td>
<td>27</td>
</tr>
</tbody>
</table>
7. ACKNOWLEDGEMENTS
8. REFERENCES
9. APPENDIX
1. INTRODUCTION

Eurypterids were marine chelicerate arthropods that first appeared in the Ordovician Period and have been extinct since the Permian Period. Their closest relatives among the arthropods include the xiphosurans (commonly called ‘horseshoe crabs’) and the arachnids (scorpions and spiders). Their fossils have fascinated paleontologists for over a century, and many questions remain relating to their interactions with other organisms and the environments in which they lived. This preliminary study focuses in great part on the question of eurypterid environment and whether or not the environment in which they were fossilized is the same as that in which they lived.

Many eurypterid fossils are likely skeletons shed during life (molts, exuviae), and eurypterid fossils have been found in a variety of environments, and this makes it problematic when seeking to determine the types of environments in which they lived (see Background). The subject of eurypterid paleoenvironments has been a matter of discussion and debate for the better part of the last century, and researchers have suggested a variety of potential paleoenvironments, from fresh water fluvial systems (rivers and streams) to brackish or hypersaline nearshore environments to open marine settings (O’Connell, 1916; Schuchert, 1916; Kjellesvig-Waering, 1979; Plotnick, 1999; Braddy, 2001; Tetlie, 2008; Vrazo and Braddy, 2011).

Eurypterid fossils are uncommon, and while they are known from a variety of environments, they are often found in rocks interpreted to represent hypersaline environments, or environments of variable salinity, such as lagoons, and various mechanisms have been hypothesized to explain the presence of eurypterid remains in such unfavorable environments (Braddy, 2001; see Background 2.3). These environments
may also have played a role in preserving the exoskeleton that otherwise might not have been preserved (Braddy, 2001; Vrazo and Braddy, 2011).

A selection of specimens from the Ciurca Collection in Yale University’s Peabody Museum of Natural History (YPM) was examined to determine the general composition of the fossil assemblage and preservational state of the fossil material, in order to begin to assess implications for environmental interpretation, potential community relationships, and eurypterid preservation. All specimens were collected from the Williamsville Formation (Late Silurian) in at Ridgemount Quarry (South), Fort Erie, Ontario, Canada. A localized environment in a narrow time range was selected in order to focus the evaluation, as this investigation serves as the groundwork for a more extensive investigation of the character of environments represented in the Williamsville Formation. The possibilities for expansion of this inquiry are numerous, and they are addressed briefly, but the focus of this work remains narrow and should be considered as preliminary work in anticipation of a more exhaustive investigation of eurypterids and the paleoenvironment of the Williamsville Formation. This investigation is primarily concerned with faunal associations and assessing their utility for determining paleoenvironment using the material from Ridgemount Quarry as a small-scale case study.

2. BACKGROUND

2.1 THE EURYPTERIDA

A full discussion of the Order Eurypterida could fill a book. This section introduces these unusual organisms with a brief explanation of what they are, how they are related to certain other organisms, and other material relevant to this investigation.
Eurypterids are extinct chelicerate arthropods, part of the Phylum Arthropoda, which also includes relatives such as the arachnids (e.g., spiders and scorpions) and the xiphosurans (despite their common name, ‘horseshoe crabs’, these organisms are not crustaceans). Chelicerata is a subphylum of Arthropoda, and like other chelicerates, eurypterids possess chelicerae, pincer-like appendages located on the ventral side of the prosoma (fig. 1).

Both eurypterids and the extant horseshoe crab belong to Class Merostomata. Historically eurypterids and xiphosurans were thought to be more closely related than eurypterids were to members of the Class Arachnida, however that has been contested, and the relationships of eurypterids to these organisms as well as to other eurypterids remains under discussion (Dunlop and Selden, 1998; Tetlie, 2007). Approximately sixty genera of eurypterids make up the class Eurypterida, of which only 5 are discussed in this work, restricted to those present in the Ciurca Collection (Sepkoski, 2002).

In order to properly discuss eurypterids, it is necessary to be familiar with several key anatomical terms and their position on the eurypterid body. For clarity, ventral refers to the underside of the organism and dorsal to the back or topside. Figure 1 illustrates basic eurypterid external anatomy. Beginning at the anterior end of the body is the prosoma (head) including kidney bean-shaped eyes on the dorsal side and chelicerae and walking legs. The two paddle-shaped appendages on either side of the body are the swimming appendages or paddles. The main portion of the body is the opisthosoma, made up of nearly rectangular segments, tergites (dorsal), and sternites (ventral). The last segment is the telson (fig. 3); the shape of the telson varies and depending on the type of eurypterid can be a long straight spike, a curved spike, or flattened dorsoventrally to form...
a paddle (fig. 3 and Appendix). Tollerton (1989) provides a thorough overview of eurypterid anatomy and morphology. Superficial similarities in overall appearance to true scorpions earned eurypterids the moniker “sea scorpions”, and the curved telsons of the Family Carcinosomatidae emphasize that similarity. They were predators, particularly the large nektonic (free-swimming) types such as members of genus *Pterygotus* that had a large, flattened, paddle-like telson for swimming and exceptionally large chelicerae (Klussendorf, 1994; Ciurca and Tetlie, 2007) (Appendix).

The carapace of eurypterids, though hard, was originally made up of the organic material chitin, but chitin does not fossilize as readily as mineralized hard parts, except in cases of exceptional preservation, as in the Williamsville Formation. A study of the composition of preserved eurypterid carapace material by Gupta et al. (2007) suggests that *in situ* polymerization of the cuticle, as a diagenetic process, is an important factor for fossilization of eurypterid remains. Similarly, Cody et al. (2011) cites the presence of a preserved chitin protein complex in a Silurian eurypterid fossil collected from Ridgemount Quarry and housed in the collection at Yale. These studies indicate a “recalcitrant” nature of the chitinous carapace that worked to protect the organic material from attack by microorganisms that would degrade the chitin, thereby providing a sort of chemical reinforcement or protection during diagenesis (Gupta et al., 2007; Cody et al., 2011).
Figure 1 Eurypterid anatomical features: (A) prosoma, (B) swimming appendages, (C) tergites, (D) telson, (E) sternites, (F) prosomal appendages (chelicerae, walking legs).

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Figure 2 Prosomas of *Eurypterus* sp. (top, YPM 207369; bottom, YPM 207378)
(Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.)
Figure 3 (top left) Fragments and telson of *E. sp.* (YPM 207356); (top right) Telson of *E. sp.* (YPM 207376); (bottom) Body segment of *E. sp.* (YPM 207362). (Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.)

Eurypterid fossils are most often considered to be molted remains, rather than the full body of a dead animal, but this sometimes is difficult to determine (Clarke and Ruedemann, 1912; Tollerton, 1997). Unlike trilobites, where the presence or absence of free cheeks can aid in distinguishing a carcass from a molt, that advantage is not present in the case of eurypterids, and few fossil specimens have been considered as dead carcasses instead of molts (Heubusch, 1962; Braddy, 2001 and references therein; Vrazo
and Braddy, 2011). It is also possible to distinguish gender in eurypterids based on the preserved external genitalia; however, which is male and which is female remains unknown (Batt, 1999; Tetlie et al., 2008). It has been suggested that the calm, hypersaline environments eurypterids are often associated with may have aided and facilitated the excellent preservation observed in eurypterid horizons of the Bertie Group rocks (Vrazo and Braddy, 2011).

2.2 THE WILLIAMSVILLE FORMATION

The Williamsville Formation is a rock unit located near the uppermost extent of the Bertie Group, a suite of Late Silurian units that contain multiple horizons that produce abundant eurypterid remains and extends from west-central New York State (USA) through southwestern Ontario (Canada). The Williamsville Formation is a dolomite unit of variable composition depending on location, particularly with regard to mud and silt content (Hamell, 1982; Plotnick, 1999). The specimens in the Ciurca Collection were collected from the lower portion designated Williamsville Bed A. The Williamsville Formation overlies the Scajaquada Formation and underlies the Akron/Cobleskill Formation. The Akron Formation is included in the Bertie Group by some authors (Tetlie et al., 2008) and in the younger Rondout Group by others (Ciurca and Hammell, 1994).

The Williamsville Formation was deposited in Late Silurian time near the edge of an inland sea (fig. 4) (Hamell, 1982). It is often interpreted as representing hypersaline or lagoon environments with variable salinity, but some workers have suggested that the Williamsville Formation represents a range of near-shore marine environments, and that hypersalinity was not its usual condition, unlike other units in the Bertie Group (Hamell, 1982; Braddy, 2001; Vrazo and Braddy, 2011). For example, Ciurca and Gartland (1975)
observed salt hopper crystals in the Williamsville Formation at Decewsville (Ontario, Canada), and they attributed this to a hypersaline environment. Hamell (1982) advocated a less hypersaline interpretation of the Williamsville Formation based on a general absence of features such as salt hopper crystals.

Figure 4 Paleogeographic map of North America during the Late Silurian (~420 Ma). Inset is a cropped view of what will be Ontario and New York; the red dot in the inset image indicates the approximate location of the collection site. (Map by Ron Blakey, NAU Geology, used with permission)
2.3 EURYPTERID PALEOECOLOGY, PALEOENVIRONMENTS, AND POSSIBLE ANOXIA

Numerous possibilities for environments inhabited by eurypterids have been postulated during the last century. In the early 20th Century, some workers made the case for a fluvial environment within which the remains were transported from the site of death to the locations where they fossilized (O’Connell, 1916; Schuchert, 1916; Romer, 1933). This view has been largely discredited, and there is no known evidence directly linking eurypterids to a freshwater lifestyle (Plotnick, 1999). Eurypterids have a nearly global distribution, including such locations as England, Pennsylvania, Wyoming (only very few specimens), Oklahoma, and perhaps most famously from the Bertie Waterlime Group in New York and Ontario (Decker, 1938; Kjellesvig-Waering, 1979; Plotnick, 1999, and references therein; Braddy, 2001 and references therein).

Kjellesvig-Waering (1979) suggested that different types of eurypterids dominate certain environments (see review in Plotnick, 1999; Braddy, 2001, and references therein). According to Plotnick (1999), Kjellesvig-Waering’s model may be valid on a general sense, as Plotnick and others noted that mixing of the proposed eurypterid biofacies has been observed (Braddy, 2001, and references therein). In reference to the Syracuse Formation, another known eurypterid occurrence, Leutze (1961) described a shallow-water environment with “highly variable salinity”.

A recently proposed hypothesis to explain the problem of eurypterid environment is the mass-molt-mate hypothesis, which presents a mating and molting behavior similar to that observed in modern horseshoe crabs, particularly the extant genus *Limulus* (Braddy, 2001; Vrazo and Braddy, 2011). Eurypterids are often compared to horseshoe
crabs, particularly in investigations of functional morphology and biology, such as respiratory function (Selden, 1985). Although they are related, some have warned against overuse of this comparison (Plotnick, 1999). The mass-molt-mate hypothesis suggests that eurypterids were not permanent occupants of the somewhat harsh environments they are often found in, and instead were temporary visitors to these environments in order to molt and mate (Braddy, 2001; Vrazo and Braddy, 2011). This hypothesis also makes use of the horseshoe crab comparison to address the issue of eurypterids being able to tolerate significant changes in salinity, as horseshoe crabs are known to be tolerant of a wide range of salinities (Reynolds and Casterlin, 1979; Vrazo and Braddy, 2011). This hypothesis treats the fossil eurypterid assemblages as the result of mass molting behavior rather than a mass mortality, particularly considering that evidence of preserved internal structures is required to distinguish a body from a molt (Braddy, 2001). Tetlie et al. (2008) also favors mass molting as opposed to mass mortality, but describes the possibility of mating also occurring as “equivocal” but still a “plausible explanation”.

Several studies note a lack of eurypterid remains in bioturbated units (Vrazo and Braddy, 2011 and references therein) and attribute the preservation to hypersalinity, which would create an inhospitable environment for bacteria that would otherwise break down the chitin carapace and also result in the lack of trace fossils. An absence of trace fossils is also potentially caused by low oxygen or anoxic bottom waters, and conditions of anoxic bottom water and oxic waters higher in the water column have been suggested for the shallow shelf seas during much of the Silurian (Wilde et al., 1991). The Silurian was known to have extensive changes in both atmospheric and oceanic oxygen content, with potential climate excursions throughout (Wilde et al., 1991).
3. MATERIALS AND METHODS

3.1 LITERATURE REVIEW

The literature review covered basic background information on eurypterids, specific information regarding the collection locality, the types of eurypterids and other organisms collected there, the Williamsville Formation, as well as that unit’s position within the Bertie Group. Historical and current views on eurypterid paleoecology and environment were included to develop a sense for how thought on these topics has changed within the last century. Journal articles were compiled through database searches, such as GeoRef, facilitated by the Marriott Library at the University of Utah, and information was also gathered through inspection of the library’s collection of books that included discussion on the Silurian, eurypterids, and other relevant information. Books included general references as well as collections of peer-reviewed papers and conference abstracts.

3.2 COLLECTION EXAMINATION

The Ciurca Collection at Yale University’s Peabody Museum of Natural History (YPM) in New Haven, Connecticut was chosen, because it is an extensive collection with known collecting localities. It contains hundreds of fossils from the Williamsville Formation alone; the nature of the collection afforded the opportunity to work with a larger sample that included both eurypterids as well as many of the other organisms reported in the literature as occurring in the Williamsville Formation. The fossil material was collected in the Ridgemount Quarry (South) (RQS) in Fort Erie Township, Ontario, Canada by Samuel J. Ciurca Jr. Mr. Ciurca is an experienced amateur collector who has collaborated on numerous scientific studies of eurypterids (e.g. Ciurca and Gartland,
1975; Ciurca and Hammell, 1994; Ciurca and Tetlie, 2007). The collection includes over 10,000 specimens, and is one of the largest in the world.

My work was a non-quantitative, collection-based inquiry into the environment in which the organisms at Ridgemount Quarry were fossilized. The key features of the examined specimens such as size can be checked against more extensive statistical studies (Tetlie, 2008; Vrazo and Braddy, 2011) done for other purposes. The objective of the study was to establish the likely environment of this location. As a preliminary step, this is addressed primarily by documenting any flora and fauna associated with the eurypterid fossils. To do this the sample of fossils was chosen to capture the widest number of species in a reasonable number rather than as a statistical sample (stratified or random). For the eurypterids, the sample was further refined by examining both complete animals (molts) and also fragments for the predominant species. This is important, as other researchers (Vrazo and Braddy, 2011) have noted that there is uncertainty related to where the molting occurs compared to where the exuviae (molts) are buried.

All these factors were kept in mind during the sample selection and examination. By restricting the location and formation in this study to look at the environment, the effects of the “Bertie Bias” (Plotnick, 1999) are not important. The “Bertie bias” refers to the excess of collected specimens that were collected in the Bertie Group, as compared to specimens originating from other locations. The overall geologic range of eurypterids extends from Ordovician to Permian, but the Bertie Group represents only the Late Silurian, as recorded by deposition in New York and Ontario. Therefore, the Bertie
Group provides only a narrow perception of potential eurypterid environments and associations.

Permission to visit and work with the collection at Yale University’s West Campus facility was granted by the Dr. Susan Butts, Curator of the Invertebrate Paleontology Collections at the Peabody Museum of Natural History. The initial visit took place in January 2013. This visit served to familiarize the author with the size and content of the collection, and identify potential specimens. The next visit was in March 2013, and a limited selection of 53 individual specimens was chosen, the information on the specimen cards recorded for reference and organization, and the specimens were photographed (see Appendix and figures for photographs). An Olympus E-410 digital camera with a macro lens attached to a copy stand for stability was used for photography of the specimens. The author took all of the 78 photographs. There are more photographs than specimens, because some consisted of multiple pieces and close up photographs were taken in certain cases. Including specimens with multiple parts, a total of 73 individual fossil samples were viewed and photographed. These photographs are the first reference images for some these specimens and are now in the archive at Yale (specimen images used in this piece have been reproduced with permission from the Peabody Museum). Photographs were edited in Adobe Photoshop Creative Suite 5.5 to crop the image frame, to boost the brightness and contrast of the original image, and to better define the fossil material from the rock matrix for clearer viewing of the details in these fossils when viewed on a printed page; original images are provided for comparison at the end of Appendix.
The sample of specimens was selected to include all available eurypterid genera and other organisms present in the Williamsville Formation (Bed A) material from Ridgemount Quarry (South), and while care was taken to include all genera, by default specimens missing identification cards were not used. Any specimens with missing cards were subsequently noted and reported. A small part of the overall collection, not only Williamsville material, is housed at Yale’s main campus. For this inquiry, and due to the large amount of material housed at the West Campus site, that material was chosen to be the focus. The expanded project described in the introduction would necessarily include a larger sample set including any Williamsville material housed at the main campus.

The eurypterid specimens were selected to include fragmentary samples and nearly complete specimens as well as examples where these occur together. Fossils of other organisms were chosen to illustrate the state of preservation and their presence at the site, in order to later assess the utility of using these organisms to inform an interpretation of the environment at this site, particularly with respect to any benefits or drawbacks to this method. Addressing the faunal association of eurypterids is not a new approach to aid in determining the environment, but it is one that requires careful consideration in order to avoid jumping to convenient conclusions. These specimens were also chosen as they represent a specific location and geologic time (Late Silurian).

For each sample, information from the specimen card was recorded, including the reported identification of the specimen, the collection location, and the collector’s name (in all cases for these samples, the collector was Samuel J. Ciurca Jr.). The specimen number was also recorded for completeness and recordkeeping purposes, particularly for revisiting and utilizing the photographs in order to avoid losing track of which photo
contained which fossil. The specimens were examined visually to describe the condition of the fossil, i.e., if it were complete, nearly complete, or fragmentary. The matrix was also examined visually for the presence of any sedimentary structures or trace fossils present in these specimens. The data was then tabulated and reviewed to assess potential environmental significance.

The sample obtained was not perfectly random, so meaningful statistical analysis is not an option until a larger, random or stratified sample can be obtained, and in this case is not a major detriment as the purpose of this inquiry is to address what these organisms indicate about the environment rather than aspects such as morphological traits of eurypterids, or abundance of these genera or species. As noted previously, while eurypterid gender can sometimes be determined with the proper skills and could be relevant to the paleoecology of eurypterids, this issue was not addressed for the purpose of this study due to the nature of the sample and the specialized knowledge required to differentiate between male and female eurypterids.

4. RESULTS

4.1 EURYPTERIDS

Williamsville fossils from Ridgmount Quarry (South) include 5 eurypterid genera and 6 species. The genera are *Eurypterus, Pterygotus (= Acutiramus), Paracarcinosoma, Dolichopterus, Buffalopterus*.

The most common eurypterids in the collection are *Eurypterus lacustris* and *E. sp.* (species undetermined). Nearly complete specimens are approximately same size (~10-15 cm) with the exception of one (juvenile?) specimen ~1.5 cm in length (fig. 6). Fossils in genus *Eurypterus* consist of fragments as well as nearly complete specimens (both dorsal
and ventral sides are represented). All fossils of eurypterids are treated here as molts rather than the whole dead animal, as it is difficult to tell them apart, and that is not the focus of this inquiry. Other less common eurypterids include *Pterygotus* (*Acutiramus*) *macrophthalmus*, *Acutiramus cummingsi*, *Buffalopterus pustulosus*, *Dolichopterus macrocheirus*, and *Paracarcinosoma scorpionis*. Remains of the other eurypterid genera are mostly fragmentary; single walking legs, chelicerae (claw-like appendage), and the telson (tail) are common. Only the specimen of *Dolichopterus* was mostly complete (fig. 5). Some data from the examined eurypterid specimens is collected in Table 1.

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<th># specimens</th>
<th>Observations</th>
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<td>species undetermined</td>
<td>27</td>
<td>Fragments and nearly complete specimens; cuticle preserved in many specimens</td>
</tr>
<tr>
<td><em>Eurypterus</em></td>
<td><em>lacustris</em></td>
<td>5</td>
<td>Fragments and nearly complete specimens; cuticle preserved in many specimens</td>
</tr>
<tr>
<td><em>Acutiramus</em></td>
<td><em>cummingsi</em></td>
<td>1</td>
<td>Fragment</td>
</tr>
<tr>
<td><em>Pterygotus</em></td>
<td><em>macrophthalmus</em></td>
<td>2</td>
<td>Fragments of prosomal appendages and telson</td>
</tr>
<tr>
<td><em>Dolichopterus</em></td>
<td><em>macrocheirus</em></td>
<td>1</td>
<td>Single nearly complete specimen, cuticle not well preserved</td>
</tr>
<tr>
<td><em>Buffalopterus</em></td>
<td><em>pustulosus</em></td>
<td>1</td>
<td>Fragment</td>
</tr>
<tr>
<td><em>Paracarcinosoma</em></td>
<td><em>scorpionis</em></td>
<td>1</td>
<td>Fragment</td>
</tr>
</tbody>
</table>

**Table 1** Eurypterid specimens from RQS, Fort Erie Township, Ontario, Canada.
Figure 5 *Dolichopterus macrocheirus* (YPM 210085). (Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.)
4.2 NON-EURYPTERID FOSSILS

Strictly marine organisms, such as orthocone nautiloids, brachiopods and prosobranch gastropods (fig. 3), are also present along with molluscs, synxiphosurans (close relatives of horseshoe crabs, fig. 3), phyllocarid crustaceans, and a hydrozoan formerly thought to be a graptolite (*Inocaulis sp.*). The terrestrial plant *Cooksonia* is also known from this site, preserved as a carbon residue (Edwards et al., 2004).
Non-eurypterid specimens examined included 3 samples of ‘Bertieca’ a problematic fossil known from and named for the Bertie Group rocks, 1 sample of the hydrozoan *Inocaulis* sp., 2 samples of the brachiopod *Stegerhynchus* sp., 1 sample of a prosobranch gastropod of undetermined genus and species, 1 sample of an orthocone (straight-shelled) nautiloid of undetermined genus and species, 1 sample of the nautiloid *Hexameroceras* sp., 1 sample of a mollusk of undetermined genus and species, 2 samples of the phyllocarid crustacean *CeratioCARIS* sp., and 2 samples of the synxiphosuran *Pseudoniscus* sp. (see Appendix for more images of the specimens).

4.3 TRACE FOSSILS AND SEDIMENTARY STRUCTURES

No primary sedimentary structures or trace fossils were observed in the rock containing the examined specimens, and the lack of observed trace fossils from the lower Williamsville Formation (Bed A) is also reflected in the literature (see Discussion for more). Specimens of physical sedimentary structures are not part of this collection and were not observed on their own or within examined specimens.

5. DISCUSSION

5.1 UTILITY OF FAUNAL ASSOCIATIONS FOR PALEOENVIRONMENTAL INTERPRETATION

In any scientific endeavor, there are often benefits and drawbacks to using a particular method or tool or assumption. In this case, the utility of using faunal associations to infer paleoenvironment from collection material must be addressed in order to illuminate any potential problems. The small and non-random or stratified nature of the selected specimen set is of no use for quantitative statistical assessment, as noted previously, so it will be considered only in a qualitative sense at this time. It is important
when working with collected material to be aware of any collection bias, and in this case the ‘Bertie bias’ has been acknowledged. However, it is not a drawback in this case, as only a single location in the Bertie Group itself is being considered; in the case of future work outside of the Bertie, this bias would be a more important consideration (Plotnick, 1999). It is important to be aware not only of what organisms are present in a collection or observed at a specific locality, but also what is absent and how the absence affects the overall interpretation. In this case, trace fossils are the absent factor, and the implications of this are addressed in section 5.2.

The Williamsville Formation has been interpreted to represent a number of different environments, as discussed in section 2.2, some of which are contradictory, such as Ciurca and Gartland’s (1975) assertion that the Williamsville is hypersaline based on observations of salt hoppers, while Hamell (1982) cites an absence of salt hoppers and determines that the Williamsville is potentially less saline than other units in the Bertie that contain structures indicative of hypersaline conditions. As eurypterids are not generally considered useful as environmental indicators (Selden, 1984), other organisms in the collection material are good indicators of various environmental conditions.

The presence of nautiloids and the prosobranch gastropod suggest marine conditions, while other organisms are not so clearly associated with a particular environment or salinity range. The unidentified mollusk is not a useful indicator of environmental conditions, because it is only generally identified as a mollusk; mollusks such as pelecypods (bivalves) can occupy a wide range of salinity conditions (euryhaline), and without a more specific identification it is difficult to say more about the conditions tolerated by that organism. Phyllocarid crustaceans such as Ceratiocaris
are associated with shallow-water marine environments during the Silurian (Collette et al., 2010; Collette and Hagadorn, 2010). Synxiphosurans have also been found associated in rocks deposited in marine environments and with marine faunal associations (Eldredge, 1974). The nature and potential implications of the ‘Bertieca’ also remain enigmatic until such a time as these unusual fossils are formally identified.

The associated fauna clearly favors a marine interpretation, as opposed to a hypersaline environment. However, this assumes that these organisms lived in the environment in which their remains are preserved. Based on the current selection of specimens, whether these organisms were endemic to this environment, were transported in post-mortem, or were a visitor of sorts is not clear, and a more definite conclusion requires further investigation of any potential transport of the collection materials using a larger sample set. Numerous studies, including those by Vrazo and Braddy (2011), have raised the possibilities listed above to explain the presence of marine organisms in environments thought to be hypersaline, and the question remains open. These possibilities are discussed in order to highlight any potential problems as well as supporting evidence.

The organisms in the collection material, in conjunction with previous work, support the assertion that the Williamsville Formation is not a hypersaline environment as previously thought, and this assertion has interesting implications for interpretations of eurypterid paleoecology and fossilization. However, this interpretation is subject to the assumption that these organisms lived at the location where they were preserved. There is some dispute as to the origin of some fossils in the Bertie, with some contending that cephalopods may have been introduced by storms as drifting carcasses or shells (Tetlie,
2008 and references therein). Tetlie (2008) noted that Braddy’s (2001) interpretation of the Bertie fossils as largely composed of exuviae was based on lack of damage due to scavenging and the pattern of dislocation. This interpretation is not contested, and unless noted otherwise all eurypterid specimens will be considered molts. Vrazo and Braddy (2011) note that Hamell (1982) suggests that eurypterids in the Williamsville Formation lived in the intertidal zone “some distance south of their final resting place”, suggesting transport of the molts and the location where they were preserved does not represent where the eurypterids actually lived or where molting occurred. Batt (1999) also cites the Williamsville Formation as being intertidal. This interpretation could be supported by the presence of fragmentary remains. However, Tetlie (2008) concluded that the occurrence of undisturbed eurypterid molt ensembles in the Williamsville Bed A Member indicated that molting location and preservation location were one and the same, and that the molted remains are consistent with a mass-molt scenario. Lack of disturbance of the delicate eurypterid material is consistent with the calm environment proposed for the mass-molt-mate hypothesis and does not lend support the proposition that the more robust aragonitic nautiloid and gastropod shells were swept in from elsewhere. However, neither does it negate the possibility of transport. An intertidal zone provides numerous microenvironments that could be represented in the Williamsville Formation. If this is the case, then salinity could have fluctuated, and the location within the intertidal zone changes with the associated fauna and presence or absence of structures such as salt hoppers.

It seems highly unlikely that a marine organism such as a nautiloid, with low tolerance for changes in salinity would venture into a hypersaline or even brackish
environment. Eurypterids may have been capable of tolerating such a change (Selden, 1985), but not the nautiloid. With that in mind, let us consider the case of a non-hypersaline environment, or at least less saline, as suggested by Hamell (1982). If the nautiloids and gastropods were not carried into the environment, and instead lived there, interactions between living biota might be inferred, such as the potential interaction between eurypterids and cephalopods, both predators. Did they compete? Or perhaps did one prey on the other? These are tempting questions to pursue, but Selden (1984) cautions that if eurypterid assemblages are considered to be molted material, then those fossils do not accurately represent the living community, and thereby any inferred community interactions would be tenuous, requiring assumptions that not only were the location of molting and preservation the same, the eurypterids would need to reside there as well. When working with specimens in collections, it is difficult to determine how the specimens were related while still in situ in the quarry. Braddy (2001) suggests that the incredible abundance of eurypterid fossil material known from the Bertie Group could be due to “taphonomic windows” and instead of being attributed to a time-averaged assemblage, and suggests that ideal conditions to produce exceptional preservation occurred over short periods, rather than a lengthy stretch of time as in a time-averaged assemblage. This suggestion was made with respect to a hypersaline environment, but the concept is sound and could potentially be applied in other environments capable of producing exceptionally preserved fossils.

This observation highlights the importance of fieldwork to accompany inspection of collection material if at all possible. Although some specimens of associated non-eurypterid fauna do occur with eurypterid molts, such as one example of *Pseudoniscus*
*sp.* (Appendix), this is not common, even in such a small sample set, and most specimens occur as multiple examples of one organism type or as a solitary fossil.

It is clear that using faunal associations to interpret paleoenvironments is mired with potential pitfalls and certain assumptions may be required in order for all of the pieces of evidence to fit, some of which are not well grounded in the available evidence.

5.2 TRACE FOSSILS, PALEOENVIRONMENT, AND PRESERVATION

The types of organisms present and described previously indicate a marine environment, in the case that the marine fauna was not transported. If this is the case it is consistent with recent suggestions in the literature for the Williamsville Formation (Hamell, 1982; Vrazo and Braddy, 2011). This point raises the question regarding why eurypterid molts would be preserved if the environment were not hypersaline.

Preservation facilitated in part by hypersaline conditions is not an unreasonable conclusion. In the mass-molt-mate hypothesis, the environment would have been calm, and the number of organisms that are capable of tolerating such high salinity would have been low, because the environment would have been a sort of safe haven (Braddy, 2001; Vrazo and Braddy, 2011). This hypothesis, in concert with the diagenetic *in situ* polymerization described by Gupta et al. (2007) as an important factor associated with preservation of the chitin cuticle, could have facilitated fossil preservation. Hypersaline conditions might deter bacteria that would otherwise break down the molted remains, but in a normal marine environment, as suggested by Gupta et al (2007), would chemical conditions be favorable for preserving a eurypterid molt? A full inquiry into that question is beyond the scope of this study, but the proposal of a marine environment appears to have an unusual characteristic that could prove beneficial for molt preservation.
Many discussions of eurypterids from the Williamsville Formation note how there are few if any trace fossils associated with the eurypterids, but this observation has not been explored further (Braddy, 2001; Tetlie, 2008; Vrazo and Braddy, 2011). The lack of trace fossils is also noted in this preliminary study, and the implications must be addressed. A lack of trace fossils indicates that the conditions in the substrate did not provide suitable living conditions for any burrowing organisms responsible for producing potential trace fossils. One possible reason that conditions might have been unfavorable is hypersalinity, which would restrict the types of organisms capable of living in that environment, and the literature often briefly makes this connection. It has been established that the associated organisms indicate dominantly marine conditions, providing that one accepts the conclusion of Tetlie et al. (2008), and the associated assumption that the marine organisms were residents, not visitors or the result of post-mortem transport. Wilde et al. (1991) notes that shallow shelf seas during the Silurian experienced low oxygen or anoxia in the bottom waters, with oxic conditions in the overlying water column. Anoxia or low-oxygen in the bottom waters and substrate may have created inhospitable conditions for burrowing organisms, and much like a hypersaline environment, may have restricted the organisms that were capable of living under such conditions. This may include chitin-eating bacteria that, according to study of modern marine varieties, function more effectively in aerobic environments than in anaerobic ones. However, anaerobic environments may not completely eliminate the possibility of such bacteria affecting the eurypterid molts (Campbell and Williams, 1951). Braddy (2001) notes that the “rate of aerobic decomposition of chitin is generally rapid”, and the hostile conditions of a low-oxygen or anoxic bottom layer coupled with
the recalcitrant nature of the eurypterid cuticle during diagensis could have functioned in tandem to promote preservation. This scenario addresses many of the same issues covered in the case of a hypersaline environment, which is part of what makes that interpretation so attractive, and it illustrates that there may be other possibilities regarding the environment in which the eurypterids were fossilized that have yet to be fully explored.

6. CONCLUSIONS

Although the data at this time and present scope of this study are insufficient to determine the specific paleoenvironment of the Ridgemount Quarry material, a number of potentially useful conclusions can be drawn. The presence of orthocone nautiloids and prosobranch gastropods implies a marine environment, which is inconsistent with the previously published interpretation of the Williamsville Formation as representing shallow, nearshore brackish to hypersaline environments, such as lagoons. Marine organisms like nautiloids and gastropods would not be living in a hypersaline environment. The interpretation of this environment representing a location with more normal marine salinity is suggested by the results, and this conclusion is consistent with recent suggestions by other workers that parts of the Williamsville Formation may not be not as saline as previously thought (Hamell, 1982; Braddy, 2001; Vrazo and Braddy, 2011). Both interpretations require several assumptions, and more work is necessary to determine the degree of transport at this site in order to assess whether the associated fauna are truly viable indicators of the environment at the site. Preservation is also a problem for an interpretation of normal marine salinity unless the bottom waters had low oxygen content or were anoxic, as suggested by the absence of trace fossils. This idea is
also invoked in the literature in support of hypersaline conditions, but their absence is not diagnostic of one interpretation over the other. A low-oxygen scenario is supported by Silurian paleooceanographic research in general (Wilde et al., 1991), but fieldwork conducted at the quarry locality is necessary to confirm low oxygen for this collection site.

Whether the environment at this location in the Williamsville Formation is hypersaline or oxygen poor, the evidence given here does support the idea of unusual conditions in a localized environment. The presence of mostly adult-sized eurypterids (genus *Eurypterus*) is generally consistent with Vrazo and Braddy’s (2011) hypothesis that the Williamsville material is located near a breeding ground, but that the locality itself may not represent one. This does not preclude the hypothesis of eurypterids molting locally, and the unusual environment may play a role in preserving the molts long enough to avoid physical or microbial destruction and fossilize.

Based on the limited collection data used in this investigation, the collection locality for the Williamsville material in the Ciurca Collection appears to indicate an unusual shallow marine environment in which are preserved numerous and well preserved fossil remains, dominated by eurypterids of the genus *Eurypterus* – represented mostly by adult organisms and some smaller specimens (potentially juvenile, though this is unconfirmed). This fossil occurrence indicates the presence of a variety of eurypterid genera as well as other marine organisms, and it also may have been a low oxygen environment as suggested by the lack of trace fossils.

This investigation aids in laying the groundwork for a more extensive study of eurypterids and the environments they are found in both at the Ridgemount Quarry site
and elsewhere in the Williamsville Formation in southern Ontario and New York State. Further study should aim to clarify the depositional environment of the Williamsville rocks, particularly related to lateral variation in environment and how these environments may aid in the preservation of chitinous eurypterids. One possible way to address the specific nature of the environment at this site is to utilize chemical fossils, i.e., organic chemical signatures of microbial life that have the potential to determine more clearly if the collection site was truly hypersaline, rather than relying on features such as salt hoppers (per. comm. Dr. Alison Olcott). The other benefit to this approach is that it works directly with the rock and poses no threat of damage to the fossils.

Future work should also focus on how environments other than hypersaline lagoons could influence eurypterid preservation, regardless of whether the collection location in this study is hypersaline. This may prove useful when addressing eurypterid horizons in other units within the Bertie Group that are more clearly defined as hypersaline as well as other eurypterid localities throughout the world.

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8. REFERENCES


9. APPENDIX

The following are photographs of all types of specimens examined. Some of these images were previously used in figures. Images may not be reproduced without permission from Yale University’s Peabody Museum of Natural History.

A1. Specimen of ‘Bertieca’; YPM 208779. Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A2. (top) Telson and other fragments of *E. sp.* (?) (YPM 207353); (bottom) Telson and connected segments of *E. sp.* (YPM 207357). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A3. Prosobranch gastropod, genus and species undetermined (YPM 212380). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.

A4. Inocaulis sp. (YPM 209601). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A5. Undetermined mollusk (YPM 209656). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A6. (top left) *Hexameroceras* sp. (YPM 212382); (bottom left) *Hexameroceras* sp. (YPM 209487); (right) Orthocone nautiloid, genus and species undetermined (YPM 186705). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A7. (top) *Acutiramus cummingsi* telson (YPM 210099); (bottom) *Pterygotus (Acutiramus) macrophthalmus* (YPM 212388). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A8. (top) *Buffalopterus pustulosus* (YPM 210111); (bottom) fragment, *Pterygotus (Acutiramus) macrophthalmus* (YPM 214083). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A9. *Paracarcinosoma scorpionis* (YPM 210109). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A10. Phyllocarid crustaceans. *Ceratiocaris* sp. (YPM 212404). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A11. Brachiopod molds. (top) *Stegerhynchus* sp. (YPM 213207); (bottom) *Stegerhynchus* sp. (YPM 213208). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A12. Synxiphosurans. (top left) *Pseudoniscus* sp. (close up) (YPM 212397); (top right) *Pseudoniscus* sp. (YPM 212397); (bottom) *Pseudoniscus* sp. (YPM 209648). Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
A13. *Dolichopterus macrocheirus* (YPM 210085), comparison of original photo to modified version. Photos taken by author and reproduced with permission from: Division of Invertebrate Paleontology, YPM, © 2013 Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA. All rights reserved.
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