

Paleoecology and Paleobiogeography of the New York Appalachian Basin Eurypterids

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Abstract

Eurypterids are a diverse group of arthropods with a wide range of body morphologies and lifestyles. They are poorly understood because their fossils are rare. However, they are quite prevalent in the Appalachian Basin, typically interpreted to be a hypersaline environment. This paper documents the temporal and geographic distribution of eurypterids in the Appalachian Basin in order to address questions of taphonomy and ecology. It aims to reveal how eurypterid communities evolved through time, as well as how their geographic distribution may have changed. By understanding these patterns, as well as ecological values such as diversity and abundance, we can better understand the role the eurypterids played in the New York and Ontario region of the Appalachian Basin during the Silurian. The Cieurca eurypterid collection housed in the Yale Peabody Museum and collected by Sam Cieurca is the largest and most complete in the world. By using a eurypterid data set to gather information about ecology, such as diversity and abundance, as well as temporal trends, the history of eurypterid assemblages through time can be reconstructed. GIS maps were developed to illustrate and quantify the geographic range, density, and distribution for each time slice as well as for each eurypterid species. A series of eurypterid pulses was detected, when the diversity, overall abundance, and species-level abundance increased markedly. The basin itself was found to be quite homogenous lithologically, a reflection of the outcrop pattern structural overprint of the region. This was also shown by the even distribution of eurypterids for every time slice. The genus *Eurypterus* was dominant geographically, temporally, and in number throughout the basin. Further map analysis demonstrated a very even distribution of eurypterids throughout the basin. Arguments about taphonomy and the nature of these assemblages are not conclusive. As a whole, this project has resulted in a better understanding of the paleoecology and paleobiogeography of a poorly studied group of arthropods.

Introduction

Eurypterids are a monophyletic group of Late Ordovician-Late Permian arthropods commonly known as “sea scorpions.” They are an interesting taxon because of their diversity in morphology and the environments in which they have been discovered. As the most diverse chelicerates in the Paleozoic, with about 235 species as listed by Tetlie (2007), they exhibit a wide range of morphologies that could reflect different lifestyles and a varied ecology. Eurypterid habitat has been widely disputed and speculated; although their fossils are commonly found in fine grained dolomitic muds and carbonates, the total variety of lithologies that eurypterids have been found in have been interpreted to range from deep marine to fluvial deposits (Braddy, 2001; Tetlie 2007; Plotnick 1999). Furthermore, their morphology, split into two groups, also supports this range of habitats: the majority, belonging to the Suborder Eurypterina, have streamlined body forms with paddle-like appendages for swimming, while Stylonurina instead have “walking” appendages, and it has been found that some species have respiratory and reproductive systems that could support an amphibious lifestyle (Braddy, 2001; Tetlie, 2007). The taxon also includes a substantial range of body sizes, from centimeter scales to 2.5 m long pterygotids (Tetlie, 2007). In addition, the environmental distribution of eurypterids varies through time; earlier fossils from the Ordovician are more often found in marine deposits, while later Permian fossils are often found in brackish estuarine or freshwater fluvial and lacustrine deposits (Braddy, 2001). This great diversity has prompted various theories about their mode of life, one of which is the following. Compared to fossils found at other localities (Kokomo, Indiana; Soom Shale, South Africa, and Gogo Formation, Australia), it is widely believed that the specimens in New York are primarily molt exuviae (Plotnick, 1999; Braddy, 1999; Tetlie, Brandt, & Briggs 2008). The dominant hypothesis about this phenomenon, Braddy’s (2001) mass-molt-mate theory, proposes that large numbers of these animals simultaneously came to shallow, hypersaline lagoon environments as a refuge to escape predation while molting and mating. Given this hypothesis that they traveled to hypersaline environments with the purpose to molt, it would be difficult to interpret eurypterid habitat since their occurrences are not indicative of their normal environment.

Eurypterid fossils have been mainly found in northern and western Europe and in northeastern North America, with a large collection from the Appalachian Basin, which includes upstate New York and southern Ontario (Tetlie 2007). Tetlie (2007) showed that eurypterids primarily lived along the coasts of the paleocontinents Laurentia (USA, Canada, Greenland, Scotland) and Baltica (Scandinavia, Baltic states, western Russia, parts of eastern Europe). Fossils are abundant in localities that have sedimentary features of restricted facies, such as marine evaporites, indicating a habitat of high salinity that prohibited decay as well as predators, ideal to protect molting individuals (Braddy, 2001). These environments have been interpreted to be a combination of near-shore marine, estuarine, fluvial, or lacustrine (Tetlie, 2007). In addition, it has been noted that biomineralized marine arthropod exoskeletons are otherwise rarely preserved, in contrast to the organic eurypterid exoskeletons, indicating an extreme environment in which these fossils were deposited (Plotnick, 1999). Furthermore, some eurypterid assemblages include terrestrial plants and invertebrates (and a lack of marine species) suggesting that some eurypterids coexisted with terrestrial organisms or were washed into this environment of deposition (Braddy, 2001).

Theories about eurypterid ecology have been complicated by eurypterid taphonomy. Their chitinous carapaces make it more difficult for fossilization to occur, resulting in an incomplete fossil record (Tetlie, 2007). Furthermore, it is not clear whether the fossils collected are true body fossils or molt exuviae; the difficulties in determining their true nature could cast doubt upon interpretations of eurypterid habitats (Braddy, 1999). It is believed that most eurypterid fossils are actually products of ecdysis, based on the conditions and the preservation of non-mineralized cuticle (Tetlie, Brandt, & Briggs, 2008). Disregarding this complication, it also seems unlikely that eurypterids – body fossils or not – actually lived in the waterlimes and highly saline environments where they are often found. In addition, specimens are primarily fragments, highlighting a taphonomic bias (Plotnick, 1999). Thus, based on Braddy's mass-molt-mate theory, it is possible that the eurypterids were preserved as molts in hypersaline waters that provided protection, as well as enhancing the fossilization potential of the exoskeleton, while the animals were at this vulnerable stage. Therefore, these assemblages may be snapshots of eurypterids at only one stage of their life, while the bulk of it was spent elsewhere where they were not as easily preserved.

The Appalachian Basin eurypterid collection at the Yale Peabody Museum, from almost 350 Silurian localities, provides an excellent way to better understand the geography, taphonomy, habitat, and evolution of these arthropods, in addition to associated taxa and sedimentary structures. The completeness of the collection provides adequate spatial resolution in the basin area. Using biostratigraphic information, this project will build and refine a better understanding of the topography and lithology of this region of the Appalachian Basin. Furthermore, stratigraphic information will be used to map the Appalachian Basin localities through time and space to track the extreme environments that eurypterids inhabited, in comparison to the non-eurypterid bearing outcrops in the Silurian also found in the basin.

Eurypterids are a poorly understood group of arthropods since they are rarely found except in select waterlimes and dolomites. However, the highly dolomitic carbonates of the Appalachian Basin are endowed with diverse and numerous deposits of eurypterid fossils. The Yale Peabody Museum's eurypterid collection, known for its completeness and extensiveness, provides a valuable resource to understand this taxon. Through lithographic information and GIS mapping, this paper aims to address the following questions in order to understand the ecology and geographic distribution of Eurypterida: How are the eurypterid communities temporally and spatially distributed within the basin? How do ecological parameters of eurypterid communities change through time? What conclusions can be made about the correlation between their occurrences and lithology? What conclusions can be made about their taphonomy and preservation? This study will help address the question of deposition – why are the eurypterids, such rare fossils, so abundant in this area?

Material and Methods

This project, which extensively utilized the Yale Peabody Museum collections, also involved field work in upstate New York, mapping localities in ArcGIS, and thin section analysis of hand samples collected from various formations in the Appalachian Basin. This novel approach is distinct from previous studies that use GIS because it also includes an analysis of individual specimens (i.e. abundance), rather than just mapping species occurrences and diversity (Rode & Lieberman, 2004). This analysis was also done on a

much smaller and focused scale than any before, centering on a detailed investigation of a single clade in an area with a good fossil record.

Yale Peabody Museum Ciurca Collection

All of the specimens studied were gathered by Samuel Ciurca and acquired by the Yale Peabody Museum (YPM). Consisting of over 10,000 specimens that were collected over a period of almost 50 years, the collection includes material from localities in southern Ontario, Indiana, Ohio, Pennsylvania, and New York. The New York and Ontario localities, which number 478 for New York localities and 730 in total, generally run along Interstate 90 (New York Turnpike), which coincides with Silurian and Devonian bedrock exposures. Specimens were collected from Buffalo in the west to Albany in the east. The collection also includes associated fauna and sedimentary structures from the localities where the eurypterids have been found. Ciurca also provided supplemental documentation in the form of field notes and annotated maps of the lithologies as well as comments on the regional stratigraphy (Ciurca, 1978; Tetlie, Tollerton & Ciurca 2007).

The Ciurca locality system is distinct from the one used by the YPM. Ciurca numbered his localities based on geographical location; for example, Ciurca locality 1 could be a roadcut with three formations exposed. However, the YPM numbering system is based on unique horizons. Therefore, one YPM locality number would be assigned to each of the three formations found at Ciurca locality 1. This discrepancy was important when linking geographic location with the YPM locality information in GIS.

Previous work done by student interns began an object and locality data set for the Ciurca collection. The KE EMu database includes information on each specimen, the number of specimens found, the locality where it was found, and the lithology of the horizon. Most had GPS coordinates. Some GPS information had been previously collected by Susan Butts and O. Erik Tetlie, with the aid of Samuel Ciurca. Erik Tetlie is a former postdoctoral associate with Derek E.G. Briggs in the Department of Geology and Geophysics at Yale, from the years 2004-2007. In order to use the data set, preliminary work was done to extract the useful data necessary for the project and organize it in a meaningful way. Other GPS coordinates were gathered by Susan Butts and the author during a field trip in 2008. To

complete the GPS information that was still lacking, online geologic maps were used to determine the latitude and longitude of Ciurca's locality descriptions in the data set.

Field Work in Upstate New York

Field work was undertaken in November 2008 by the author and Susan Butts to examine Ordovician and Silurian localities in upstate New York along an east-west transect. With the help of Samuel Ciurca, various localities were visited to take GPS information that was missing from the data set, gather hand samples, take notes about the lithology and stratigraphy pertaining to eurypterid horizons, and become familiarized with the Silurian deposits of the area. Photographs were taken at each site visited to visually record the lithology (some examples are included in the appendix). The lithology and stratigraphy information were used to create a stratigraphic chart for the region, along with information from the literature and help from Sam Ciurca (**Figure 1**). The hand samples from eurypterid horizons were used in thin section analysis.

ArcGIS Mapping

ArcGIS is a program that allows the user to map localities and develop spatial relationships between points. GPS data are plotted as a shapefile, and certain features in the data to be highlighted can be included in a separate map layer. For example, to highlight a particular set of eurypterid localities in a shapefile of fossil localities, a layer can be created where only those localities are shown. Data in ArcGIS are stored in tables, and this information can be linked to other tables through relationship classes. This allows the user to create complex links between the geographic information and object information. Further information can be obtained at ArcGIS Desktop Help 9.3.

The Peabody data set includes GPS information and/or latitude and longitude coordinates determined from map points for each of Ciurca's localities. Once the information was formatted into a usable form, this information was plotted in ArcGIS 9.3 to produce a map which displayed the spatial relationship between the localities. The underlying maps included bedrock geology shapefiles obtained from the New York State

Museum website (which can be accessed at: <http://www.nysm.nysed.gov/gis/>). These were used as guidelines for the exposed bedrock patterns of the localities visited.

Because there could be more than one YPM locality for every Cieurca locality, a one-to-many relationship class was used to link the YPM localities to Cieurca's localities. This was done so that selecting one of the localities presented on the map would allow the user to navigate to the YPM localities. The YPM localities have lithological and formation information. Another one-to-many relationship class was created to link the specimens to the YPM localities. This provided a further link that allows the user to see what specimens were found at each YPM locality. The user may choose between viewing all taxa (community) or only specimens belonging to Eurypterida.

Layers were then created to allow for analysis by time and by species, allowing the user to see the Cieurca localities associated for each time segment and for each species. First, layers were made for each "time slice." These time slices were based on the stratigraphic chart for the region (**Figure 1**). For example, time slices were created for the Wanaka Shale Member of the Ludlowville Formation and for the older Union Springs Member of the Marcellus Shale Formation. The Cieurca localities found in the Union Springs Member allow the user to see the specimens that are relatively older than the specimens found in the Wanaka Shale Member. This was created as an interactive map, called "Time.mxd." Likewise, layers were made for each eurypterid species, so that the spatial and temporal occurrences for each species can be examined. For example, the *Eurypterus remipes* layer provides the localities where it is found, and by clicking on those localities, the user can glean temporal data. The user can then compare this information with *Eurypterus lacustris*, to observe the differences between the two species. This was created as a map called "Specimens.mxd." These maps will be available on the YPM website, as well as presented on a CD as an appendix to this report.

Thin section Analysis

Lithological samples from 66 eurypterid horizons collected during the field trip and by Erik Tetlie on earlier field trips were cut into billets and then sent to Vancouver GeoTech Labs to be made into 27 x 46 mm, 30 µm standard thin sections. Many of the thin sections

indicated sedimentary orientation. About a third of each slide was then stained with Alizarin Red-S to distinguish between dolomite and calcite crystals (Tucker, 1988). Based on the Alizarin Red-S staining, which binds to calcium in a chelation process that increases birefringence, calcite appears pink/red under white light and dolomite is colorless (Tucker, 1988). The slides were stained for two minutes. The thin sections were examined under a petrographic microscope with cross polarizers and a gypsum plate. They were examined for silt, estimated dolomite/calcite abundance, and textural features. Other features such as the occurrence and type of bioclasts were also recorded. The HCl test was performed on the corresponding billets to provide further lithologic information. The lithology information was used in the analysis to understand the more nuanced details between the time slices, and was added to the maps.

Data Analysis

A data matrix was made to compare the presence of different species at the various stratigraphic levels, which represent successive time slices (**Figure 2**). This was repeated with ‘ghost’ ranges, where 0’s were used to represent the absence of species – species that were not present in this part of the basin even though other occurrences reveal that their stratigraphic range extends through this interval (**Figure 3**). A similar matrix was created, including taxa other than eurypterids, to analyze the community assemblages (**Figure 6**). Members were used as the stratigraphic units where possible, but formations were used where they are not subdivided into members (and in cases where data on occurrences in members were not recorded). A similar problem applies to species. While many specimens were identified to the species level, in some cases only the genus could be identified (*Genus* sp. = Genus determined, species undeterminable) or taxonomic determinations were questionable. Therefore, to maintain that information, some species “categories” are actually genus-level designations that include all specimens that fall into that genus. Where such categories are used in the analysis they are noted.

Next, a stacked column was created to analyze the diversity and abundance of the different species over the stratigraphic time slices (**Figure 4**). The x-axis contains the stratigraphic time slices and their corresponding lithologies, while the y-axis represents

abundance. Each species was assigned a color based on their superfamily, and the height of each bar in the stacked column represents the abundance of that species. The species included in the abundance analysis were all species that could at least be identified to the genus level; unidentified specimens were omitted from the analysis. Over each column (**Figure 4a**) is a number that indicates the diversity for that time slice. To make the graphs easier to read, the most abundant species were removed and plotted separately: the genus-level category *Eurypterus* sp., and the species-level categories *Eurypterus lacustris*, *Eurypterus remipes*, and *Hughmilleria socialis*.

To analyze the distribution, a series of maps were produced using ArcMap. The localities were plotted on both a modern map as well as a paleomap georeferenced in ArcMap (**Figure 7**, map obtained from Ron Blakey with permission, <http://jan.ucc.nau.edu/~rcb7/namS420.jpg>). A graticule grid was made with latitude and longitude lines for each degree. This allowed geographic range to be approximated; for every box in the grid that a selected locality crossed, it was counted as part of the range. To simplify this approximation, it was assumed that each locality was the same size (i.e. the size of the selected icon, about 1/9 of each grid). This method is in contrast to the polygon system used by Rode & Lieberman (2004); the linear aspect of the outcrop pattern makes the grid system much more viable. Layers were then made for each stratigraphic unit, and the eurypterid prevalence was estimated by dividing the number of eurypterid grids by the total number of grids for each time slice. An example of this map is included in the appendix as **Figure 10**. In a similar method, layers were also made for each species category. The number of grids for each species category was counted, and the approximate density for each species was calculated by dividing the number of specimens by the number of grids (specimens/area). An example is also included in the appendix as **Figure 11**. A scale of relative density was designated given the natural breaks in the data; high density = 75 specimens/grid or greater, medium density = 10-75, and low density = 1-10. Maps were then made to show the geographic distribution through time for *Eurypterus lacustris* and *Eurypterus remipes*. These two were chosen because they were the only species categories to be present in more than four time slices. A map was made for each time slice that specimens were found in, in order to trace the changes in distribution through time for *Eurypterus lacustris* and *Eurypterus remipes*.

Study Site

Eurypterids reached their peak of diversity during the Middle Silurian to the Early Devonian (Tetlie, 2007). The most diverse assemblages and the majority of specimens have been found in eastern North America and Europe, which may reflect true distributions on the paleocontinents of Laurentia and Baltica but may also be a result of collection bias (Tetlie, 2007). The Cieurca collection comes almost entirely from the Appalachian Basin in upstate New York and Ontario. Silurian and Devonian bedrock exposures occur in a narrow strip that runs from Syracuse west on NY Interstate 90 through Rochester and Albany into the Niagara region of Ontario. A significant number of these exposures have yielded eurypterid fossils, as well as other assemblages. Based on paleogeographic reconstructions and sedimentology, it is estimated that this ribbon of fossil localities was on the edge of the Appalachian Basin and they are interpreted to be mainly near-shore environments (Carl Brett pers comm., 3/25/09; R. Blakey map, accessed at <http://jan.ucc.nau.edu/~rcb7/namS420.jpg>). The basin extended to deeper waters further to the south and west, and land was located to the north, in present day Canada.

This section of the Appalachian Basin consists of the following major groups in stratigraphic order: Medina, Clinton, Lockport, Salina, Bertie, Onondaga, Helderberg, and Hamilton (**Figure 1**). The earliest eurypterids in the basin are found in the Lockport (Cieurca & Tetlie, 2007); however, eurypterids are most abundant in the Bertie. The Bertie consists almost entirely of dolomites and waterlimes, fine-grained dolostones, and very rare beds of limestone. As a whole, the Silurian outcrops other than the Bertie are carbonate shales or limestones, with an important evaporite formation, the Syracuse Salt, in the Salina Group. In the Devonian groups – Onondaga, Helderberg, and Hamilton – the lithologies are also carbonate shales and massive limestones. Below is a stratigraphic chart of the study area, with correlations from western beds near Buffalo to eastern beds near Syracuse (**Figure 1**).

Outcrops of the Bertie Group run almost directly west-east through New York, especially along NY-90, displaying a slight dip toward the south-southwest at about 9 meters to the kilometer (Belak, 1980). Thus, during the Upper Silurian, the northernmost edge of the Appalachian Basin runs nearly along the interstate. This erosional window applies to the

other stratigraphic units in the Silurian and the Devonian, resulting in a two-dimensional outcrop pattern for this time period. The position of most of the eurypterid localities along the roads does not necessarily point to a sampling bias but can be explained by the basin architecture.

The correlation between basin structure and sampling also indicates that each formation represents a distinct and homogenous depositional environment. Belak (1980) described the basin undergoing transgression and regression from the Scajaquada to the Chrysler (**Figure 1**). He interpreted the Scajaquada to be supratidal deposits, the Williamsville to be intertidal, and the lower Cobleskill-Akron Dolomites to be subtidal during the transgression event. During the regression event, the upper Cobleskill-Akron represents intertidal deposits and the Chrysler Limestone represents a supratidal environment. Belak (1980) also interpreted the coastline to consist of shallow slopes, approximately one inch to the mile, which would have resulted in a very broad intertidal zone – estimated to be at least 6 km – along the nearly 300 km of the basin edge. This extreme shallow depth resulted in the restricted facies where the eurypterids are found. Since the sea level was not high, it was impossible to form strong currents to mix the water (Belak, 1980). In addition, the shallow tides resulted in high levels of evaporation (Belak, 1980). This conclusion is supported by the presence of enormous salt casts and other halite structures, and euhedral dolomite crystals, especially in the Syracuse Salt and the Manlius Limestone (Belak, 1980, Sam Ciorca pers. comm., 2/17/09).

The Appalachian Basin was a continental shelf, resulting in an outcrop pattern that makes it difficult to analyze the basin morphology itself. In addition to the east-west nature of the deposits, the shallow beds all dip very gently, resulting in few outcrops for each formation. Therefore what has been exposed is not necessarily representative of the area covered by the depositional environments present, making it difficult to draw any conclusions about paleobiogeography. However, a positive conclusion of the outcrop pattern is that the linearity of the localities is not due to sampling bias.

<i>WEST – Buffalo</i>				<i>EAST – Albany</i>			
Group	Formation	Member		Group	Formation	Member	
Hamilton	Ludlowville	Wanakah Sh		Hamilton	Ludlowville	Wanakah Sh	
	Marcellus Sh				Marcellus Sh	Union Springs	
Onondaga	Onondaga Ls	Edgecliff		Helderberg	Manlius Limestone	Elmwood	
<i>unconformity</i>						Olney	
			<i>Silurian/ Devonian boundary</i>		Chrysler Limestone	Thacher	
Bertie	Moran Corner Waterlime					Bertie	Moran Corner Waterlime
	Akron Dol		Cobleskill Dol/Ls				
			Oxbow Dolomite				
	Williamsville Waterlime		Williamsville Waterlime				
	Scajaquada		Forge Hollow Dol				
	Fiddlers Green Dolomite	Ellicott Creek Breccia	Fiddlers Green Dolomite		Phelps Waterlime		
		Black shale marker bed					
		Victor Dol			Victor Dol		
	Morganville Waterlime		Morganville Waterlime				
	Oatka Wl			Salina	Camillus Shale		
	Fort Hill Wl						
					Syracuse Salt		
Salina	Vernon Shale				Vernon Shale		Barge Canal
					Ilion Sh	Pittsford Sh	
						Farmers Mills	
				Lockport	Lockport Dolomite		
							Sconodoa
				Clinton	Rochester Shale		
Clinton	De Cew Dol						Irondequoit Ls
					Reynales Limestone	Wallington Ls	
						Maplewood Sh	Furnaceville
				Medina	Kodak Sandstone	Brewer Dock	
						Grimsby Formation	
Medina			<i>Ordovician – Silurian boundary</i>				
	Whirlpool Ss (base of group)	Ridgelea					

Figure 1. Silurian stratigraphy of New York. Formations are correlated from the west (near Buffalo, NY) to the east (near Albany, NY). (Ciarra, pers. comm.; Ciarra 1978; Tetlie & Tollerton, 2007; Rickard, 1962; Goodman & Brett, 1994). Lithologies are abbreviated as: Sh = shale, Ls = limestone, Wl = waterlime, Dol = dolomite, Ss = sandstone.

Results

Temporal Distribution of all Eurypterid Species

Eurypterids occur nearly continuously from the Whirlpool Sandstone near the Ordovician-Silurian boundary to the lower Devonian Ludlowville Formation (**Figure 2**).

Based on **Figure 2**, it is clear that Eurypteroidea is the most diverse superfamily, with 12 species present. The Pterygotoidea is the second most represented superfamily, with 9 species found, followed by Mixtoperoidea with 4 species. Only 1 species of Stylonurina and 1 species of Waeringopteroidea were found in this part of the Appalachian Basin. The phylogenetic position for *Borchgrevinkium* sp. could not be determined, as it is possible that they actually belong to a sister group to eurypterids (Tetlie, 2007).

Figure 3 depicts the ‘ghost’ lineages of the species found. This allows for the extrapolation of the temporal range of the species. Their absence within the stratigraphic range indicates that either they did not live in the environment of deposition or taphonomic factors prevented them from being preserved. This diagram shows that the Pterygotoidea had the longest time range, present from the Pittsford Shale to the Ludlowville Formation, the youngest formation sampled. This is mainly due to the presence of the genus *Pterygotus*, most examples of which could not be identified to the species-level. Of the identifiable species, however, most seem to have only lived in the basin for short periods of time, either when the Pittsford Shale was being deposited or from the top of the Fiddlers Green to the Williamsville.

The Waeringopteroidea, which is represented by only one species, was present for a short time during the deposition of the Vernon Dolomite and the Syracuse Salt. The Mixtoperoidea were the first eurypterids to appear in this northern area of the basin, generally occurring from the Rochester Shale to the Williamsville Formation. However, there are many gaps in between, indicating an absence during much of the deposition of the basin. One species, *Mixtopterus multispinosus*, was only present during the Vernon. The Eurypteroidea show a varied presence in the basin. *Eurypterus pittsfordensis* was the first species to appear, but it is only present in the Pittsford Shale Member of the Vernon. *Eurypterus lacustris* and *Eurypterus remipes* both first appear in the Syracuse Salt and persist until the Onondaga Limestone. *Buffalopterus pustulosus* occurs from the Ellicott Creek Breccia (ECB)/Phelps Waterlime Member of the Fiddlers Green to the Williamsville, and *Eurypterus dekayi* from the Williamsville to the Moran Corner Waterlime. The other species, which were deposited from the ECB/Phelps to the Olney Member of the Manlius Limestone, were not present in more than 2 formations.

The Stylonurina are only found from the ECB/Phelps to the Williamsville.

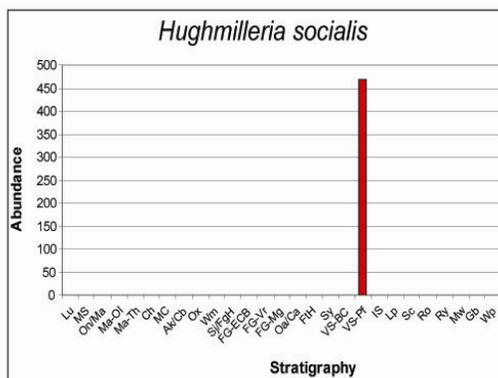
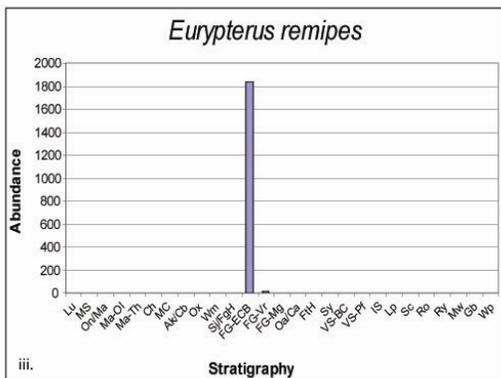
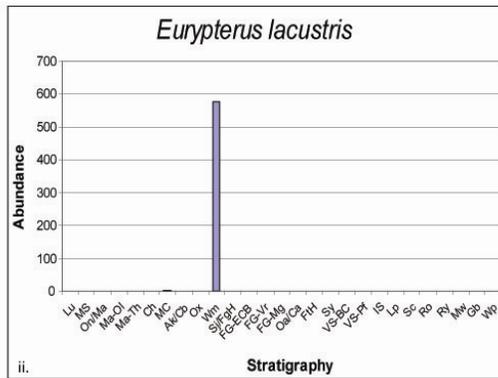
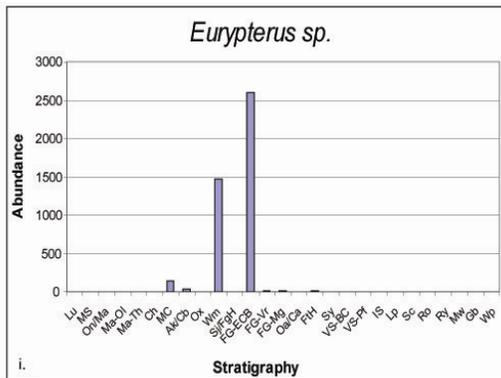
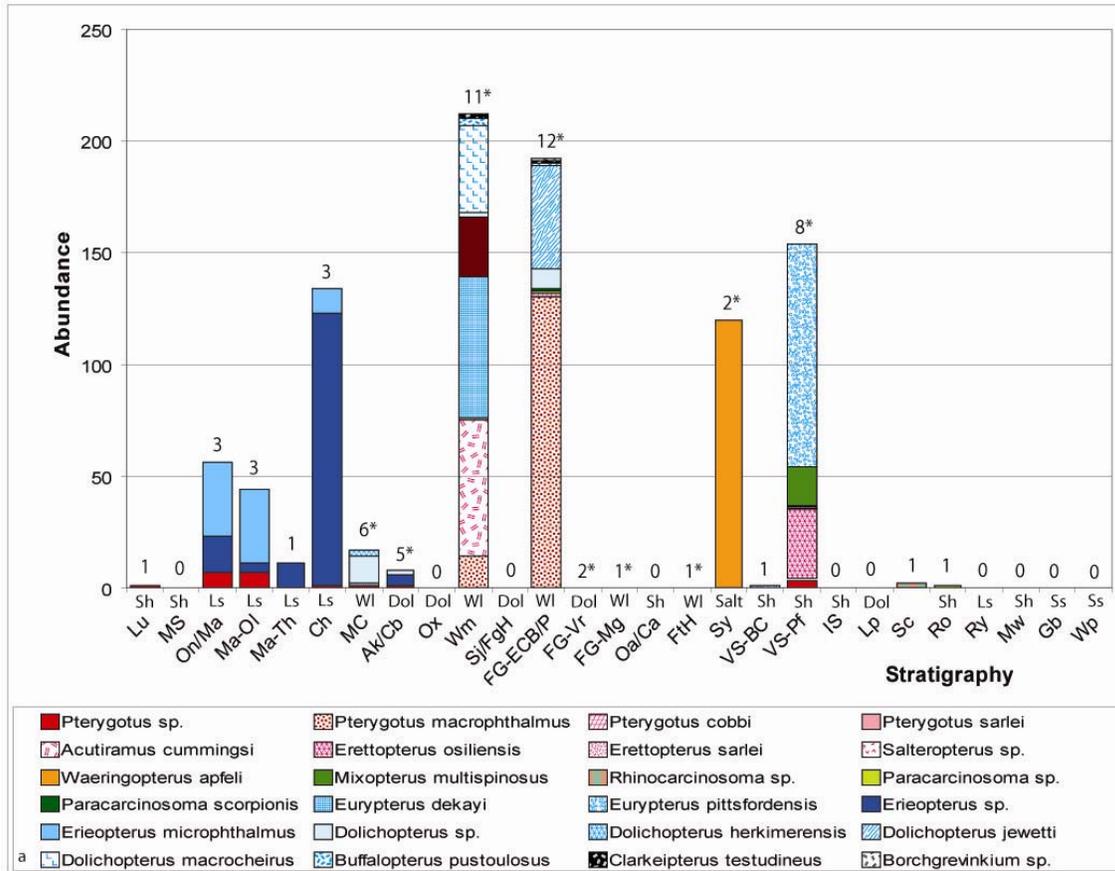
Diversity and Abundance

The most obvious observation is that periods of high diversity and high abundance tend to occur in the same stratigraphic units (**Figure 4**). These periods occur in pulses that do not correlation well with lithology.

Overall abundance and diversity

As revealed by the individual graphs in **Figure 4b**, the most abundant and diverse stratigraphic units were the Williamsville Waterlime, the Ellicott Creek Breccia /Phelps Member of the Fiddlers Green and to a lesser degree, the Pittsford Member of the Vernon Shale. The Williamsville yielded 11 species with over 2200 total specimens, the Ellicott Creek Breccia /Phelps of the Fiddlers Green 12 species with over 2700 total specimens, and the Pittsford Member of the Vernon Shale 8 species with over 620 specimens. Three more stratigraphic time slices yielded more than 100 specimens; the Chrysler with 134 specimens, the Moran Corner with 158, and the Syracuse with 124 specimens. The Moran Corner showed the greatest diversity with 6 species, while the Chrysler had 3 species, and the Syracuse only 2. There were quite a few stratigraphic units with few specimens but a higher diversity: the Onondaga/Manlius unit yielded 58 specimens from 3 species, the Olney Member of the Manlius 44 specimens from 3 species, and the Akron/Cobleskill 44 specimens from 5 species. The Victor Member of the Fiddlers Green had 32 specimens of a single species. The following had abundances less than 20 specimens and only 1 species: Ludlowville, Thacher Member of the Manlius, Morganville Member of the Fiddlers Green, Fort Hill Waterlime, Barge Canal Member of the Vernon Shale, Sconondoa, Rochester, and Reynales.

No clear pattern emerges in the relationship between lithology and abundance/diversity. Although the two most diverse and abundant lithographic units, the Williamsville and the Ellicott Creek Breccia /Phelps, are both waterlimes, the other waterlimes do not seem to exhibit these characteristics, as the Moran Corner Waterlime had a significantly smaller yield with about 158 specimens and the Morganville and Fort Hill Waterlimes yielded none. Waterlimes are simply very fine-grained dolomites, and the eurypterid faunas of the dolomites in this sequence were neither especially diverse nor



b

Figure 4. Abundance and diversity data. Each species category is represented by a different color, and has been plotted given its occurrence in different stratigraphic units. The abundance is indicated by the y-axis. The diversity of the stratigraphic unit is given by the number above the column. The lithology of each time slice is given below the column. A. represents the least abundant species, while B. represents the individual graphs of the most abundant species, which were separated so that the data does not overwhelm the information in A. Stratigraphic abbreviations: Lu = Ludlowville, MS = Marcellus, On/Ma = Onondaga/Manlius, Ma-Ol = Olney Member of the Manlius, Ma-Th = Thacher Member of the Manlius, Ch = Chrysler, MC = Moran Corner, Ak/Cb = Akron/Cobleskill, Ox = Oxbow, Wm = Williamsville, Sj/FgH = Scajaquada/Forge Hollow, FG-ECB/P = Fiddlers Green, Ellicott Creek Breccia and Phelps Members, FG-Vr = Fiddlers Green, Vernon Member, FG-Mg = Fiddlers Green, Morganville Member, Oa/Ca = Oatka/Camillus, FtH = Fort Hill, Sy = Syracuse, VS-BC = Vernon Shale, Barge Canal Member, VS-Pf = Vernon Shale, Pittsford Member, IS = Ilion, Lp = Lockport, Sc = Sconodoa, Ro = Rochester, Ry = Reynales, Mw = Maplewood, Gb = Grimsby, and Wp = Whirlpool. Lithological abbreviations: Sh = shale, Ls = limestone, Wl = waterlime, Dol = dolomite, Ss = sandstone.

abundant: Akron/Cobleskill was the most diverse with five species, and Victor Member of the Fiddlers Green had two, while Oxbow, Scajaquada/Forge Hollow, and Lockport yielded no eurypterids. After the waterlimes, the second most abundant stratigraphic unit was the Pittsford Member of the Vernon Shale, with many specimens of *Hughmilleria socialis*.

Examining the other shales, however, shows that while about half of the stratigraphic units of this type yield eurypterids, they are only in small numbers. The Ludlowville, Rochester, and Barge Canal Member of the Vernon Shale all had less than 10 specimens of a single species. The Marcellus, Oatka/Camillus, Ilion, and Maplewood Shales all lack eurypterids. The limestone units generally were relatively diverse; the Onondaga/Manlius, the Olney Member of the Manlius, and the Chrysler Limestones all yielded three species and at least 40 specimens each, while just one species is known from the Thacher Member of the Manlius. Of the limestones only the Reynales lacks eurypterids. The Grimsby and Whirlpool Sandstones both did not have any identified eurypterids. The Syracuse Salt – the only “Salt” unit – had only one species, *Waeringopterus apfeli*, but it is quite abundant. The Syracuse Salt was observed by Ciurca to have extremely large salt crystals and salt hoppers (**Figure 5**).



Figure 5. Salt hoppers. The cubic structure of the halite is clearly shown. The crystallized area is about 6 x 8 cm. Photo courtesy of Sam Ciurca.

Superfamily Pterygotoidea

The most abundant pterygotoid species is *Hughmilleria socialis* (**Figure 4biv**). Over 450 specimens were found in the Pittsford Member of the Pittsford Shale. The occurrence of other pterygotoid species is shown in **Figure 4a**. *Pterygotus macrophthalmus* was present in the Williamsville (14 specimens) and Ellicott Creek Breccia /Phelps (130). *P. cobbi* was found in only the Ellicott Creek Breccia/Phelps, and with only 2 specimens. *P. sarlei* and *Erettopterus sarlei* only had 1 specimen in the Pittsford Member of the Vernon Shale. *Acutiramus cummingsi* was found in the Williamsville, represented by 61 specimens. Both *Erettopterus osiliensis* and *Salteropterus* sp. were found in the Pittsford Member of the Vernon Shale represented by 31 specimens and 1 specimen, respectively.

Superfamily Waeringopteroidea

The only species represented in this region, *Waeringopterus apfeli*, was found only in the Syracuse Salt. 120 specimens were found.

Superfamily Mixopteroidea

Mixopterus multispinosus was found only in the Pittsford Shale, with 17 specimens. *Rhinocarcinosoma* sp. was found in the Williamsville (1 specimen) and in the Sconodoa (2 specimens). *Paracarcinosoma* sp. was found in the Ellicott Creek Breccia /Phelps (1) and the Rochester (1). *Paracarcinosoma scorpionis* was found in the Williamsville (63) and in the Ellicott Creek Breccia /Phelps (1).

Superfamily Eurypteroidea

The genus *Eurypterus* occurs almost continuously through the sequence from the Moran Corner Waterlime to the Fort Hill Waterlime (**Figure 3bi**). Examining the abundance graphs of the two most abundant *Eurypterus* species, *Eurypterus lacustris* and *Eurypterus remipes*, reveals that there are huge fluctuations in individual populations. However, it must be noted that a significant number of *Eurypterus* specimens could not be identified to the species level (2519 specimens). *Eurypterus lacustris* was very abundant only during the Williamsville, with almost 600 specimens found (**Figure 4bii**). No more than twenty specimens were also found in the Moran Corner Waterlime, the Akron/Cobleskill Dolomite, the Ellicott Creek Breccia /Phelps Member of the Fiddler's Green, and the Syracuse Salt. Similarly, the vast majority of *E. remipes* occur in the Ellicott Creek Breccia or Phelps Waterlime (which are stratigraphically equivalent) of the Fiddlers Green, where over 1800 specimens have been found (**Figure 4biii**). A small number (<30) were also found in the Ellicott Creek Breccia /Phelps Member of the Fiddlers Green.

Figure 4a provides information about less abundant species. A few specimens of *Eurypterus dekayi* were found in the Moran Corner but 27 were found in the Williamsville. A few specimens of *Eurypterus pittsfordensis* are known from the Barge Canal Member of the Vernon, but 100 specimens have been found in the Pittsford Shale Member of the same formation. The genus-level *Erieopterus* sp. is represented by a few specimens from the Onondaga/Manlius, the Olney and Thacher Members of the Manlius, and the Akron/Cobleskill, but 122 specimens are known from the Chrysler. *Erieopterus microphthalmus* is known from less than 40 specimens in the Onondaga/Manlius, the Olney Member, and the Chrysler. The genus-level *Dolichopterus* sp. is present in 5 units: Moran Corner (12 specimens), Akron/Cobleskill (2), Williamsville (2), and Ellicott Creek Breccia

/Phelps (9). *Dolichopterus herkimerensis* is only found in the Moran Corner where 3 specimens have been found. *Dolichopterus jewetti* occurs in the Ellicott Creek Breccia /Phelps (46 specimens) and *Dolichopterus macrocheirus* in the Williamsville (39 specimens). *Buffalopterus pustulosus* is not abundant; 3 specimens have been found in the Williamsville and 1 at the Ellicott Creek Breccia /Phelps.

Suborder Stylonurina and others

Only one species belonging to the Stylonurina was found. *Clarkeipterus testudineus* occurs in the Williamsville (2 specimens) and in the Ellicott Creek Breccia /Phelps (1).

The phylogenetic position of *Borchgrevinkium* sp. is currently unknown. Only 1 specimen was found in the Ellicott Creek Breccia /Phelps.

Community Information

A coarse analysis was done of the community assemblages. The matrix illustrated in **Figure 6** shows the occurrence of the eurypterids, as well as other arthropod classes and other taxa found by Ciurca, in the stratigraphic units studied. Information beyond phyla and class is not used due to the lack of identification. The first observation is that within the stratigraphic units under consideration, eurypterids are the most common fossil; no other taxonomic category occurs in as many time slices. However, this may reflect a sampling bias on the part of the collector, Sam Ciurca. In addition, of the 9 stratigraphic units that do not yield eurypterids, other fossils appear in only 3 of them, and these include brachiopods, echinoderms, cnidarians, and some ichnofossils.

These units, which were deposited in the Lower Silurian, are the most siliciclastic rocks of the ones studied. The remaining 6 units are barren of all fossils. The stratigraphic units with the greatest eurypterid diversity – Williamsville, Ellicott Creek Breccia /Phelps, and Pittsford Shale – also have the most diverse communities. Of the 18 taxonomic categories that occur, 12 are present in the Williamsville, 8 are present in the Ellicott Creek Breccia /Phelps, and 7 in the Pittsford Shale. The Rochester Shale, not one of the eurypterid-diverse units, also has a high diversity of taxa, with 9 species. The Chrysler Limestone is notable in being the only one to yield both Porifera and Annelida.

The second map, “Specimen.mxd,” was created with layers for each species, as well as for other taxa in order to compile community assemblage information. Selecting the layer displays the locations where those species were found.

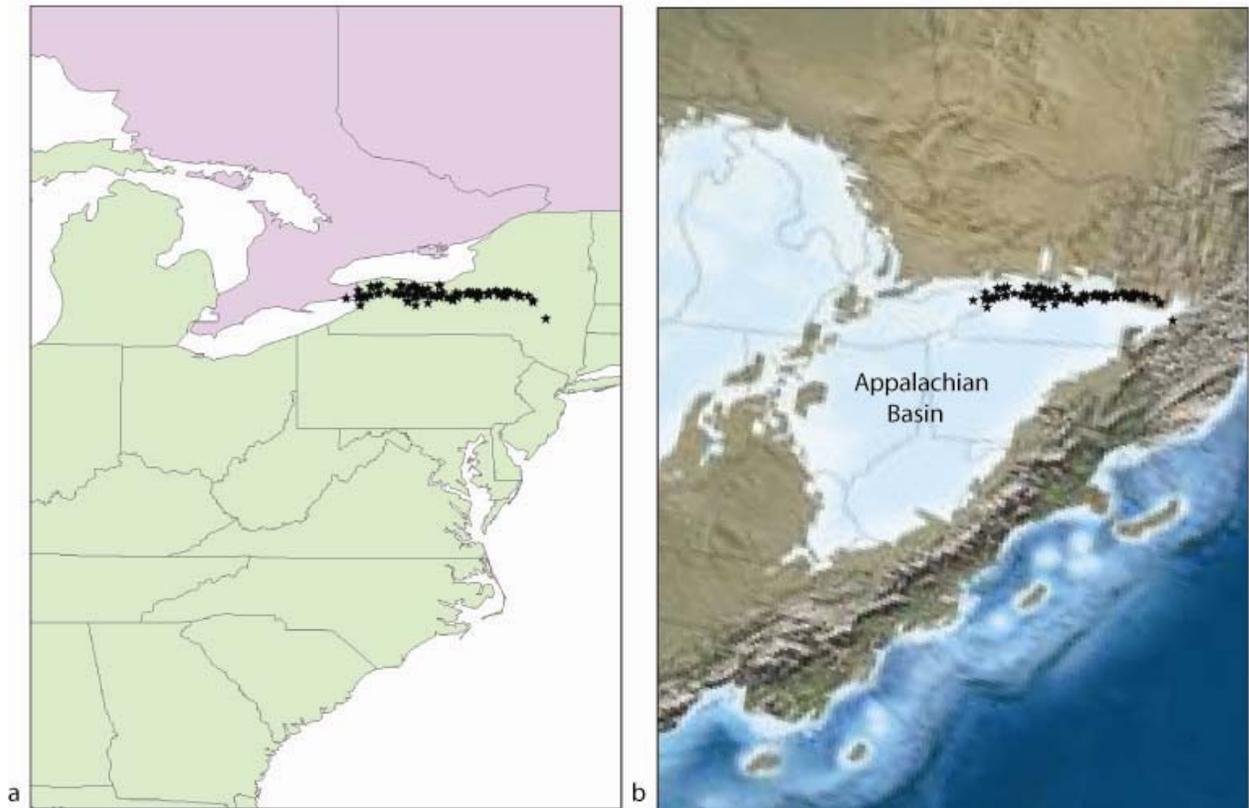


Figure 7. Localities in the Appalachian Basin. a. The localities mapped on the modern political map; the localities are mostly in the region between Albany and Buffalo, as well as in the Niagara region of Ontario. b. The localities mapped onto a paleogeographic reconstruction of the Late Silurian (map was obtained from Ron Blakey with permission: <http://jan.ucc.nau.edu/~rcb7/namS420.jpg>. Georeferencing was performed in ArcMap).

The localities are concentrated along a narrow west-east transect that runs through the Niagara region of Ontario to Albany, NY (**Figure 7a**). This ribbon of exposures also runs along NY-90, which is not shown on this map. This is a result of the outcrop pattern mentioned above; due to the dipping of the beds, all the outcrops of this time period appear in this linear, two-dimensional fashion. The eurypterids are found along the northern edge of the shallow basin (**Figure 7b**). As a result, it can be inferred that almost all of the specimens were deposited in littoral and shallow-marine environments. The occurrence of localities on

land in **Figure 7b** is an anomaly resulting from georeferencing or the spatial resolution of the paleogeographic maps. These localities should also be aligned with the shore and shallow marine environments. Other maps from Blakey's collection show that this northern rim of the Appalachian Basin does not move significantly between the Lower Silurian and the Middle Devonian. Thus, it is clear that the outcrops are concentrated in shallow near-shore settings, and the linearity of the outcrop pattern does not provide sediments from deeper environments.

Geographic Range

Stratigraphy	Lithology	Total Grids	Eurypterid Grids	Percentage
Ludlowville	Shale	1	1	100
Marcellus	Shale	2	0	0
Onondaga/Manlius	Limestone	26	18	69.23
Manlius-Olney	Limestone	10	5	50
Manlius-Thacher	Limestone	9	6	66.67
Chrysler	Limestone	13	4	30.77
Moran Corner	Waterlime	2	2	100
Akron/Cobleskill	Dolomite	29	21	72.41
Oxbow	Dolomite	2	0	0
Williamsville	Waterlime	30	17	56.67
Scajaquada/Forge Hollow	Dolomite	17	12	70.59
Fiddlers Green-Ellicott Creek Breccia/Phelps	Waterlime	23	21	91.30
Fiddlers Green-Victor	Dolomite	13	12	92.30
Fiddlers Green-Morganville	Waterlime	5	5	100
Oatka/Camillus	Shale	6	0	0
Fort Hill	Waterlime	6	6	100
Syracuse	Salt	8	8	100
Vernon-Barge Canal	Shale	2	2	100
Vernon-Pittsford	Shale	3	3	100
Ilion	Shale	4	0	0
Lockport	Dolomite	5	1	20
Sconondoa		2	2	100
Rochester	Shale	4	0	0
Reynales	Limestone	3	0	0
Maplewood	Shale	2	0	0
Grimsby	Sandstone	1	0	0
Whirlpool	Sandstone	1	1	100

Table 1. Stratigraphic time slices and eurypterid distribution. The stratigraphic units are arranged with the most recent at the top of the table and the oldest at the bottom.

Table 1 indicates the percentage of grids per stratigraphic unit that yielded eurypterid specimens. It demonstrates the prevalence of eurypterids within the outcrop of each stratigraphic unit. With the exception of the Chrysler Limestone, where only 31% of its total exposures were eurypterid-bearing, and the Lockport, with 20%, at least half the area of the outcrops for each stratigraphic unit yielded eurypterids. Of the 19 total eurypterid-bearing stratigraphic units, 15 of them had at least 66% of their exposure area populated by eurypterids fossils. There is no obvious correlation between the proportion of coverage and the lithology of a unit.

Table 2 presents similar information. However, rather than comparing the presence of eurypterids in different time slices, the geographic range of each species was counted by proxy based on the number of grids that the localities occupied. The total number of specimens was then divided by this grid number to calculate an approximate density. The density is not relative to individual time slices but to overall time.

For eurypterids in general, there were 138 specimens found in each grid, quite a high density and driven by the most abundant species. The genus-level *Eurypterus* sp. category also shows a high density, as did *Eurypterus remipes* and *Eurypterus pittsfordensis*. *Hughmilleria socialis* was the densest – for each grid where the species occurs, there were about 250 specimens. In general, the Pterygotoidea showed a low relative density, although some species, such as *Pterygotus macrophthalmus*, *Acutiramus cummingsi*, and *Erettopterus osiliensis* showed slightly higher densities (10-48 specimens/grid). Waeringopteroidea, represented by *Waeringoptera apfeli*, showed a medium density of 15 specimens/grid. Mixopteroidea showed a medium density as well, although *Rhinocarcinosoma* sp. was very low. Eurypteroidea had very mixed results. Within *Eurypterus*, density was medium to high, although *Eurypterus dekayi* showed a low density. *Eriopterus* showed a medium density. *Dolichopterus* showed a low-medium density, and *Buffalopterus pustouloosus* was low. The density of species in the suborder Stylonurina, *Clarkeipterus testudineus*, was low.

Species Category	Grids	Specimens	Approximate Density	Relative Density
All	52	7175	137.981	High
<i>Hughmilleria socialis</i>	2	498	249	High
<i>Pterygotus sp.</i>	16	166	10.375	Medium
<i>Pterygotus macrophthalmus</i>	3	144	48	Medium
<i>Pterygotus cobbi</i>	3	3	1	Low
<i>Pterygotus sarlei</i>	1	1	1	Low
<i>Acutiramus cummingsi</i>	6	63	10.5	Medium
<i>Erettopterus osiliensis</i>	2	32	16	Medium
<i>Erettopterus sarlei</i>	1	1	1	Low
<i>Salteropterus sp.</i>	1	1	1	Low
<i>Waeringopterus apfeli</i>	9	132	14.667	Medium
<i>Mixopterus multispinosus</i>	3	19	6.333	Low
<i>Rhinocarcinosoma sp.</i>	4	3	0.75	Low
<i>Paracarcinosoma sp.</i>	10	110	11	Medium
<i>Paracarcinosoma scorpionis</i>		103		
<i>Eurypterus lacustris</i>	9	585	65	Medium
<i>Eurypterus remipes</i>	16	1874	117.125	High
<i>Eurypterus pittsfordensis</i>	3	226	75.333	High
<i>Eurypterus dekayi</i>	4	29	7.25	Low
<i>Eurypterus sp.</i>	36	5240	145.556	High
<i>Erieopterus sp.</i>	13	229	17.615	Medium
<i>Erieopterus macrophthalmus</i>	5	61	12.2	Medium
<i>Dolichopterus sp.</i>	13	119	9.154	Low
<i>Dolichopterus herkimerensis</i>	1	1	1	Low
<i>Dolichopterus jewetti</i>	3	47	15.667	Medium
<i>Dolichopterus macrocheirus</i>	4	43	10.75	Medium
<i>Buffalopterus pustulosus</i>	3	4	1.333	Low
<i>Clarkeipterus testudineus</i>	4	4	1	Low
<i>Borchgrevinkium sp.</i>	1	1	1	Low

Table 2. Geographic range distribution for each species. High relative density = 75 or greater, Medium = 10 to 75, Low = 1-10.

Geographical Distribution

Figure 8 shows the distribution of outcrops yielding *Eurypterus lacustris* through time. During the deposition of the Vernon Shale, the species was deposited across the basin with slightly more deposited in the west. This is also true during the Ellicott Creek Breccia /Phelps, although there is a heavier concentration in the west. This western concentration is consistent during the Akron/Cobleskill, although some still occur in the east. Although it appears that the species appears in the middle of the basin during the Moran Corner, the

extent of Moran Corner outcrops is limited. In the Onondaga/Manlius time slice, *E. remipes* is only present in the west, despite the prevalence of outcrops of this stratigraphic unit.

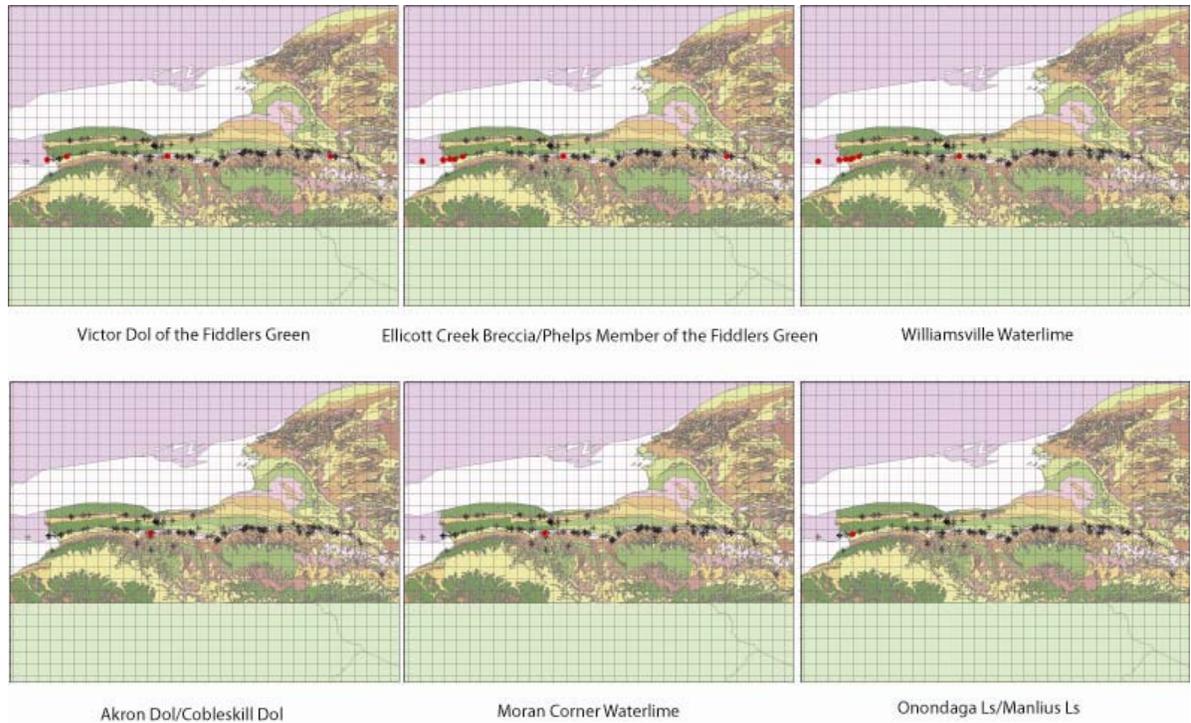


Figure 8. Temporal distribution of Eurypterus lacustris. Each map represents a different time slice, from oldest to youngest from left to right and top row to bottom. The blue dot indicates a locality with Eurypterus lacustris, while the other dots are other eurypterid localities.

Figure 9 presents the same progression for *Eurypterus remipes*. In general, there are fewer localities with *Eurypterus remipes* than with *Eurypterus lacustris*. Distribution during the Fort Hill time slice is limited to the western and central parts of the basin region. During the Victor time slice, distribution is now even among the western, central, and eastern parts. Even distribution remains during the Ellicott Creek Breccia /Phelps. During the Williamsville, the distribution has now shifted westward, with specimens present in the west and in the central areas. However, during the Akron/Cobleskill, the distribution is again even through the three regions. Finally, during the Onondaga/Manlius time slice, the species is present in the west and in the central regions.

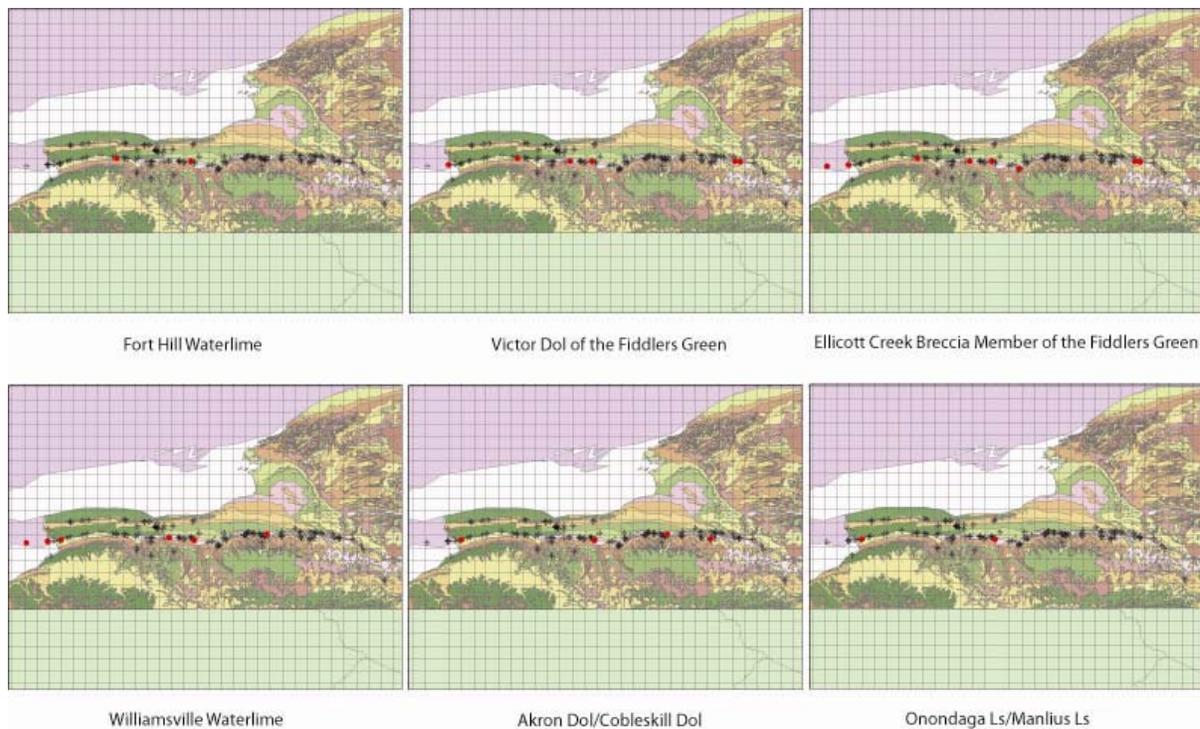


Figure 9. Temporal distribution of *Eurypterus remipes*. Each map represents a different time slice, from oldest to youngest left to right and top row to bottom. The blue dot indicates a locality with *Eurypterus remipes*, while the other dots are other eurypterid localities.

Lithology and Thin Section Analysis

Table 4 in the Appendix describes the lithological characters observed in the thin sections. In general, hand samples from each formation show some distinguishing characteristics, although all were fine-grained, micritic carbonates with a slightly varying mixture of calcite and dolomite. For example, within the 9 thin sections made from the Chrysler Limestone, 5 had strong reactions to 5% HCl, while 2 had slight reactions and 2 exhibited no reaction. In general, all the rocks were very fine grained, with almost the whole sample consisting of micritic, muddy matrix. The amount of visible grains ranged from 0-25% of the total slide, most of which was quartz silt. The texture of the rocks varied primarily with the formation sampled. The oldest unit sampled, the Syracuse Salt, could be distinguished by frequent silica and carbonate mud interbedding. The slightly younger Fort Hill Waterlime also had a high incidence of silica interbedding. Next, after a gap of time, the Victor Member of the Fiddler Green lacked a consistent texture, with some samples

consisting of almost pure micrite while some included granular material. The Ellicott Creek Breccia Member of the Fiddlers Green exhibited some mud clasts but otherwise showed no significant textural characteristics. Further into the Bertie Group, the Williamsville Waterlime and the Cobleskill Dolomite were almost all very fine muds. After the Bertie, the lithologies begin to include biological material. Some of the samples from the Chrysler show silica interbedding, as well as potential ostracod clasts. The lithology of the Thacher Member of the Manlius yields bioclasts, dolomite rhombs, calcite crystals, and silica silt. The bioclasts in the Thacher could be identified as ostracods and *Howellella* brachiopods in one sample. The Olney Member of the Manlius Limestone was similar to the Thacher. In addition to bioclasts and dolomite rhombs, relatively large calcite grains and lamination were found. Therefore, although the lithologies are all quite micritic with little overall siliciclastic input, some trends can be detected in thin section. Some photos of representative thin sections can be found in the appendix.

Discussion

Paleoecology

The presence and absence of eurypterids through time demonstrates some interesting trends in taphonomy and migration of eurypterids within this region of the Appalachian Basin. Based on **Figure 3**, there seems to be three pulses where the eurypterid community changed and many species entered the basin, as well as one possible regional extinction. These pulses are summarized in **Table 3**.

The first pulse of eurypterid invasions occurred during the deposition of the Rochester Shale and the Sconodoo, when specimens of Mixopteroidea were first found. In general, Mixopteroidea were not very diverse, with only 4 species categories present. Nonetheless, two of them, the genus-level *Paracarcinosoma* sp. and *Paracarcinosoma scorpionis*, are represented by over 100 specimens. The other two, *Mixopterus multispinosus* and *Rhinocarcinosma* sp., were both less abundant. With the exception of *Mixopterus multispinosus*, which only was present in the Vernon Shale, the other Mixopteroidea

Pulse	Units	Previous Diversity	New Diversity	Origination	Species (first occurrence)	Abundance
1	Rochester Shale	0	3	3	<i>Rhinocaracinosoma</i> sp., <i>Paracaracinosoma</i> sp., <i>Paracarcinosoma scorpionis</i>	Low
2	Pittsford Shale of the Vernon Shale	3	12	9	<i>Hughmilleria socialis</i> , <i>Pterygotus</i> sp., <i>P. sarlei</i> , <i>Erettopterus osiliensis</i> , <i>E. sarlei</i> , <i>Salteropterus</i> sp., <i>Waeringopterus apfeli</i> , <i>Mixopterus multispinosus</i> , <i>E. lacustris</i> , <i>E. remipes</i> , <i>E. pittsfordensis</i> , <i>Eurypterus</i> sp.	High
3	Ellicott Creek Breccia/ Phelps of the Fiddlers Green and the Williamsville Waterlime	7	14	7	<i>Pterygotus macrophthalmus</i> , <i>P. cobbi</i> , <i>Acutiramus cummingsi</i> , <i>Eurypterus dekayi</i> , <i>Erieopterus</i> sp., <i>Erieopterus macrophthalmus</i> , <i>Dolichopterus</i> sp., <i>D. herkimerensis</i> , <i>D. jewetti</i> , <i>D. macrocheirus</i> , <i>Buffalopterus pustouloosus</i> , <i>Clarkeipterus testudineus</i> , <i>Borchgrevinkium</i> sp.	High

Table 3. Summary of the three pulses seen in the eurypterid fossil record. Diversity indicates increase in species and was gathered from Figure 3. Abundance is from Figure 4.

were present in the basin for a long time, until the Williamsville. This pulse is distinct in that it marks the first occurrence of eurypterids in the basin. As a result, the diversity increase is large, but diversity and abundance are comparatively much less than the later pulses.

The second pulse was the Pittsford Shale Member of the Vernon Shale Pulse, where almost all Pterygotoidea species and some Eurypteroidea first entered the basin. *Hughmilleria socialis* and both species of *Erettopterus* first occur in this member, as well as *Salteropterus* sp. and one species of *Pterygotus*. However, all Pterygotoidea species that were present in the Pittsford Shale Member of the Vernon Shale were exclusively present in the Vernon Shale. This is also true for *Waeringopterus apfeli*, which was found in the Vernon Shale and in the Syracuse Salt. Eurypteroidea, however, are more widely distributed in time. Only the *Eurypterus* genus was involved in this pulse. Although *Eurypterus pittsfordensis* was only present during the Vernon, but both *Eurypterus remipes* and *Eurypterus lacustris* arrived at the Syracuse and persisted until the Onondaga/Manlius. The exception to this pattern is *Eurypterus dekayi*, which was only present much later, at the Williamsville.

The third pulse occurred at the Ellicott Creek Breccia/Phelps Member of the Fiddlers Green and after. This event is more widespread among the superfamilies as the more diverse

Pterygotoidea, Eurypteroidea, and Stylonurina species were involved. Of the Pterygotoidea, *Pterygotus macrophthalmus* and *Pterygotus cobbi* entered the basin. *Acutiramus cummingsi* appeared later, in the Williamsville. Of the Eurypteroidea, both the genus *Dolichopterus* and *Buffalopterus pustulosus* were part of this pulse. There were also other species that entered later, including species of the genus *Erieopterus*, that could potentially be a fourth pulse if more new species are found in the Chrysler Limestone. Finally, the sole representative of the Stylonurina, *Clarkeipterus testudinus*, appeared in this third pulse.

While many species periodically became regionally extinct during the Silurian, at only one point does there seem to be a pattern. Although not as clear, there seems to be a regional extinction event after the Williamsville was deposited; of the 28 species categories studied, eight disappeared from the basin after the Williamsville. However it is not clear if this was because of habitat change during the Oxbow, when no species are present at all, or later on during the Akron/Cobleskill.

Gaps or absences occur between the pulses (**Figure 2**). For example, there are few specimens of any taxa found between the Ilion Shale and the Sconodoa. Using the ‘ghost’ ranges (**Figure 3**), however, it can be inferred that eurypterids were present in the basin. To explain this, there could have been a mass migration of practically all eurypterids to another part of the basin. However, this seems unlikely, especially since other organisms are found in the basin at these times (**Figure 6**). Therefore, it is most likely that this absence is the result of taphonomic bias, rather than a migration of almost all eurypterids to other regions of the basin. This is probably true given that other shelly organisms found in the basin have a higher preservation potential than eurypterids, and perhaps the taphonomic conditions favored shelly preservation rather than the cuticle preservation that characterizes the eurypterid fossils. Another gap occurs between the Victor Member of the Fiddlers Green and the Syracuse Salt. In this case, other organisms are absent. This lack of life could indicate an inhospitable environment to many life forms, including the eurypterids, which prevented these organisms from living here. This may not be surprising given the enormous salt crystals found in the Syracuse, indicating extreme hypersalinity. Therefore, it does seem likely that taphonomy is important, supporting Braddy’s mass-molt-mate hypothesis that these were not areas where eurypterids spent most of their lives.

The entrance pulses also seem to coincide with pulses in increased overall abundance, especially pulse 2 (Pittsford pulse) and 3 (Ellicott Creek Breccia /Phelps pulse). The three most abundant and diverse stratigraphic units were the Pittsford Shale, the Ellicott Creek Breccia /Phelps, and the Williamsville. In addition to having many species enter at the Pittsford and the Ellicott Creek Breccia /Phelps, the greatest abundance of individual species also occurs in these units. Therefore, it seems likely that some environmental variable in the basin changed, where many new species entered and did so in large numbers. Examination of the lithologies using thin sections does not explain this pattern, as the Ellicott Creek Breccia thin sections did not show any distinguishing characteristics. However, this analysis is not complete as the crumbly Pittsford Shale could not be made into thin sections. The abundance graph (**Figure 4**) also shows that overall abundance generally dropped after each pulse, within three time slices. This seems likely to be due to changes in lithology. For example, at the third pulse, both the Ellicott Creek Breccia /Phelps and the Williamsville have very high abundances, yet during the Akron/Cobleskill and after, the abundance dropped significantly. The lithology also changed, from a dolomitic regime to a limestone regime. This could indicate shifts in sea level, gradually changing the environment of deposition. A surprising conclusion is that although some species had a long temporal distribution, their abundance peaked at only one time slice. This is true for the three most abundant species, *Eurypterus lacustris*, *Eurypterus remipes*, and *Hughmilleria socialis*. This could be an indication of evolving species dominance, as species compete for resources in the basin.

Diversity and abundance information on the superfamily level shows that the eurypterids in the Appalachian Basin were dominated by Eurypteroidea, and more specifically, the genus *Eurypterus*. Of the specimens for each time slice, the largest proportion consistently belonged to this superfamily. The Pterygopteroidea, while having a long temporal range, only dominated with *Hughmilleria socialis* in the Pittsford Shale member and to some degree in the Williamsville and Ellicott Creek Breccia /Phelps. The Mixtoperoidea are surprisingly abundant despite their low diversity, although only during the beginning of pulses 2 and 3. The Waeringopteroidea and the Stylonurina are represented by only one species in the basin, but *Waeringopterus apfeli* is relatively abundant during the one time slice it appears.

Conclusions about taphonomy are not completely clear. While these environments are hypersaline, many other species were found along with eurypterids in these stratigraphic units (**Figure 6**). In addressing the question about whether these are taphonomic assemblages or represent the eurypterids' true habitat, it seems more likely that this is a taphonomic assemblage. The presence of other species does not support the idea that eurypterids preferred hypersaline environments, because many of them would not have been able to survive in such saline waters. However, the number of these other organisms is generally very low, especially when considering their abundances in other marine assemblages of this time period. Many of the other taxa, such as brachiopods, are not body fossils but molds, while the eurypterid fossils are exoskeleton cuticle, thought to be chitin (Gupta et al., 2007). This indicates that preservation was influenced by the environment or by diagenesis; while calcareous shells were dissolved, eurypterid exoskeletons survived. The chemistry that allowed for this preservation could be an indication of the environment in which the fossils were deposited. As a further complication, it was very rare to see eurypterid fossils mixed in with other organisms; for example, the *Howellella* bed in the Thacher Member of the Manlius is a highly concentrated, few centimeter thick bed. There was no mixing with the eurypterid fossils found above and below. This separation of eurypterids and other organisms seems to indicate that these are taphonomic assemblages. This could be an indication of Braddy's mass-molt-mate hypothesis, or simply a fact that eurypterids were better preserved in these environments. Further study to develop a hypothesis of taphonomy could include an analysis of the specimens in the YPM to see if there is any evidence of transport.

Changing environments in the basin could also affect the taphonomic trends in the basin. Based on the well preserved but incomplete specimens found in the Bertie group localities, many consider these fossils to be molt exuviae rather than carcasses (Braddy, 2001; Tetlie, Brandt, & Briggs, 2008). While many of the specimens have been found in the Bertie group, changes in eurypterid species before and after the Bertie group could also be an indication of a different taphonomic environment. For example, it has been observed in other studies that most of the *Eurypterus* species disappear at the Silurian/Devonian boundary after the Bertie group, and younger units yield *Erieopterus* and *Acutiramos*, as well as the brachiopod *Howellella*, and this is thought to be an indication of a transition to a more

marine environment (Tetlie, Brandt, & Briggs, 2008). Therefore, it is also possible that as the depositional environment changed, so too did the taphonomic conditions, although there is currently not enough data to make such conclusions.

Paleobiogeography

One of the limiting factors of the biogeographic analysis was the outcrop pattern of the basin. As is evident in **Figure 7**, the Silurian and Devonian outcrops of the basin run parallel to the basin shore, and generally are not very thick. These sediments also dip toward the south. As a result, the environments that can be examined during this time period only include shallow marine deposits, since the inland sediments have been eroded away and the deeper marine sediments have not yet been exposed. This outcrop pattern makes it difficult to make any conclusions about the paleogeography of the basin. Luckily, the paleogeographic reconstruction also shows that there was no geographic sampling bias involved; the fact that specimens were collected near NY-90, which runs east-west, was not due to sampling convenience but represents the outcrop pattern. The map also shows what was confirmed by thin section analysis. Practically all of the lithologies of this region are carbonate rocks with minor siliciclastic input. Occasional silt input and bedding are probably due to sea level progradation and regression. All samples for thin section analysis were taken only from eurypterid horizons. Despite varying in time and geography, the lithologies presented little variation: very muddy, with few carbonate crystals and occasional siliciclastic input. With the exception of the Devonian units, there are few bioclasts, and little texture beyond occasional laminae and interbedding. An end-member pattern of silty carbonaceous muds at one end of the spectrum and bioclastic input at the other does appear. This could correlate with time, as the oldest unit studied in thin section, the Chrysler, had some silica silt and carbonate mud interbedding. The units of the late Silurian, such as the Williamsville and the Ellicott Creek Breccia, were almost completely carbonate muds that were too micritic to distinguish their mineral composition. The youngest units, the Thacher and Olney Members of the Manlius Limestone, had a high occurrence of bioclasts. This basic pattern could be an indication of changing basin sea level conditions.

The GIS maps were also used to estimate geographic range. At first glance, it may seem as if eurypterids are concentrated at the western end of the region (**Figure 7**). However, this is actually a reflection of where outcrops can be found. For each stratigraphic unit, the percentage of map grids that had eurypterid specimens was calculated. This percentage represents the pervasiveness of eurypterids in that time slice. Of note is that the percentages were high; for the most part, if eurypterids are present in a unit, they are present almost everywhere that the unit is exposed. This is not entirely surprising because each time slice essentially is the horizontal equivalent of the same environment. This is true for the entire area, and not localized. There was no pattern between eurypterid prevalence and the pulses. In another attempt to use the GIS maps, the total number of specimens for each category was divided by the number of map grids that they were found in, providing a measure of approximate density (species/area). For this parameter, the dominance of the genus *Eurypterus* is evident. The density of all the species in this genus was high or medium except for *E. dekayi*. For the most part, the relative density for each species category was very similar to their abundance levels. Because the density takes into account the area range in which the species has been found, it demonstrates that the abundance patterns described earlier is not a factor of belonging in a formation that had many outcrops. In other words, the density patterns were normalized for area. Since the abundance and density patterns seem to be similar, the abundance data described earlier are not a relic of outcrop exposure but reflect the community ecology of the species. A result of this could be indications of the eurypterid trophic structure of the basin ecology. All eurypterids were predators, and predators typically can only sustain smaller populations than their prey (Gotelli, 2001). Density can also give insight into the trophic structure within the eurypterids as well. The pterygotids are the largest eurypterids found, and their enlarged, toothed chelicerae indicate an especially developed predatory morphology (Ciurca & Tetlie, 2007). Therefore, their relatively lower densities could be because of their larger size and ecological role as a secondary predator, maybe even of other eurypterids. The high density of *Eurypterus* could be an indication of a lower trophic position; perhaps their prey was smaller. Further analysis of body size and morphology gathered from the specimens in the YPM collection may refine our understanding of community ecology.

The maps were also used to examine the temporal geographic distribution of *Eurypterus lacustris* and *Eurypterus remipes*. These two were chosen because they were the most abundant. They also had the longest temporal range, and were the only species that were present in more than four stratigraphic units (not considering the genus-level categories). As mentioned before, the genus *Eurypterus* was also the most dominant in this region of the Appalachian Basin. The geographic distribution of *Eurypterus lacustris* does seem to change through time. During the middle Silurian, specimens can be found throughout the region. As time progresses, the species concentrates in the western areas. *Eurypterus remipes* follows a slightly different pattern. Initially it is distributed in the west and central areas, then expanding to all areas. At the final time slice, however, it has once more become concentrated in the western and central basin.

Further work with this data set includes a cluster analysis to better gauge the differences in the stratigraphic units. This will provide a more concise view of the ecology and environment of the region, as well as a better understanding of how the sea level patterns may have affected eurypterid ecological parameters. Perhaps this can shed light on what environmental changes allowed the pulses described above to occur.

Summary

This study took a close look at the paleoecology and paleobiogeography of the eurypterids in the upper Appalachian Basin. Presence and absence data were used to determine the temporal ranges for each species. From this data, a pattern of eurypterid pulses could be detected. The abundance and diversity data also supported these pulses, characterized by invasions by new species, and drastic increases in diversity and abundance. The diversity and abundance data also demonstrated the dominance of the genus *Eurypterus* in the basin. GIS was used to map eurypterid localities and study the geographic distribution for each. It was found that distributions were quite even; if eurypterids were present in a time slice, they were pervasive throughout the outcrops of that stratigraphic unit. Specimen density was also calculated using the data on the maps; it was found that the density of a species (specimens/unit area) mirrored the abundance as well. It is difficult to make any

conclusions about the nature of the fossil specimens themselves. It seems likely that these are taphonomic assemblages, but such a conclusion is not yet clear.

From these analyses, a basic understanding of Appalachian Basin eurypterids was formed. There seemed to be three pulses where the basin environment became favorable for diverse eurypterids to enter in large numbers. Within this region of the basin, the eurypterids were evenly distributed, further proof that this area was quite homogenous. This was also supported by a study of thin sections. From each perspective of the basin ecology, it was obvious that the superfamily Eurypteroidea, and more specifically, the genus *Eurypterus* dominated the abundance, diversity, range, and density of the eurypterids in Silurian New York. Although it is difficult to make interpretations about the true biogeography of the basin due to the outcrop patterns, further study may shed more light on the paleoecology, including why the pulses occurred.

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Appendix

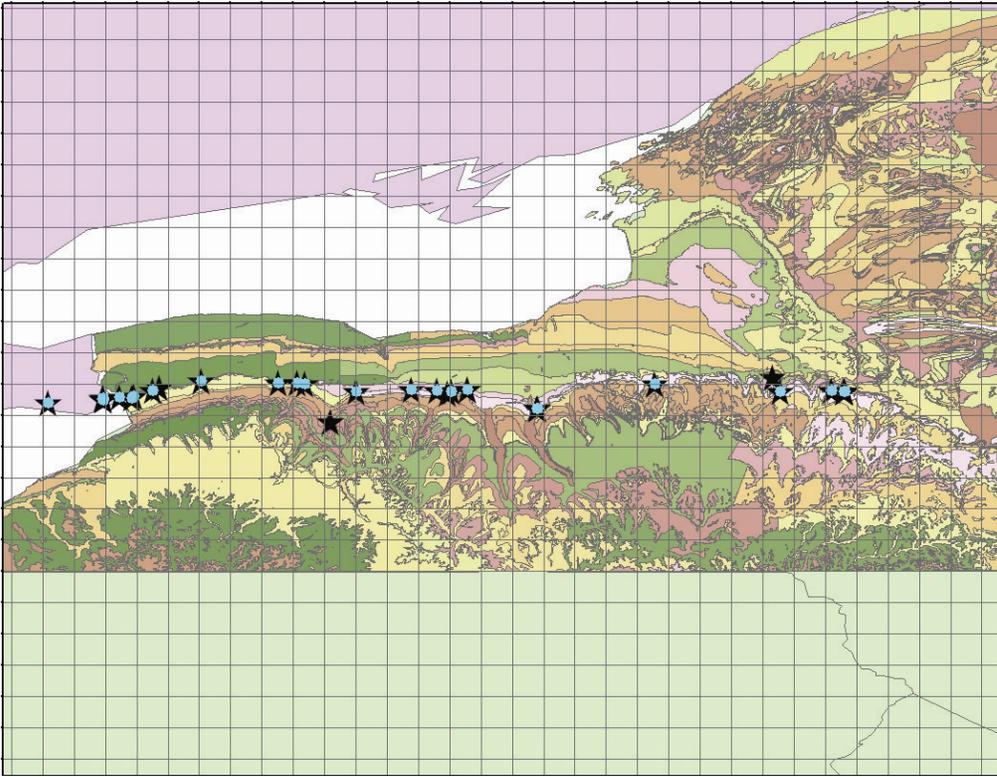


Figure 10. Geographic range for the Ellicott Creek Breccia/Phelps. The star represents the outcrops for this time slice, while the teal circles represent the localities where eurypterids were found. The grid system was used to estimate range. The pervasiveness of eurypterids in the ECB/Phelps was calculated by dividing the eurypterid grids by the total grids.

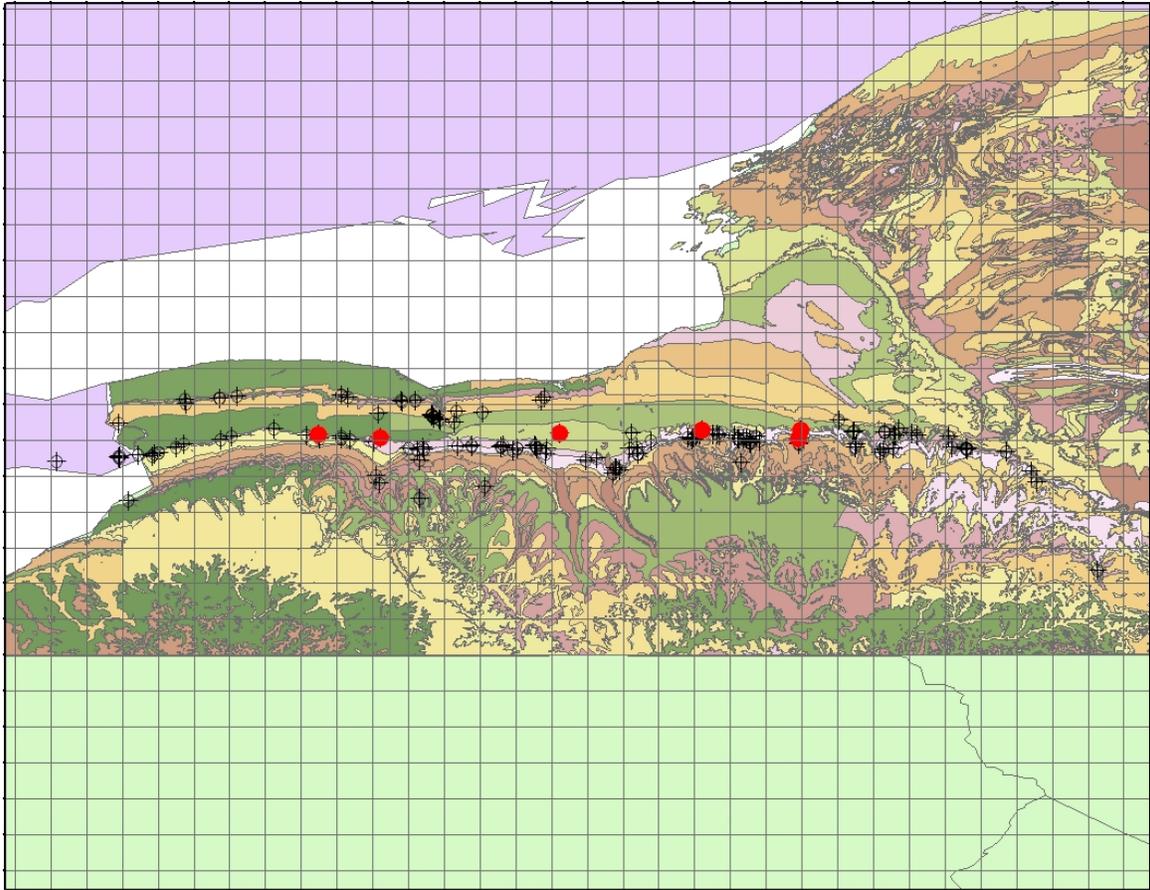


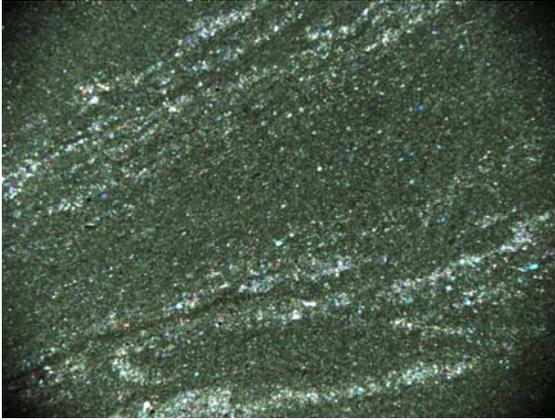
Figure 11. Geographic range for Waeringopterus apfeli. The dots on the map represent localities where this species was found. The grid was then used to estimate the range for this species. Density was calculated by dividing the total number of species by the number of grids.

Formation	Acid	Grains				Mud	Notes
		Silt	Calcite	Dolomite	Lithics		
Manlius-Olney	yes				100		dark blob with fossils?, large calcite grains, carbonate matrix with lineated fabric
Manlius-Olney	yes	5	40	30	25	25	bioclasts in beds (10% total), dolomite rhombs
Manlius-Thacher	yes	3			97	99	3 very large, well developed calcite grains
Manlius-Thacher	yes	20	20		60	70	bioclasts (15%), some silica silt, highly calcitic
Manlius-Thacher	yes	5	20		75	20	ostracods, brachs, laminated bioclast layers (40%), bedded
Manlius-Thacher	yes	15	40	30	15	20	some determinable Howellella brachiopods, lots of dolomitized bioclasts, dolomite rhombs, silt
Chrysler	slight	3	30		67	99	silica and carbonate mud interbedding
Chrysler	yes	15	25	45	15		bedding, coarse-grained silica, dolomite rhomb
Chrysler	no	7	40		53	70	
Chrysler	no	20			80	75	stylolites, silica and carbonate mud interbedding
Chrysler	slight	25	10		65		silica and carbonate mud interbedding, dolomite rhomb
Chrysler	yes	10	90		0	90	porous
Chrysler	slight	20	10		70	75	ostracods?, dolomites
Chrysler	yes				100	30	laminated brachs, ostracods
Chrysler	yes	10	30		60		bedded bioclasts (brachs?) 30%, silty lamina
Chrysler	yes				100	99	
Akron	yes	20	35	25	20	80	
Cobleskill	yes	3	45		52	99	slight coarser matrix
Cobleskill	no		50		50	99	poor lamination
Cobleskill	yes	3	40		57	99	some silica lamina
Cobleskill	yes				100	99	porous
Cobleskill	yes		40		60	99	silica and carbonate mud interbedding
Cobleskill	slight		30	30	40	99	sparry texture
Cobleskill	slight				100	99	stylolite, almost pure dolomite with some rhombs (no stain)
Cobleskill	yes		40		60	90	predominantly mud clasts, some potential bioclasts
Williamsville	no	5	30		65	99	some silica and carbonate mud interbedding
Williamsville	no		30		70	99	
Williamsville	yes	5	45		50	95	
Williamsville	slight		30		70	99	
Williamsville	yes		30		70	99	bedding of unidentified black grains
Williamsville	slight	15	40		45	80	
Williamsville	no	20			80	80	large silica grains
Williamsville	slight	3	20		77	90	
Williamsville	no		30		70	99	fine mud lamina
Williamsville	slight	5	25		70	95	
Williamsville	no				100	99	
Williamsville	yes	3	50		47	95	
Williamsville	no	10	20	35	35	32	a few dolomite rhombs

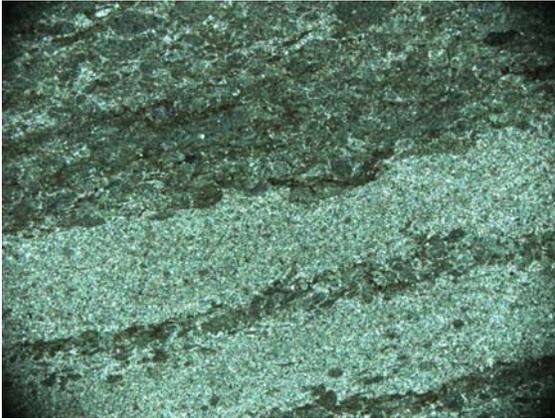
FG-Ellicott Creek	yes		20		80	99	
FG-Ellicott Creek	no		50		50	95	mud clast lamina
FG-Ellicott Creek	no		25		75	95	rounded mud clasts
FG-Ellicott Creek	no	10	40	15	35	32	bedding, silt
FG-Ellicott Creek	slight	10	25	10	55	45	silt, mud clasts
FG-Ellicott Creek	no	5	30	30	35	35	
FG-Ellicott Creek	yes		40	20	40	39	black seams
FG-Ellicott Creek		15	15	10	60	60	
FG-Ellicott Creek		3	50	10	37	22	mottled surface and scratches
FG-Ellicott Creek	no	1	25	25	49	48	
FG-Ellicott Creek	yes				100	95	lamina
FG-Victor	yes	3	70		27	95	mud veins?
FG-Victor	yes		80		20	99	
FG-Victor	no	5	40	55	0		silica and carbonate mud interbedding
FG-Victor	yes				100	99	
FG-Victor	yes				100	99	dolomitic rhombs
Fort Hill	no	20	10		70	70	silica and carbonate mud interbedding
Fort Hill	yes	20	15		65	80	silica and carbonate mud interbedding
Fort Hill	slight	20	15	20	45	52	
Fort Hill		10	0	10	80	80	silica bedding
Syracuse	no	3	15		82	99	interbedding, rounded mud clasts with some silica in the matrix
Syracuse	no	20	20		60	80	well formed silica beds interbedded with mud
Syracuse	slight		10		90	95	silica and carbonate mud interbedding
Syracuse	yes		30		70	99	stylolites, bedded subrounded mud clasts, calcite crystals
Syracuse	slight	10	10		80	90	silica and carbonate mud interbedding
Syracuse	slight	5	20		75	99	mud lamina
Syracuse	no	7	20		73	95	
Syracuse	no	5	20	20	55	50	

Table 4. Thin section analysis. Observations made from thin sections taken from selected eurypterid horizons.

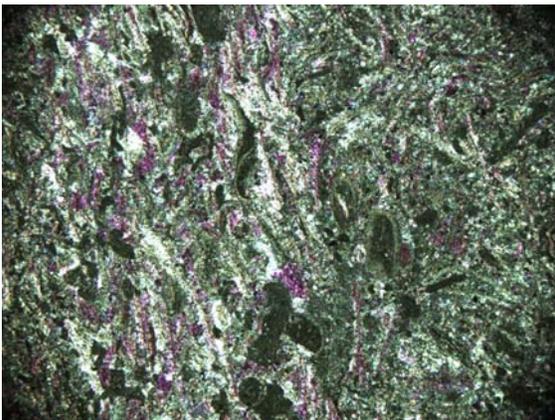
Representative Thin Section Photos



Chrysler Limestone, 40x, 25% zoom



Ellicott Creek Breccia Member of the Fiddlers Green Formation, 40x, 25% zoom



Thacher Member of the Manlius Limestone, 40x, 90% zoom

Photos from field trip, November 2008



Photo of the Olney Member of the Manlius Limestone, near Clockville, NY



Photo of the Williamsville Waterlime, Glen Park, Buffalo, NY



Conchoidal fracturing at the top of the Ellicott Creek Breccia, Neid Road Quarry