

The Silurian Experience

Second Edition



*Paul Chinnici
and
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A pictorial documentation of the fossils from the Rochester Shale formation at the Caleb Quarry in Western New York State.

Stratigraphy and Paleoenvironments of the Rochester Shale
in Western New York.

- By Carlton E. Brett

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Introduction

Extraordinary fossil assemblages, sometimes called fossil Lagerstätten (Seilacher et al., 1985), are celebrated for the richness of detail they provide about ancient life. Despite their rarity, Lagerstätten (literally fossil mother lodes) yield significant insights into paleobiology and ancient organism communities. The fossil assemblages from the Rochester Shale, illustrated in this book, well qualify for that elite category as they reveal exquisite snapshots of Silurian life.

The Rochester Shale was already, and justifiably, famous for its fossil fauna in the days of James Hall. In 1852 Hall described the prolific fossil assemblages of the Silurian in the Fourth District (western New York). He mentions collecting a bushel basket full of the nut-like thecas of the cystoid *Caryocrinites ornatus* during excavation for the locks of the Erie Canal at Lockport. Hall also acquired the extensive collections of Colonel Jewett of Lockport, which also contained many new species. Among the more than 300 species described in this great monograph about two thirds were from the Rochester Shale. Many other researchers have discussed various aspects of the Rochester fauna (Ringueberg, 1882, 1886, 1888a, b; Bassler, 1901; Gillette, 1947).

Throughout much of its range, the Rochester Shale carries an abundant and diverse fossil assemblage, typically dominated by brachiopods and locally, bryozoans and echinoderms. In the outcrop belt of western New York and southern Ontario, Canada the lower Rochester and especially the upper Lewiston Member, contains thin lenses and biostromes of ramose (twiggy) and fenestrate (lacy) bryozoans (Grabau, 1901; Bassler, 1901). The fauna of these beds is exceptionally diverse and more than 200 species have been reported including diverse bryozoans, brachiopods, mollusks, echinoderms, and trilobites as well as a few corals, conulariids, dendroid graptolites, worm tubes and other miscellaneous rare fossils.

Although moderately well known, the fossil assemblages of the Rochester Shale were less famous than other middle Silurian echinoderm and trilobite rich beds such as those of the Much Wenlock Limestone of the Dudley area of Great Britain and the highly diverse assemblages of Wenlock and Ludlow age from the island of Gotland, Sweden (see Hess et al., 1999). The extraordinary preservation of Rochester Shale fossils at some levels has been documented in previous studies (Brett, 1978a-c; Taylor and Brett, 1996; Brett and Taylor, 1997). However, the most extraordinary assemblages were only revealed through excavation of large surface areas of bedding planes at the shale pit opened in the mid-1990s by Brent and Rose Caleb, in making a pond near Middleport, NY. It is those assemblages that are highlighted in this book. These assemblages not only provide extraordinary glimpses of Silurian life but an exceptional opportunity to document fossil occurrence, paleoecology and depositional processes of the lower Rochester shale. With this book, the Rochester biota and its occurrence is better documented than has ever been possible previously. This chapter is intended to provide an overview of the stratigraphy, geological setting and depositional environments of the Rochester Shale in western New York, as well as the taphonomy and paleoecology of the rich fossil assemblages with an emphasis on new insights from the exposures in the Middleport area.

Geologic Setting and Climate of the Middle Silurian Wenlock Interval

The Rochester Formation and associated sediments accumulated in the southern Subtropics at about 25 to 30°S in the Appalachian foreland basin (Cocks, 2001; Blakey, 2011) adjacent to carbonate platform environments to the west and northwest (in modern directions; Figure 1). Climates were relatively warm, typical of the Subtropics, and probably affected by easterly Trade Winds. In the mid-continent more arid environments existed and these conditions ultimately gave rise to deposition of evaporites such as gypsum and halite, especially in the Michigan Basin and later also in New York State. However, the climates in the foreland basin were probably somewhat more humid and rivers emanating from highlands to the southeast carried a load of eroded sediment into the adjacent basin. Tropical storms and hurricanes would have been typical of this area owing to high sea surface temperatures and their storm tracks took them across the northern end of the foreland basin in present day western New York.

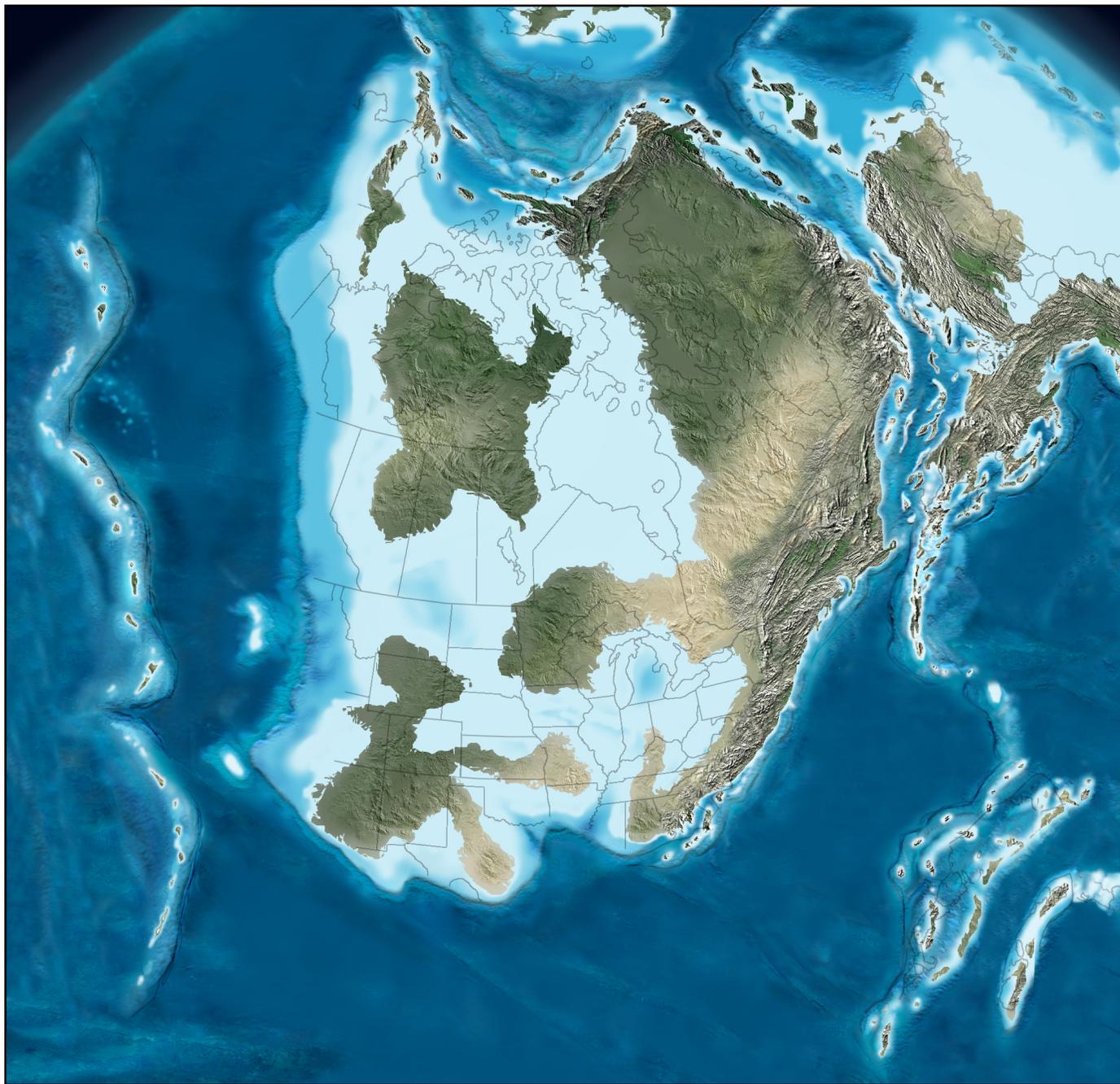


Figure 1

Palaeogeography of Laurentia (Ancestral North America) during late Silurian time.
Note the mountainous terrain to the east of New York.
Map by Ron Blakey, Colorado Plateau Geosystems, Arizona USA.
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Figure 2 - facing page

Correlated stratigraphic sections of the lower Rochester Shale (Lewiston Member) along the Niagara Escarpment in western New York from the Niagara Gorge in the west, to Brockport, NY in the east, approximately 60 miles (96 km), showing the widespread correlation of marker beds and units. Lettered intervals A to E refer to informal submembers of the Lewiston Member. Datum or reference horizon is Lewiston B-C submember boundary. Modified from Taylor and Brett (1996).

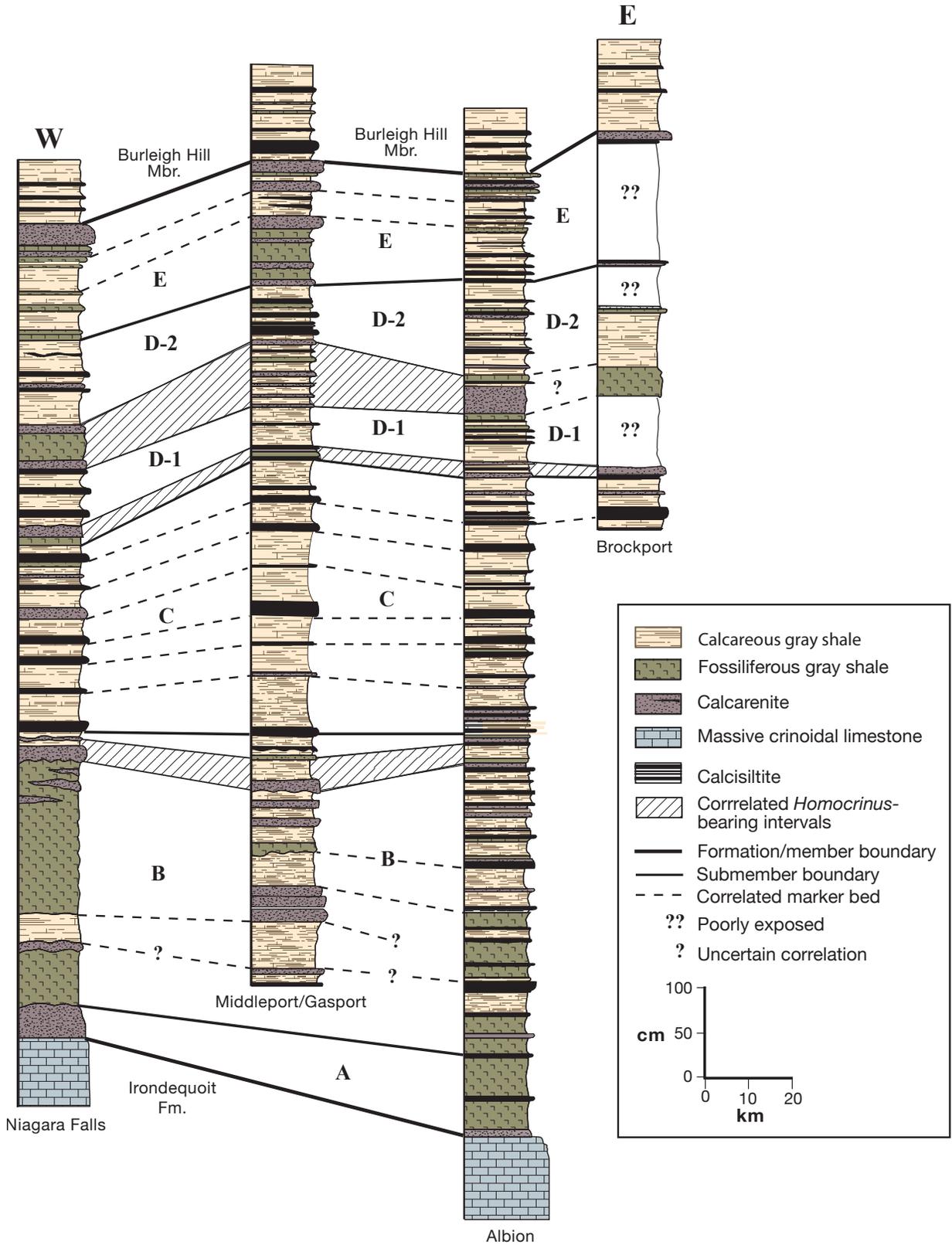


Figure 2

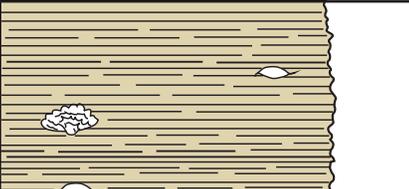
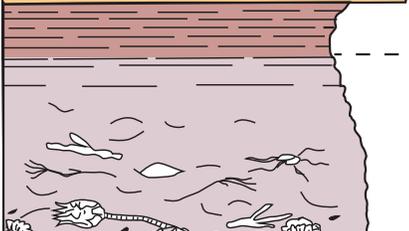
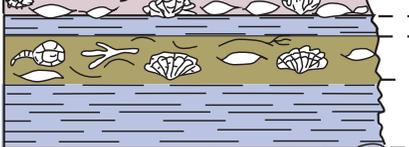
During the Middle to Late Ordovician Period, Laurentia or ancestral North America, collided along its southeastern side (essentially the modern east side) with the Taconic island arc, a series of volcanic islands. An accretionary wedge of sediments and volcanics off scraped from the Iapetus (Protoatlantic) was overthrust onto the edge of the continent (Ettensohn, 2008). The landmass was uplifted to Alpine heights and shed sediments onto Laurentia. By the middle Silurian the Taconic Mountains had largely been eroded to relatively low relief cutting back the supply of siliciclastic sediments and leading to deposition of "homegrown" limestone sediments in the basin. However, during the Wenlock Epoch a new collision was under way, with a narrow peninsula-like continental area, Avalonia, which now forms the parts of the Eastern Seaboard of Canada, impinging upon eastern Laurentia. Siliciclastic mud and silt comprising the Rochester Formation was shed from highlands produced during an early tectophase of the so-called Salinic Orogeny (Ettensohn and Brett, 1998; Ettensohn, 2008), which uplifted mountainous terrains to the east of present day New York State. This orogeny also produced gentle subsidence of the foreland basin that propagated to the northwest and permitted accumulation of a substantial thickness of muds, silts and sands. The fine-grained sediments that comprise the Rochester deposits graded to the east, near present day Utica, NY, with nearshore sands of the Herkimer Formation. Contemporaneous with the Rochester deposition, shallow water carbonate banks with minor patch reefs, somewhat like the modern Bahama Banks, existed in the midwestern regions of the Laurentian continent (Figure 1). Thus, Rochester muds interfingered with carbonate skeletal sands and silts to the northwest and locally shelly organisms, especially bryozoans and brachiopods, produced sufficient skeletal debris to form thin limestones.

Stratigraphy of the Rochester Shale

The Rochester Shale is a classic unit in North American stratigraphy, as the first formally designated formation. James Hall (1839) applied the name to a gray shale unit, about 100 feet thick, exposed below High Falls in the Gorge of the Genesee River at Rochester, NY. This designation effectively established the practice of naming stratigraphic units for well-defined type sections or reference localities, a practice that has been formalized in the North American Code of Stratigraphic Nomenclature. In this sense, the Rochester Shale, or Rochester Formation, is an icon of stratigraphy.

The Rochester Shale consists of medium gray, calcareous mudstone, which weathers shaly (marl of European usage) interbedded with lenticular to tabular, muddy limestones (packstones), as well as some clean, skeletal limestones with little mud (grainstones) and calcisiltites (beds composed of silt-sized calcitic grains). Much of the "shale" is barren or sparsely fossiliferous and in some localities much of the Rochester Formation is sparsely fossiliferous (Figure 2). The unit ranges in thickness from about 43 meters (140 feet) east of Rochester, NY to just 0.6 meters (2 feet) at Clappison Corner, Ontario prior to its pinchout to the northwest (Brett, 1983a, b). To the east of Syracuse, NY the Rochester Shale begins to interfinger with fine-grained sandstones and east of Utica, NY it undergoes a transition into the Herkimer Sandstone (Gillette, 1947), locally, a massive quartz sandstone (Zenger, 1971). Along the outcrop belt the Rochester Shale persists northwestward to near Hamilton, Ontario, despite strong thinning and in the subsurface, the unit is known in southern Ontario and northern Ohio (Figure 3); in southern Ohio and Kentucky its equivalent is mapped as an informal shaly member of the Bisher Formation (Brett and Ray, 2005). To the south it persists into Pennsylvania, Maryland, West Virginia and northern Virginia as a medium to dark gray shale unit. Thus, the Rochester Shale was a very widespread interval of mud and silt deposition over eastern Laurentia (ancestral North America).

The Rochester Shale sharply, but conformably (no major time gap) overlies a 2 to 4 meter (6.5 to 13 feet) thick interval of fossiliferous limestone, termed the Irondequoit Limestone (Figure 2), a dolomitic packstone to the west, crinoidal packstone and grainstone (i.e. with or without muddy matrix between the fossil grains) in western New York and muddy packstone near Rochester, NY. The Rochester Formation is overlain, throughout western New York, by the DeCew Formation, a fine-grained, silty to sandy, laminated dolostone, typified by spectacular soft sediment deformation and slumping (Brett et al., 1990; McLaughlin and Brett, 2006).

UNIT	SCHEMATIC SECTION	T (cm)	DESCRIPTION
V		2	Barren to sparsely fossiliferous mudstone, shale
		3	Fossiliferous mudstone (<i>Striispirifer</i> , <i>Homocrinus</i> association)
IVA		3	Barren shale; silty transitional zone at base with <i>Caryocrinites</i>
		6	Planar and, hummocky cross-laminated burrowed calcisiltite band
IV		2.5	Barren, silty shale
III		4	Fossiliferous silty mudstone with basal shell layer (<i>Striispirifer</i>) Main <i>Homocrinus</i> -bearing horizon
		0.5	Barren shale
II		1.5	Fossiliferous mudstone, basal shell layer, <i>Homocrinus</i> association
		2	Barren shale
I		5	Bryozoan biostrome; abundant ramose bryozoans in mudstone matrix (top of B submember)
Base of Section			

Symbols:

	Planar laminae		Brachiopods (plane and cross section)		<i>Homocrinus</i>
	Cross laminae		Ramoses bryozoans (plan and cross section)		<i>Asaphocrinus</i>
	Unbedded mudstone		Burrows		<i>Caryocrinites</i>

Figure 3

Detail of stratigraphic section showing the transition between Lewiston B and C submembers, in the "*Homocrinus* bed" based on a section excavated at Lockport, NY.

The Rochester Shale of western New York was formally subdivided into two members, the Lewiston and Burleigh Hill, by Brett (1983a, b). The lower, or Lewiston Member, was named for exposures along the east side of the Niagara River Gorge about a mile south of the village of Lewiston, Niagara County, NY. Here and elsewhere, the member consists of calcareous shale and fossiliferous, muddy limestone. The upper, or Burleigh Hill Member as recognized for a large road cut exposure along Burleigh Hill Road at the Niagara Escarpment near Thorold, Ontario, Canada. This interval consists of about 10 meters (30 feet) of barren to sparsely fossiliferous calcareous to dolomitic shale with thin dolomitic calcisiltite beds that increase in thickness and frequency upward. This member has very few fossiliferous limestone beds and bears a sparse, low diversity fauna, with small, thin-shelled brachiopods, *Amphistrophia*, *Coolinia*, as well as the trilobites *Dalmanites limulurus* and *Trimerus delphinocephalus*, but generally lacking bryozoans and echinoderms.

Brett (1983a, b) further divided the Lewiston Member into five informal submembers, designated Lewiston A-E (Figures 2 and 5). The Lewiston A represents approximately 1 meter thick transitional facies of muddy limestone and very calcareous shale at the base of the formation which is characterized by a fauna of atrypids, *Eoplectodonta* and large *Leptaena* and some unusual echinoderms; it is less rich in bryozoans than overlying mudstones. Locally, small mounds of micritic limestone and leaf-like fistuliporoid bryozoans protrude upward from the Irondequoit Limestone into the Lewiston A submember. Lewiston B consists of lenses of medium dark gray, muddy, bryozoan-rich limestone (packstone) and interbedded sparsely fossiliferous, calcareous mudstone; in most localities the B is about 5 meters thick and displays a middle portion that is more sparsely fossiliferous mudstone. Upper and lower portions tend to yield specimens of the rhombiferan cystoid *Caryocrinites* and the coronoid *Stephanocrinus angulatus*. The transition of the Lewiston B into overlying C beds is abrupt but typically marked by a distinctive thin interval (typically < 10 cm) with exceptionally preserved crinoids, cystoids and other fossils. Because this interval typically shows articulated specimens of the tiny disparid crinoid *Homocrinus parvus*, it has been informally termed the *Homocrinus* beds (Figure 3). Lewiston C is a distinctive sparsely fossiliferous interval characterized by an absence of lenticular bryozoan limestone and the presence of abundant thin, tabular, laminated calcisiltites. This portion of the Lewiston closely resembles the upper Rochester or Burleigh Hill in lithology and fossil content. The D submember rather closely mirrors Lewiston B with lenses of bryozoans, mainly *Chilotrypa* and bedding planes covered with the brachiopod *Striispirifer niagarensis*. *Caryocrinites* is locally abundant again at this level (Figures 1 and 2). Lewiston E corresponds with the "bryozoa beds" of Grabau (1901), a package of about 1-2 meters of stacked bryozoan-rich limestones with abundant ramose as well as fenestrate bryozoans and thin calcareous shale and a diverse assemblage of brachiopods, echinoderms, and trilobites. The upper contact of the Lewiston E beds with the overlying basal Burleigh Hill Member is typically very sharp; the highest bryozoan-rich limestone is abruptly overlain by barren dark gray shale. The five divisions of the Lewiston Member have been recognized approximately from Brockport, NY westward to near Jordanville, Ontario and the position of the E beds or "bryozoa beds" can be correlated still farther east and west.

The Rochester Shale is of middle Silurian age, belonging to the early Sheinwoodian Stage of the Wenlock Series - both terms derived from the classic Silurian in the Welch Borderland area of Great Britain. It is, in part, equivalent to the rather similar Coalbrookdale Shale of England, while the underlying Irondequoit Limestone is equivalent to a rather similar Buildwas or Woolhope limestone in Britain. These correlations are based upon the occurrence of conodonts, tiny tooth-like elements of small, eel-like proto-vertebrate animals. These tiny (< 1 mm) apatite (calcium phosphate) elements can be extracted from limestones and limey mudstones like the Rochester Shale, using weak acids such as muriatic acid to dissolve the calcium carbonate and release the conodonts. Conodonts of the *Kockellella ranuliformis* and *Ozarkodina sagitta rhenana* zones are present in the Rochester Shale with the boundary of the two zones occurring approximately at the upper part of the Lewiston Member (Cramer et al., 2005). These conodont species also occur in the type area of the Silurian in England and permit age assignment. The base of the Sheinwoodian is presently dated at approximately 431 to 433 million years old based upon U/Pb radiometric dating of zircon crystals obtained from volcanic ash layers close to the boundary with the underlying Telychian Stage of the Llandovery Series (Melchin, 2012). The Rochester deposition may record approximately a million years of geologic time.

Taphonomy of Rochester Shale Fossils

Taphonomy is the study of processes and patterns of fossil preservation. The exquisite fossils of the Rochester Shale have inspired a number of studies of taphonomy or fossil preservation (see Taylor and Brett, 1997). Distinctive modes of preservation typify different groups of fossils. Calcitic fossils, such as brachiopods, bryozoans, echinoderms and corals tend to preserve very well, with much detail except in areas where the Rochester Shale has undergone late stage dolomitization; there, the fossils tend to be "ghosted" (shells partially dissolved) and their detail obscured. Originally aragonitic fossils, such as some bivalves, tend to be poorly preserved, highly flattened molds. Most beds also show strong compaction of fossils, which has deformed them to varying extents.

Biostratinomy includes the study of processes that are imposed upon organic remains essentially from the death of organisms to their final burial; these include mortality itself and necrotic (decay) processes. Sources of organic remains include both normal and mass mortality as well as the shedding of parts during the lifetimes of some types of animals, such as molt parts of trilobites. Rarely, skeletons are buried precisely in life position and there are examples of probable live burial in the Rochester Shale, including complete cystoids that are simply toppled where they stood. More commonly, skeletal remains may be reoriented. Bodies or skeletons may become preferentially oriented by currents or waves or even by bioturbation (burrowing and other disturbance by organisms) prior to burial. The dish-shaped valves of brachiopods are most stable in convex up orientations and are commonly preserved in convex upward pavements of *Striispirifer* valves (Figures xxvii - xxix and 93). Rarely, when valves are suspended by storm waves and allowed to settle from water they will flip and land convex downward. The occurrence of edrioasteroids on the undersides of convex downward shells from the Rochester Shale implies such a mode of emplacement; the shells were lifted off the seafloor at the final moment and then re-settled burying the edrioasteroids on the bottom side (Brett, 1983).

Fossils with a long axis commonly show a slightly to strongly preferred alignment. This may affect conical shells such as cephalopod, which tend to rotate such that their long axis parallels the current direction with the apex pointing upstream. Multiple specimens of *Dalmanites* trilobites on some bedding planes appear to show a high degree of parallel alignment (Figures xxvi and 395). These patterns may reflect slight current orientation of dead carcasses in the aftermath of storms during which gradient currents flowed basinward following storm surges.

Soft tissues degrade very rapidly upon death even in anoxic settings; connective tissues are somewhat more resistant than most soft parts but still tend to breakdown in days to months, releasing articulated skeletal parts. Brachiopods had various potentials for disarticulation. In spiriferids like *Striispirifer* the pedicle and brachial valves would have become readily separated after death. In contrast, the interlocking hinge teeth of rhynchonellid and some atrypid brachiopods (Figures 98 and 99; 69 and 70) would have maintained valve articulation for prolonged periods. The hinge teeth would have to have been physically broken to allow these brachiopods to disarticulate, and consequently they are commonly intact even in beds in which all other brachiopods occur as separated valves. Thus, different species show distinct differences in preservation. For example, in bulk samples from the *Homocrinus* beds at Lockport, Brett (1978a) found that all specimens of *Atrypa reticularis* and *Stegerhynchus* were articulated, whereas of 343 specimens of *Striispirifer niagarensis*, 85 were articulated but 258 occurred as separated valves.

Following disarticulation, skeletal parts may become fragmented and abraded, especially in high-energy settings or chemically corroded, mainly in deeper water settings. Many of the densely packed shell-bryozoan beds show evidence of substantial disarticulation of brachiopods and some fragmentation of valves and most bryozoans. This probably represents prolonged periods of normal mortality and residence of skeletal remains on the seafloor. These are time-averaged deposits representing mixtures of the remains of multiple generations of organisms that occupied the seafloor and accumulated.

The presence of small, broken and abraded fragments of shells and bryozoans in many of the limestones of Lewiston E probably reflect multiple periods of reworking of old skeletal debris by storm waves and currents.

Organisms with multi-element skeletons, such as crinoids, trilobites and starfish are especially sensitive indicators of burial rate. In general, these types of skeletons are partially disarticulated within a few days after death unless buried. Some of these organisms, such as ophiuroids ("brittle stars") and asteroids (starfish or sea stars) (Figures 218 - 236) are extremely delicate and can only be preserved if buried very rapidly, probably within just hours after their death or while alive. The latter is particularly interesting for these mobile organisms. Experiments have shown that ophiuroids can burrow out of layers of up to 10 cm of sediment accumulated in just a few hours. This is one reason that these organisms are so rare in the fossil record. Specimens in the *Homocrinus* beds were commonly found above the main buried seafloor level with crinoids and other fossils. They appear to have expired while attempting to disinter themselves from burial layers. In other cases, the organisms may have been killed prior to sediment accumulation.

Even many of the best-preserved crinoids in the Rochester Shale show evidence of very minor decay prior to burial (Figure 260a and 285). More resistant modules, such as segments or pieces of columns and calyxes/thecae of crinoids and cystoids, may resist decay for longer periods. Evidence from encrustation of calyxes of the common Silurian crinoid *Eucalyptocrinites* by bryozoans, other crinoid holdfasts, and worm tubes (Liddell and Brett, 1982) indicate that these cups could remain unburied on the seafloor for periods of many months, but ultimately they would collapse along the sutures of plates. Many partially articulated crinoids and cystoids are known from the Rochester Shale. These cups accumulated along with mainly articulated brachiopods and bryozoans. In some cases, the lower portion of a crinoid that was partially buried in sediment was well preserved, whereas the upper part was exposed and underwent decay and disarticulation (Brett and Baird, 1986).

Trilobites likewise, would probably disarticulate into cephalons, pygidia and single segments if not buried quickly. In many other deposits where trilobites are well preserved, for example, the famed Devonian Harragan beds of Oklahoma or those of Morocco, they are found in semi-enrolled to enrolled configurations and/or occur in random orientations, including vertical and oblique positions within the sediments. These specimens appear to have been caught up in mudflows or density currents that flowed along the seabed (Brett et al. 2012). Conversely, in other types of obrution deposits, including most in the Rochester Shale, the trilobites are parallel to bedding and subhorizontal, very few are enrolled even among trilobite genera that are commonly enrolled, such as *Calymene*. Some show incipient decay or evidence of gentle orientation prior to burial. This suggests that the source of mortality was separated in time from the burial. Brett et al. (2012) suggest that these (type A) trilobite beds reflect mass mortality produced by other effects (such as temperature or salinity changes) associated with storm events prior to their burial. In these cases the muddy sediment may have been suspended for a period of time, as plumes of mud carried seaward by currents along boundary zones of different water density. However, following the dispersal of the muddy plume the fallout of muddy sediment evidently was rapid. Clays may have become aggregated as brackish water from flood runoff mixed with saline water producing chemical reactions that caused the clays to become flocculated into larger grains, which settle much more rapidly than clays. Scanning electron microscope (SEM) study of Rochester mudstone layers that rest upon buried well-preserved fossils show "flocs" or aggregate grains of clay flakes (O'Brien et al., 1994).

Several beds excavated at the Caleb Quarry display nearly perfect articulation of numerous organisms. At least 15 such horizons are recorded in this book. This extraordinary preservation, recording rapidly smothered seafloor conditions or obrution Lagerstätten (Brett and Seilacher, 1991), provides "snapshots" of the skeletonized communities on the sea bottom and is not typical of most sedimentary deposits nor even most of the Rochester Shale. In two decades of study of the lower (A-B) and upper (D-E) units of the Lewiston Member, the author collected nearly 300 cystoids and almost 1000 specimens of *Stephanocrinus*, the two most common echinoderms.

Yet, of these collections, columns and feeding appendages were found in fewer than ten specimens and no complete specimens of these or any crinoids were ever found. Likewise, articulated trilobites were found to be very rare. In contrast, within a few thin beds in about 20 cm of the transitional B-C a large number of complete crinoids and cystoids were found (Figures 293, 296, 301 - 303). This was long ago recognized by the famous crinoid paleontologist Frank Springer (e.g. Springer, 1926) and his veteran collector, Frederick Braun, who discovered these beds in a small gully at Lockport. Careful tracing of these beds by the author eventually resulted in discovery of similarly well preserved fossils at the same level for over 100 km along the Niagara Escarpment. Subsequently, similar horizons of exceptionally preserved fossils were discovered in the Lewiston B and C-D transition between Middleport and the town of Gates, west of Rochester, again in a narrow zone not more than 2m thick. The C-interval is generally very sparsely fossiliferous or completely barren so the chances of finding obrution beds are low even if the sedimentological conditions favorable to forming these deposits were common.

Evidently, the best conditions for fossil preservation occurred in a narrow environmental window in which organisms of various types were relatively abundant and conditions for rapid burial with minimal disruption of seafloor communities could take place, probably near the deeper end of storm wave base, the greatest depth at which strong storm waves touched down on the seabed. This "sweet spot" lay in somewhat deeper water near the lower end of tolerance of many organisms including *Caryocrinites* and some crinoids. Thus, the well-preserved fossils reflect a biased sample of the spectrum of fossil communities. Only certain types of organisms are present in these well-preserved assemblages. For example, these settings were apparently too low energy, deep or muddy for some sensitive forms like *Stephanocrinus* and callocystitids and therefore the opportunity to see these organisms as perfectly preserved specimens was rarely attained. The constraints on the Rochester taphonomic window probably include downramp settings that were shallow enough to have normal oxygenation and to sustain abundant life and yet deep enough that the bottom was not too heavily torn up and disrupted by storm waves and where abundant sediment winnowed from upslope area was rapidly dropped out, probably as a backwash of flocculated muds. Evidence of some current alignment in elongate fossils, such as trilobites (see below), suggests that some of this sediment came in the form of dense, bottom flowing currents.

Paleoecology and Depositional Environments of the Rochester Shale

The depositional environment and paleoecology of the Rochester Shale has been previously discussed in some detail (Brett 1983, 1999; Taylor and Brett, 1996, 1999, Tetreault 1994) and will be briefly summarized here with an emphasis on new data from the Caleb Quarry that provides some important new insights.

During deposition of the Rochester Shale the depositional strike (or orientation of environmental or facies belts) in western New York and Ontario was nearly east-west and water depth increased gradually from north to south (Brett, 1983b; 1999; Figure 4). In the present (east-west) outcrop belt of the Niagara Escarpment, facies are very similar for considerable distances. Indeed every bed of the thin (~30 cm) *Homocrinus* beds transition (Figure 3), including centimeter-thick crinoid beds was found to be traceable between Lockport and St. Catharines, Ontario (Brett and Taylor, 1997). And yet the nearly continuous north-south outcrops along Niagara Gorge show that the Rochester Shale facies change gradually but rather rapidly to the south, such that the fossil rich lower and upper parts of the Lewiston Member thin while the Lewiston C division thickens and most of the interval becomes nearly barren, dark gray shale near Niagara Falls. This evidence shows that the ramp was relatively steep to the south and that the environments to the south were deeper, dysoxic (low oxygen restricted) and nearly lifeless zones. Had the erosion of the Niagara Escarpment moved it a few miles further south, the Rochester would be viewed as a nearly barren shale unit.

Figure 4 - facing page

Reconstructions of the northern Appalachian basin during the deposition of the Rochester Shale in the mid Silurian; note general parallelism between the facies belts and the present day Niagara Escarpment belt and deepening to the southwest. A) reconstruction for deposition of the Lewiston Member, B submember. B) reconstruction of Lewiston E; note bryozoan belt to the north, approximately along the Niagara Escarpment outcrop belt. Names of communities or biofacies (communities) belts are based on common brachiopods and other fossils characteristic of particular fossil assemblages. Dotted lines are isopachs showing the thickness of the Rochester Shale at different localities.

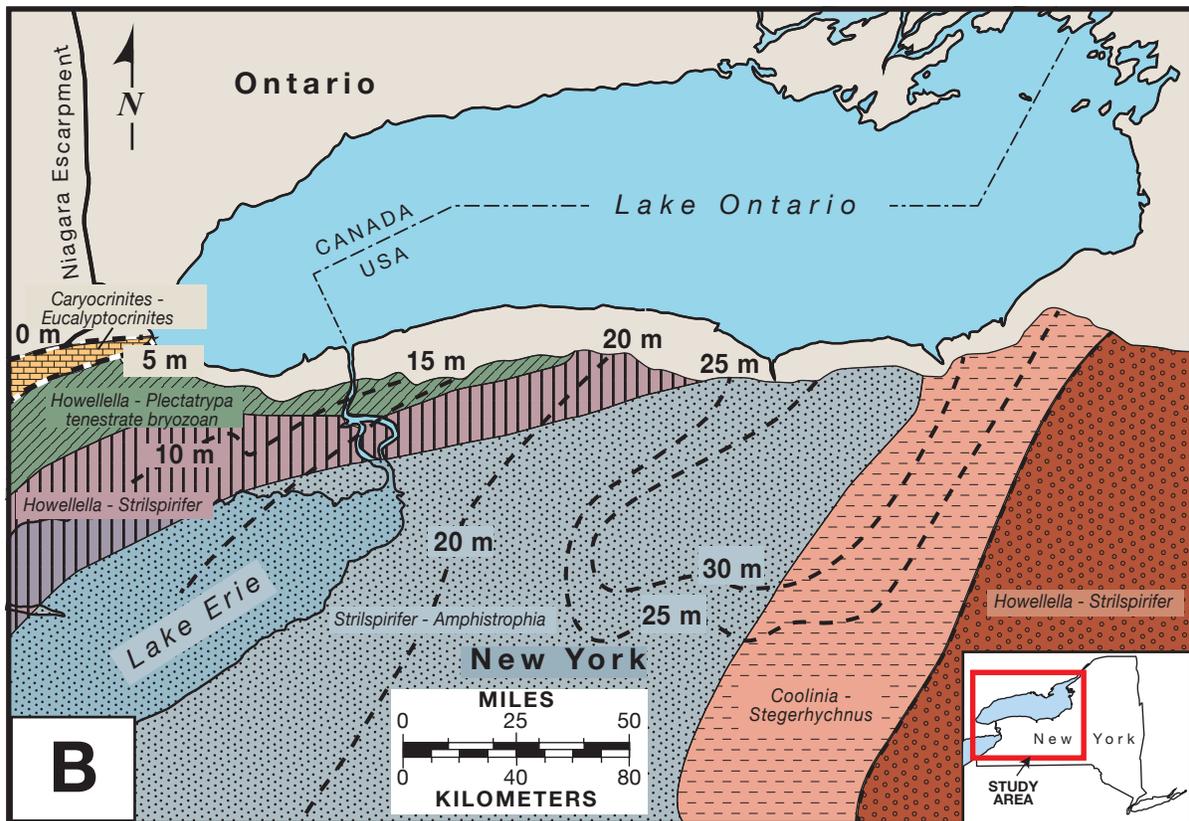
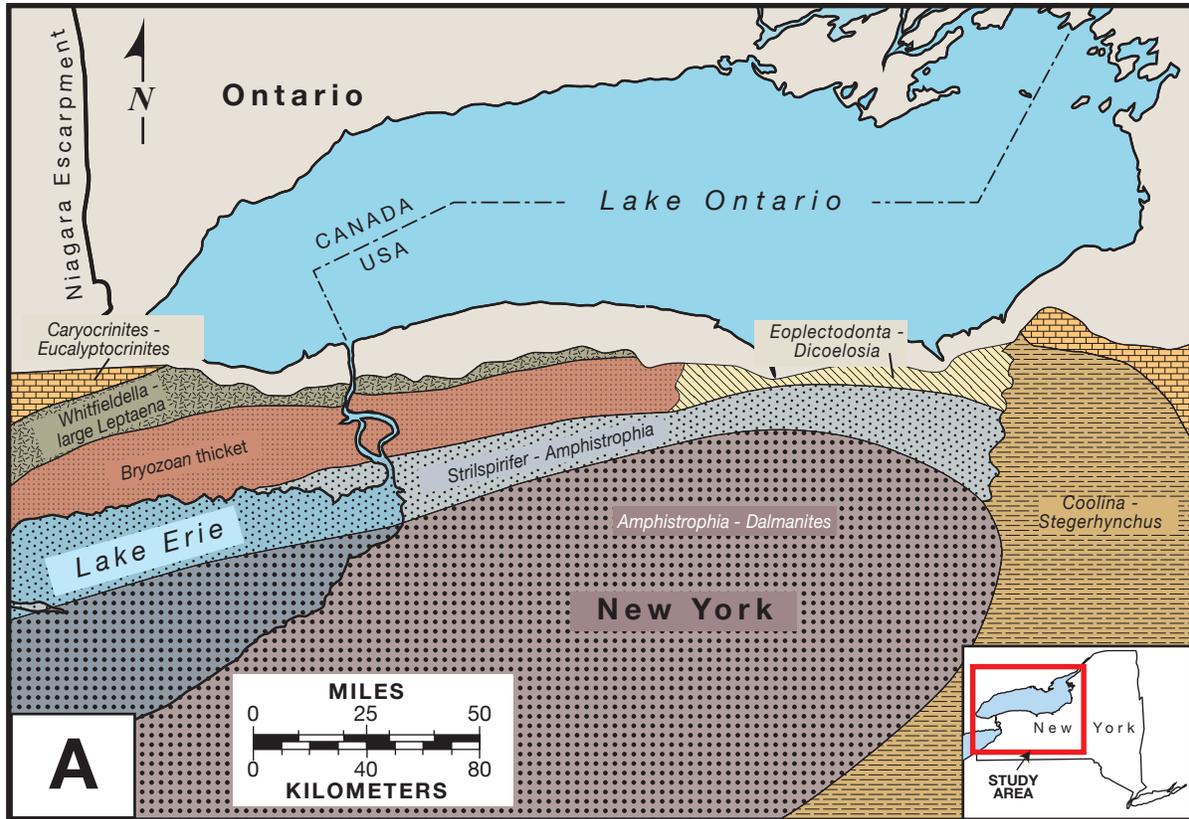


Figure 4

Figure 5 - facing page

Detailed stratigraphic section of the middle Lewiston Member of the Rochester Shale at the Caleb Quarry showing distribution of fossil beds. Curves to the right show inferred depositional cycles of the lower Rochester Shale, aligned with the stratigraphic column. Solid line shows short-term fluctuations in relative sea level; dashed line shows overall or averaged pattern of deepening and shallowing through Lewiston submember C to E. Abbreviations above curves are for indicators of relative water depth (see text for discussion of depths): Br: bryozoan thicket biofacies (communities); Tr: transitional biofacies; local patches of bryozoans with cystoids and other fauna; St: *Striöspirifer* brachiopods dominate; minor bryozoans, small crinoids such as *Homocrinus*; Ba: largely barren, except for rare trilobites, small brachiopods and trace fossils. Sequence stratigraphic interpretation on far right gives inferred patterns of shoreline shift for the overall, large-scale cycle: transgression; shoreline migrating up slope, toward north; MFS: maximum flooding surface; Highstand; sea level high and relatively stable, with increasing mud sedimentation offshore; regression, sea level is falling overall shoreline is migrating down slope to south.

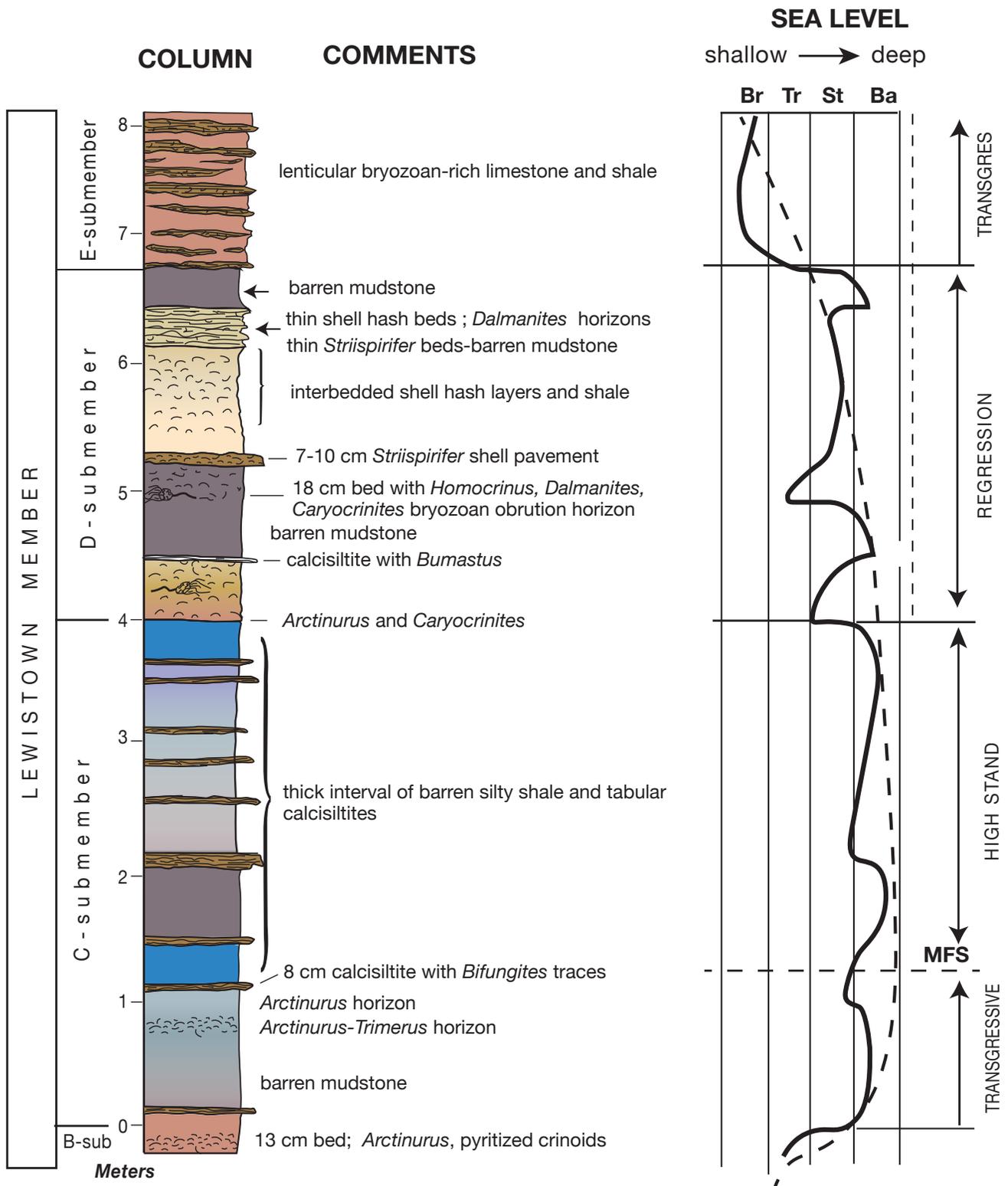


Figure 5

Water Depth: Of particular interest in any study of ancient marine environments is the issue of water depth, because depth is correlated with many other variables (e.g. temperature, light, environmental energy) that have a strong controlling influence on benthic (bottom dwelling) organisms. Unfortunately, depth is also a difficult parameter to assess, as there is little direct information on water depth. The Rochester Shale shows abundant evidence of deeper storm wave-current deposited sediments. These include thin (1 to 10 cm) tabular calcisiltite beds that show sharp soles with tool marks and scours, micrograding, planar to small scale hummocky cross stratification, all indicators of deposition from gradient currents and/or combined flows that involve minor wave action. These deposits of silt-sized carbonate sediment were swept into the muddy basin during times of strong backflow currents or gradient currents. This places the seafloor within the reach of storm-generated currents and the presence of hummocks suggests interference of wave effects. These silty beds were probably deposited toward the deeper end of storm wave-current effects, i.e., at deep storm wave base. For shallow interior seas this position may have been as much as 50 meters (~150 feet) or slightly more but clearly the seafloor was not in very great depths. Very gentle distal ends of gradient currents may have reoriented and aligned the carcasses of trilobites such as *Dalmanites* into "windrows." Certain mass occurrences of *Dalmanites* show preferred orientations. However, the currents were not strong enough to impart a very strong preferred orientation. In shallower depths, storm waves locally broke up colonies of bryozoans and shells and reworked them into local lenses of slightly broken debris.

Shallower water sediments are indicated in some of the higher Lockport Group above the Rochester Formation. For example, the Gasport Limestone that occurs above the Rochester Shale shows bimodal or herringbone cross bedded crinoidal sand and gravel; such evidence indicates deposition in water shallow enough to be affected by strong, reversing tidal currents, probably no more than 10 to 15 meters of water. These beds also contain locally abundant colonial corals and stromatoporoid sponges that probably required shallow, well-lit waters. Rochester sediments accumulated in considerably deeper water.

Light intensity: Evidence for ancient light levels is more tentative. Small mounds or bioherms at the top of the Irondequoit Limestone that protrude upward into the Rochester Shale are composed of clotted lime mud or micrite, as well as leaf-like *Lichenalia* bryozoans. The clotted muds resemble thrombolites produced by the blue-green cyanobacterium *Girvanella*, though more detailed study is needed. These structures thus imply a position within the euphotic (well-lit zone) at least for the basal transition into the Rochester Shale. If the forms, such as *Inocaulis* (Figures 120 - 122) are actually green algae and not dendroid graptolites then these would also imply a position in the euphotic zone. Certain units yielding assemblages of brachiopods similar to those of the Rochester Shale, such as those in the Silurian of Gotland, have yielded abundant microborings of algae and cyanobacteria ("blue green" bacteria). Since these organisms require light for photosynthesis they provide evidence for deposition in the photic zone (Glaub and Bundeschuh, 1997; Glaub et al., 2007). However, Rochester fossils have not yielded these sorts of traces to date. The presence of relatively sophisticated schizochroal (multi-faceted, with discrete, non-distorting lenses) turreted eyes in the abundant trilobite *Dalmanites* points to the presence of some light, as organisms living in perpetually dark settings (such as cave crayfish) tend to have weak or non-existent eyes. Eyes of dalmanitids were adapted for forming clear images and this requires sufficient light. The large size of the eyes, on the other hand may indicate relatively low light levels to which the organisms were adapted. Given that the Rochester seafloor was no doubt muddy and prone to high turbidity this indicates depths of just a few tens of meters. Together these lines of evidence suggest deposition in the dysphotic to lower euphotic zone, at depths of perhaps 30 to 60 meters of water, shallowest to the north where the Rochester Shale pinched out into carbonate shoals with sediments resembling the Irondequoit Limestone and deeper to the south where Rochester facies were mainly dark, barren shales, reflecting stagnant, dysoxic environments.

Salinity: Salinity in the Rochester depositional basin was mostly normal marine (about 35 parts per thousand salinity) as evidenced by the numerous organism groups that are known to be quite intolerant to conditions other than normal salinity, such as echinoderms and cephalopod mollusks. However, the barren character of certain portions of the Rochester despite evidence, in the form of burrows, for benthic oxygenation suggests that somewhat stressed conditions existed at least locally near the basin center.

Substrates and Sedimentation: The substrates were mainly soft muds but with local accumulation of skeletal hard parts. It is clear that the distribution of certain organisms was more specifically controlled by substrate. Direct colonization of the muddy sea bed was difficult for many organisms, but some mobile forms such as the trilobite *Dalmanites*, were able to survive here, and other sedentary forms have morphologies that aided in support on soft, muddy substrate. The thin, flattened forms of many of the most widespread brachiopods probably allowed them to rest freely on the mud. Likewise, the broad flattened shape of some bryozoan colonies, such as *Lichenalia* may have been adaptive for spreading out on muddy sea floors. *Dendrocrinus* possessed flexible rootlets (Figure 272) that may have permitted adjustment of attachment sites and facilitated colonization of the soft seafloor directly.

Other brachiopods (attached by pedicle stalks), bryozoans, corals and a majority of echinoderms and worm tubes required hard substrates for settlement. In some areas stable hard substrate was provided by skeletal debris, particularly brachiopod shells. The cystoid *Caryocrinites* appears to have preferentially settled on branching bryozoans and the occurrence of these cystoids therefore mirrors the occurrence of small patches of *Chilotrypa* and *Hallopora* bryozoans (Figures 7 - 13a). Other echinoderms utilized small fragments of skeletal material as an initial substrate. Both *Caryocrinites* and certain crinoids like *Eucalyptocrinites* possessed strongly branched radicles or rootlets that penetrated into soft substrate (Brett, 1978c). In turn, these organisms provided substrates for other organisms such as the small coral *Favosites parasiticus* (Figures 55 and 56), which encircled the columns, and even other echinoderms, which were attached by distal coils or cemented holdfasts to their hosts.

The process of "taphonomic feedback" (Kidwell and Jablonski, 1983) played a critical role in the build-up of local patches of more diverse organisms. This means that the accumulation of dead shells, initially of "pioneering" mud dwelling brachiopods, trilobite molts, etc, provided substrates for more diverse communities, including twig bryozoans and echinoderms, which, in turn, may have been favored by intervals of drier climate and/or minor to more major sea level rise. The rise of base level affects offshore sedimentation by creating bays and estuaries that may serve as coastal "traps" for sediment delivered by rivers from Taconic highlands. Thus, many of the thicker shell beds in the Rochester Shale probably accumulated during times of offshore sediment starvation, preferentially associated with intervals of sea level rise following shallowing episodes. The amalgamation of shelly debris was further aided by occasional storms or hurricanes, during which large waves touched down on a normally quiet water area and fragmented, winnowed and concentrated accumulating skeletal debris. Thus, some shell beds have sharp, scoured bases and rippled tops. These features were the mark of the final process that disrupted and concentrated shelly debris and sometimes whole, live organisms that had accumulated during previous periods of up to centuries duration.

Environmental Energy: Most Rochester seafloor settings were predominantly low energy (current velocities generally not exceeding 20 cm/sec). Low current energy means that organisms could be relatively weakly attached to the seafloor and still maintain their position. Some crinoids such as *Dimerocrinites* (Figures 294 - 306) simply laid a section of the column or a distally coiled area on the seafloor for adequate support in low energy environments. Other organisms were free lying or weakly tethered by small holdfasts, cemented pads or pedicle stalks (brachiopods). Evidently, this was adequate anchorage for stability during the majority of the time. However, during the rare storm events such weak tethering became a major weakness as storm waves and currents disrupted the normally quiet seafloor, dislodging millions of individuals of bryozoans, echinoderms, and brachiopods, and other organisms and in some instances rapidly burying them in layers of muddy sediment resuspended by waves from shallower areas.

Other weaker storm currents, in deeper areas slightly below the reach of waves, merely toppled crinoids and other organisms more or less in their life positions. Such preservation is typical of the cystoid bed where whole *Caryocrinites* were more gently uprooted and knocked over without being torn apart.

The normally low current and wave energy settings of deeper Rochester environments may have limited certain organisms that required water movement to provide feeding currents, such as most echinoderms. It may also have promoted a multi-tiered community in which different groups of organisms fed at different levels above the seafloor (see Ausich and Bottjer, 1982). Brachiopods and bryozoans, which could produce their own filter feeding currents (active filter feeders) may have benefitted from living close to the seafloor where suspended food was concentrated by gravity settling, whereas crinoids that relied strictly on external currents (passive suspension feeders) survived by elevating their crowns up away from the stagnant boundary zone near the sediment surface and into levels of at least some current energy.

Modes of Life of Silurian Organisms and Community Paleocology

Marine ecologists classify organisms into guilds or generalized modes of life based upon their: a) position with respect to their life in the water column, planktonic (floating) and nektonic (swimming) or on seafloor, benthic as well as b) their feeding or trophic types. Benthic organisms are further identified as infaunal (living within the sediment) or epifaunal (living on the sediment surface). Many, such as brachiopods and crinoids, are sessile or sedentary, while others like gastropods, are vagrant, crawling on the seafloor.

All ecosystems have complex interactive webs or trophic pyramids that require an external energy source, generally sunlight, primary production by autotrophic organisms, mainly photosynthetic green plants and algae, consumers (heterotrophs) animals that feed on plants, or other animals, and decomposers, primarily bacteria, that degrade organic matter and recycle its contained nutrients. Such relationships based upon modes of feeding are called trophic systems. In the case of marine systems, common trophic modes include removal of suspended planktonic algae and zooplankton or particulate organic detritus from seawater. Such *suspension feeding* may include passive suspension feeding, as in crinoids, which rely upon external currents in seawater to bring food particles to sticky feeding surfaces, and active *filter feeding* in which organisms create their own feeding currents using movements of flagella (as in sponges), cilia (e.g., in brachiopods and bryozoans) and/or whole limbs as in certain arthropods. Infaunal organisms, termed *deposit feeders*, live in the substrate and actively ingest sediment and extract food from it. In addition, other organisms are *scavengers* or *grazers*, rasping or scraping up dead or living organic matter typically plants. Still others are *predators*, mainly active or vagrant swimming or crawling forms that kill and consume other animals for food.

Attached epifauna may show *tiering*, feeding at different levels above the sediment surface. Low-level organisms occupy a zone of abundant suspended food particles just 1 or 2 centimeters above the seafloor. Intermediate level suspension feeders such as many bryozoans, and some crinoids are elevated about 5-10 cm above the bottom, while some long stemmed crinoids may feed at levels exceeding a meter above the seabed.

Exquisite preservation of Rochester Shale fossils from the Caleb Quarry and elsewhere provides rare glimpses of ancient organisms preserved very nearly in life position permitting virtual snapshots of a Silurian seafloor. Interpretation of the modes of life and ecology of ancient ecosystems involves a combination of functional morphology that uses the form of skeletons to infer their function, in conjunction with direct evidence from fossils and surrounding sediments and information on the biology of mostly closely related living organisms.

The primary producers in Rochester Shale ecosystems are poorly represented in the fossil record but given the abundance and diversity of suspension feeding organisms we must presume that a large base of green phytoplanktonic algae provided the basis for the food web. In fact, fossil acritarchs, organic-walled microfossils of probable planktonic algae are abundant in the Rochester Shale (Thusu, 1972). Possible green benthic algae may be represented by *Acanthograptus* and *Inocaulis* (Figures 118 - 122; LoDuca and Brett, 1997, S.T. LoDuca, personal communication 2014).

Infaunal deposit feeders within the Rochester seafloor are represented primarily by trace fossils, particularly the feeding burrows *Planolites* and *Chondrites* that are abundant and/or well preserved in silty beds. These are traces of sediment mining worms. The rare machaeridian *Lepidocoelus* (Figures 198 - 203) may have been an armor plated deposit-feeding worm. Certain trilobites may also have been deposit feeders. Illaenids like *Bumastus* (Figures 369 - 375) are common dwellers on Silurian reefs and bioherms and seem to have occupied pockets in these structures feeding from the sediment (Sarle, 1907).

The most abundantly represented trophic groups are suspension feeders. This category takes in a wide array of filter feeders, including the varied brachiopods and bryozoans and probably also the dendroid graptolites. Most of these are low tier sedentary organisms.

Brachiopods and bryozoans generate feeding currents using ciliated tentacles on their looped or coiled lophophores that produce rhythmic beats that propel water and suspended particles. Many of these organisms have morphological strategies that may have aided in water flow. For example, the groove at the center of the valves (fold and sulcus) in *Striispirifer*, *Howellella*, and other spiriferids, as well as rhynchonellids such as *Ancillotoechia*, *Rhynchotreta*, and *Stegerhynchus* (Figures 104, 106 and 78), served to funnel the wastewater away from the lateral incurrent streams and may have had some Venturi effect that helped to promote water flow. Likewise the bumps or monticules on the surfaces many of the bryozoans (e.g., *Trematopora tuberculata*, Figures 35 and 36) may have promoted water flow off the surface of larger colonies to prevent stagnation of filtered water. Many brachiopods may have initially settled on small hard substrate objects; however, as adults, these organisms often were free-resting on the seafloor. The large, broad surface area of shells in forms like *Coolinia* and *Amphistrophia* helped to spread out the weight of the free-resting brachiopods like a snowshoe to prevent them sinking into soft muds. The concentric growth rings or rugae of *Leptaena* (Figures 74 and 75) not only provided increased frictional contact with the substrate but may have strengthened the shell against physical damage or predation. *Striispirifer* appears to have been an opportunistic form that thrived in somewhat stressed low energy settings. It may have possessed a functional pedicle stalk at least initially, but its broad interarea also provided a base to help stabilize the shell. The rhynchonellids (e.g. *Stegerhynchus*) were attached by pedicle stalks and may have initially settled on shell fragments and other skeletal materials. They were evidently even capable of attaching to living substrates, as they have been found in life position on the exoskeletons of *Arctinurus* trilobites (Taylor and Brett, 1996 and Tetreault 1990, 1992).

Certain bryozoans, such as *Chilotrypa* (Figures 7 - 9), were capable of surviving in relatively muddy seafloor environments not only because of active filter pumping but also elevation of growing portions of their colonies into areas above the low energy seafloor. Their slender branching shapes, adaptive for low energy environments may also have helped in shedding sediment from the surfaces of colonies. However, most bryozoans are sensitive to high turbidity, probably because suspended silt may clog their delicate filtration meshes. In slightly more energetic settings represented by the Lewiston E bryozoa bed limestones, other growth strategies aided in feeding. For example, the mesh-like networks and fan or funnel shapes of fenestrate bryozoan colonies (Figures 15,16 and 23 - 26) promoted water flow through the colonies.

As noted, echinoderms do not generate their own feeding currents; therefore, many, such as edrioasteroids (Figures 237 - 243a) and stalked crinoids and cystoids were passive suspension feeders dependent upon external currents to bring suspended food particles into the vicinity of their food grooves, which were covered with tube feet and mucous to trap these particles.

Although crinoids are generally considered to be passive suspension feeders, Silurian echinoderms may have had rather varied modes of feeding.

By analogy with living stalked crinoids many Paleozoic forms with long pinnulate arms, such as *Dimerocrinites* and *Macrostylocrinus*, are interpreted as having formed filtration fans. Modern crinoids are "leeside" suspension feeders; that is, they recurve the backsides of their arms into the strongest water currents. Water flushes through the spaces between pinnules and forms a low-pressure zone on the other side where the ambulacral grooves are amply supplied with sticky tube feet. Particles spiraling in these eddies are captured on the tube feet and propelled into the cilia-lined food groove; a combination of food and mucous then makes its way to the mouth, like the flow from various branches coming together like tributaries of a stream drainage systems. Camerate crinoids, such as *Macrostylocrinus* and *Dimerocrinites*, may have fed in approximately this way, although the lack of muscular articulations in their arms, in contrast to modern articulate crinoids, must have limited arm mobility. An intriguing discovery came from the excavations at Caleb Quarry: complete specimens of the crinoid *Catatonocrinus halli* (Figures 244 and 245) revealed, for the first time, the arm structure of this remarkable, rare crinoid. *Catatonocrinus* was almost unique among the disparid crinoids in possessing pinnulate arms, the large number of small side branches provided a relatively large surface area for food gathering.

Densely pinnulate arms do appear to have been efficient to food capture, but only if sufficient currents existed in the environment to force water through the relatively dense meshwork of arms and pinnules. Such crinoids are often thought to be restricted to high-energy environments, but the Rochester Shale crinoids seem to contradict this. Most of the densely pinnulate camerate crinoids and *Catatonocrinus*, which are preserved almost in life position, evidently did not inhabit high-energy environments as they occur in mudstones. Evidently they were able to collect enough food even without strong current flushing and in fact they appear to have been successful in quite a range of environments.

Although modern crinoids have yielded much insight into crinoid feeding behavior, it is evident that not all Paleozoic crinoids could have formed efficient parabolic feeding fans. Most of the small disparid crinoids, such as *Homocrinus*, most calceocrinids, and myelodactylids (Figures 283, 244 and 264 - 268), lacked pinnules, possessed low flexibility, stick-like arms, and may have used large sticky tube feet to capture particles from low energy water. Flexible crinoids like *Lecanocrinus* and *Ichthyocrinus* (Figures 261 - 263 and 255 - 260b) had broad, space-filling brachials in the arms that ended in tendril like branches, but lacked pinnules. Their arms are often preserved as tightly coiled, like a clenched fist. It has been suggested that these crinoids were raptorial, actively capturing larger plankton with their flexible arms and pulling it into the mouth.

Most blastozoans such as the callocystitid cystoids and *Stephanocrinus* lacked arms and instead had tiny coiled, thread-like brachioles. These were so slender that there was little or no space for tube feet and it has been suggested that these organisms lacked tube feet altogether (Sprinkle, 1973). If so, they must have fed in a very different way than crinoids, perhaps using mucous secretion and cilia to trap microplankton. The small size of their food collecting appendages may have confined these organisms to higher energy or more food-rich shallower environments. These are among the groups that do not extend into Rochester deeper water environments and they may have required shallower more agitated settings.

Caryocrinites is an exception that tests the general rule. This cystoid convergently evolved elongate appendages resembling crinoid arms (Figures 311 - 324). They are not made of evolutionarily related (homologous) parts. The arm plates are actually cystoid ambulacral floor plates, which normally run along the surface of the theca, as in the Rochester Shale genus *Callocystites* (Figures 338 - 344) and their apparent "pinnules" are actually brachioles homologous to those seen in the callocystitids. Nonetheless, *Caryocrinites* had much greater food gathering capabilities than other cystoids, such as *Callocystites*. This may have given *Caryocrinites* great versatility and, indeed, this cystoid occurs in a broader range of environments than do most blastozoans or short-armed crinoids.

In modern crinoids respiratory gas uptake occurs through the thin walled tube feet on the arms. Perhaps for this reason crinoids generally required no specialized respiratory structures. In contrast, the blastozoans, which had greatly reduced or lost the tube feet generally, possessed complex respiratory structures to improve gas exchange. Thus, the callocystitids had three pairs of rhomb-shaped areas called pore rhombs, each with slots leading to thin walled calcite tubes that extended into the theca. Presumably these allowed seawater to come into contact with the cystoid's body wall in a large surface area. Likewise, *Stephanocrinus* had u-shaped pore canal systems that extended into their thin walled coronal crests (Brett et al., 1983). These structures were also probably canals for gas exchange.

Development of columns in most crinoids and cystoids enabled their feeding and respiratory structures, at least in adults, to be elevated into currents strong enough to permit feeding. Even the the undescribed Rhenopyrgid edriosteroid (Figures 237 - 242) developed a turreted theca to elevate feeding surfaces several millimeters above the substrate.

Certain short-stalked crinoids, such as *Gazacrinus* and the cystoid *Callocystites*, must have fed from an intermediate position elevated a few centimeters above the seafloor. Others, such as *Macrostylocrinus*, *Eucalyptocrinites* and the cystoid *Caryocrinites* (Figures 288, 277 and 311) apparently fed from a level as much as 20 cm above the seabed. Still others, notably the slender armed *Dendrocrinus* and some *Dimerocrinites* (Figures 269 and 294) had a much more elevated feeding strategy with columns occasionally running as much as 50 cm long. These crinoids were especially adapted to elevating the crown as rapidly as possible above the inhospitable mud bottom. Not surprisingly, these crinoids are occasionally found in large numbers in units such as the upper Rochester Shale (Burleigh Hill Member) where other echinoderms are never found. These were opportunistic crinoids that could survive and even thrive in settings inimical to most benthic life and their elevated strategy together with relatively flexible attachment strategies at least for the dendrocrinids (which had whorled cirri on the distal stem; Figures 272 and 275) were surely important for this mode of life.

Surprisingly, however, certain crinoids reversed the trend of feeding above the substrate and fed close to the seafloor. For example, the calceocrinids ("slipper crinoids"), such as *Catatonocrinus halli* apparently had a recumbent column that lay upon the seafloor; their crowns were hinged on the basal plates and could be folded down against the column. This was very likely a defensive strategy for an organism that lived close to the seafloor. In particular, during times of storm current stirring of mud the feeding surfaces of the arm could be shut down rather effectively.

In an analogous way, *Crinobrachiatus* lived close to the substrate with a coiled column and stout cirri that not only aided in anchoring the crinoid in the substrate but also enshrouded the delicate crown when the animals withdrew the crown into the coils of the stem. We reconstruct this crinoid as having lived with the stem oriented parallel to the substrate and propped up by the stiff, branching cirri, which are progressively longer from the posterior tip forward (Eckert and Brett, 1988).

Gastropods had varied modes of life. Most were active organisms that utilized a muscular foot to crawl on the seabed and a rasping tongue or radula for feeding. Some of the more typical platyceratids in the Rochester assemblages, such as *Naticonema* may have lived as active benthic scavengers or predators. However, the majority of this group was adapted to an unusual mode of life. These organisms attached, probably as juveniles, to the tegmens of certain crinoids (Figures 461 - 463), especially *Macrostylocrinus*, *Dimerocrinites* and *Lyriocrinus* and the cystoid *Caryocrinites*, and lived a dependent, sedentary life attached to their hosts. These gastropods were positioned over the anal vents of the echinoderms where they apparently fed upon fecal material expelled by their hosts; that is, they were coprophagous. They have generally been interpreted as commensals that benefitted from their hosts but did them little or no harm. However, some authors have argued that these snails could also be parasitic. At least by the Devonian there is evidence that some platyceratids used their radulas to drill into the gut of their hosts and rob them of some food (Baumiller and Gahn, 2002).

Rochester Shale crinoids also had other parasites. In some assemblages a very high proportion of *Ichthyocrinus* specimens had their columns and calyx plates riddled by circular, parabolic pits (Brett, 1978b), a trace fossil referred to by Brett (1985) as *Tremichnus*. These pits, which were probably formed by some type of worm, were most certainly harmful to their hosts and like many parasites were quite specific to particular host crinoids. *Ichthyocrinus* was the most frequently infested but *Tremichnus* occurs less commonly in a few other crinoids, including calceocrinids and *Eucalyptocrinites*.

Carnivores in the Rochester seafloor communities were relatively uncommon and surely not as significant as in modern communities. Trilobites may have been partly detritivores or scavengers, feeding on decaying organisms; they lacked biting mouthparts and so were constrained to feeding on relatively soft food. Certain trilobites, however, were probably predators on soft-bodied organisms. By analogy with modern horseshoe crabs, trilobites may have utilized the bristly inner joints of their legs (gnathobases) to grasp soft bodied organisms, such as worms, from within the sediment and pass them forward to the mouth, which was underlain by a wedge-shaped plate, the hypostome. In some cases, trilobites may have worked the food between anterior legs and the hypostome to break it down into small pieces to be ingested by a suctorial mouth. In rare cases the coffee bean shaped trace fossils of trilobites (*Rusophycus*) (Figure 429) from the Rochester Shale and elsewhere have been observed to intercept a worm burrow in the sediment and it is likely that these represent hunting traces of trilobites (Tetreault 1990). Forms like *Trimerus* that had smooth, spade-like cephalae may have been adapted to furrowing in sediment after prey; they match in size and shape some associated *Rusophycus* traces (Tetreault 1990). Large *Arctinurus* were evidently rather slow moving and molted infrequently, as evidenced by the presence of encrusting worm tubes bryozoans and small attached brachiopods (Figures 483 - 485) on their dorsal exoskeletons (Tetreault 1990, 1992) as do modern large horseshoe crabs, and may have scuttled on the surface in search of detritus.

Ophiuroids or brittle stars were also probably actively crawling scavengers and predators, using their entire slender sinuous rays to propel themselves along the seafloor in search of organic matter and microorganisms, which they processed with the small "jaws" at the corners of their star shaped mouths.

Starfish or sea stars are known to be important predators in modern communities. These animals actively crawl using tube feet and some forms are capable of wrapping their arms around bivalved prey such as clams and exerting a pull with tube feet. Eventually, these animals weaken their prey sufficiently to allow a portion of the starfish stomach lining to be inserted and start digesting their victim's tissues. This same mode of life may have been present in *Palaeaster* (Figures 218 and 219) from the Rochester Shale.

The master predators of the Silurian seafloor in the absence of any fishes, were probably nautiloid cephalopods. Based on modern analogs, notably the chambered *Nautilus*, these were streamlined, actively swimming predators. *Dawsonoceras* could be up to a meter long and up to 10 cm in diameter. By analogy to *Nautilus* it probably swam using a form of jet propulsion by taking water into its mantle cavity and forcing it out through a narrow nozzle referred to as a hyponome. Relatively sophisticated eyes enabled nautiloids to track prey. Nautiloids had a cluster of tentacles for seizing other organisms such as trilobites. These surrounded a mouth equipped with a sharp, parrot-like beak that could tear into their prey. A number of trilobites illustrated in this book show scallop-shaped divots in their exoskeletons that are interpreted as bite marks. These may very well record predatory strikes by large nautiloids; however, some of these trilobites clearly survived the attacks and lived to partially heal their wounds. Jawed fishes would become a more important element in the Middle Devonian, and they may have had a strong influence on prey taxa, but they were only just coming on the scene during the later Silurian and none lived in the Appalachian basin seas.

Cyclicality and Community Replacement in the Rochester Shale

Large-Scale Cycle: Overall, the Irondequoit Limestone, Rochester Shale and DeCew Dolostone form a large-scale deepening-shallowing cycle on the scale of perhaps a million years. It is an unconformity bounded package or depositional sequence, identified by Brett et al. (1990, 1998) as Silurian sequence V. This sequence is bounded below by a sharp unconformable contact of the basal crinoidal limestones of the Irondequoit and at the top by a distinctly erosional contact at the base of the crinoid-rich and reefy Gasport Limestone of the Lockport Group. This unconformity progressively and rapidly cuts out the DeCew Formation and the thin Rochester Shale northwest of Hamilton, Ontario.

Like most depositional sequences, Sequence V is not symmetrical probably because the types and rates of sedimentation vary predictably during a rise and fall of base level. During transgressions, the effect of raising base level is to starve offshore areas of mud and silt, which is trapped or sequestered in shallow bays and estuaries leading to clean platforms offshore. The net effect of this offshore starvation of mud and silt is to allow buildup of skeletal limestones, such as the Irondequoit Limestone. Conversely, during sea level stillstand and fall, seaward regression of the shoreline occurs allowing greater amounts of increasingly coarse clastic sediments to be deposited offshore, as recorded in the upper Rochester (Burleigh Hill Member) and DeCew formations.

The Irondequoit-Rochester succession has been traced widely in eastern North America and may have counterparts in Europe and elsewhere. As noted above, a similar succession of limestone into shale is recorded in the Welsh Borderland of Great Britain, which during the Silurian, was on a separate microcontinent termed Avalonia, and a very similar succession exists in strata of the same age in the Swedish island of Gotland and in northwestern Estonia (Brett, unpublished), which were parts of the paleocontinent of Baltica or Ancestral Europe (Cocks, 2001). The occurrence of similar transgressive-regressive successions on at least three separate paleocontinents strongly indicates that this fluctuation was produced by a global or eustatic cycle of deepening and shallowing on the scale of tens of meters of water. And even smaller scales of cycles appear to be correlatable. If so, this provides possible evidence for glacial retreat and buildup in the middle Silurian, as this is the primary mechanism responsible for global rise and fall of sea level. Ancient glacial tillite deposits are known from the early Silurian strata of the Paleandes in South America, which were then closer to the South Pole (Caputo et al., 1998). One of the later glacial deposits may correspond with the unconformity below the Irondequoit.

Smaller-Scale Cycles: Nested within the Irondequoit-Rochester-DeCew large-scale cycle (10 - 40 meters) are two smaller cycles (Irondequoit to lower Lewiston and upper Lewiston E-submember to DeCew sequences), and a series of even smaller meter-scale cycles. The Lewiston Member was long recognized to record a nearly symmetrical cycle of sedimentation probably associated with water depth change of a few tens of meters (Brett 1982, 1983), and reflected in cyclic changes in biofacies (Tetreault 1994). New data from the Middleport area provide strong support for this hypothesis and add important details (Figures 2 and 5).

The lower Rochester cycle starts with a strong deepening recorded in the upper Irondequoit Limestone into the lower Lewiston Member. The sharp contact between the Irondequoit and the basal Rochester Shale is interpreted as a flooding surface, associated with rather rapid rise of sea level, which produced the effect of sediment starvation offshore. Commencing with shallow shelf conditions near normal wave base (~5 - 10 meters of water) water deepened into deeper subtidal conditions occasionally scoured by storms but not effected by fair weather waves. The occurrence of mounds of fine, micritic limestone and bryozoans at the surface attests to a period of upward growth by organisms during a time of clear water and probably base level rise. Certain organisms were closely related to the Irondequoit mounds.

The lower Lewiston Member (A and B submembers) records continued upward deepening although probably at a lower rate. The extent of deepening is uncertain, but probably ranges from near normal wave base to deep storm wave base or a few tens of meters. Maximum water depth was attained near the boundary of units B and C of the Lewiston Member and we interpret the B-C boundary as a maximum flooding zone. Lewiston C, like the upper Rochester Burleigh Hill Member, is interpreted as representing highstand conditions. That is, maximum depth was attained near the base of the unit and that minor gradual shallowing took place through the unit. A further implication is that the rate of siliciclastic sedimentation was gradually increasing. Here depths were generally too great and conditions too turbid and muddy to support abundant shelly organisms so that skeletal limestones are essentially absent. However, at some levels, remains are found of small thin shells (e.g. *Amphistropbia*) and mobile animals including trilobites such as *Dalmanites* and *Trimerus* and, rarely *Arctinurus*, as well as soft-bodied worms, which left trace fossils, especially in silty deposits and very likely formed important food for predators including the trilobites. Beds of carbonate and/or siliciclastic silt are abundant within this interval. These beds show clear evidence of deposition by deep storm gradient currents with slight interference from waves. Such currents scoured the muddy seafloor removing loose muds and depositing slightly graded, hummocky laminated silt transported out of shallower areas to the north.

Near Whirlpool Bridge in Niagara Falls, NY, exposures of Rochester Shale in the upper C-D units show thicker (up to 40 cm), channelized and somewhat deformed siltstones/calcsiltites that closely resemble the DeCew Formation at the top of the Rochester (Brett, 1983). These units are both interpreted as rapidly deposited, coarse sediment that was poured into the basin during a time of falling sea level, analogous to the falling stage conditions. No hint of this silty package occurs in the Lewiston D submember at Middleport, or for that matter, at the north end of the Niagara Gorge. Presumably it was confined to local submarine channel fills along the southward trending slope or ramp into deeper parts of the Rochester basin. Regardless, this evidence strongly suggests that the Lewiston D submember represents a falling stage deposit - i.e. deposited during a regression forced by an actual and probably eustatic sea level fall. The Lewiston E, "bryozoa beds" limestone package was formerly interpreted as the maximum shallowing. However, reconsideration of this situation suggests that it may actually record the very initial transgression following a shallowing. As noted above, during transgressions terrigenous sediments tend to become trapped or sequestered in coastal areas leading to offshore starvation of siliciclastic sediments and promoting growth of carbonate-forming organisms. The sharp upper contact of the Lewiston E is interpreted as a maximum flooding surface associated with rapid rate of rise. It is analogous to the top of the Irondequoit limestone.

Interestingly, patterns very similar to those in the Rochester Shale are found in Ancestral Europe or Baltica, for example, the Jaani Formation, of essentially the same age seen in cliff sections along the island of Saaremaa, in Estonia. The basal shaly Mustjala Member, resembling lower Lewiston Member, is followed by bryozoan and crinoid rich limestones in the Ninase Member, as in similar aged Lewiston E strata, and these are, in turn, overlain by gray shales and calcsiltites of the Paramaja Member (Männik and Nestor, 2014) that very closely resemble the Burleigh Hill Member of the Rochester. This suggests that even the smaller scale cycles of the Rochester may have been produced by eustatic sea level changes.

Community Succession: The succession of changing environments and biofacies (communities) in the middle Lewiston Member is particularly well displayed at Middleport (Figure 5). By combining data and observations from nearby creek exposures with the excavations at the Caleb Quarry we can reconstruct a remarkably symmetrical transition of fossil assemblages from relatively shallow to deeper environments and then back again.

Exceptionally weathered exposures in the lower Rochester Lewiston B occur along banks of Jeddo Creek in Middleport. These were studied in detail by the writer both by sieving the weathered mudstone in the creek to collect all resistant fossils, and by collecting slabs from the banks; this sampling revealed an exceptionally rich fauna in several bryozoan-rich beds, separated by sparsely fossiliferous shale (Brett, 1978a).

In particular, these beds showed a high diversity of brachiopods (27 species), including atrypids, *Striispirifer*, rhynchonellids, and *Leptaena* and abundant, tiny bilobed shells of *Dicoelosia* and pyramidal *Skenidioides*. Echinoderms of 18 species, included *Caryocrinites*, and abundant *Stephanocrinus angulatus*. Crinoids included *Macrostylocrinus*, calceocrinids and rare *Ichthyocrinus* and *Lecanocrinus*. Trilobites were under-represented in washings because they tend to breakdown to unrecognizable fragments but inspection of bedding planes showed that the most common forms were *Bumastus*, *Calymene*, and *Dalmanites*.

Unfortunately, the level of the Lewiston B-C transition is poorly exposed at Middleport, but it is well represented near Lockport where these beds, referred to as the "*Homocrinus* beds" (Figures 4 and 6; Taylor and Brett, 1996, 1999) yielded a very distinctive fauna of moderate diversity (about 40 species), including a great abundance of the spiriferid brachiopod *Striispirifer niagarensis*. Distinctive echinoderm elements include the delicate disparid crinoid *Homocrinus parvus*, the small flexible crinoid *Asaphocrinus ornatus*, the ophiuroid *Protaster* and the edrioasteroid *Hemicystites parasiticus*, typically cemented to *Striispirifer* valves, as well as more widespread elements: *Caryocrinites*, *Crinobrachiatus*, *Macrostylocrinus*, and *Ichthyocrinus laevis*. Conversely, *Stephanocrinus*, calceocrinids, and many less common crinoids, were completely absent. This distinctive fauna must have occupied a relatively narrow belt of transitional conditions between the highly diverse, bryozoan-rich thickets in shallower water to the north and the nearly barren Lewiston C facies to the south. This also appears to be the optimal facies for the large lichid trilobite, *Arctinurus*.

Moving to slightly deeper, muddier facies the fauna drops off rapidly, with scattered patches of *Striispirifer* giving way to small flat brachiopods, such as *Amphistrophia*, *Coolinia* and *Leptaena*. Upward, the mudstones of the upper B submember of Lewiston showed an abruptly decreased diversity and the addition of new elements, in particular large dendroid graptolites, *Conularia*, the trilobite *Arctinurus* and the crinoids *Dendrocrinus* and *Dimerocrinites* were present with fewer bryozoans or *Caryocrinites*.

The only trilobites that typify these deeper facies were *Dalmanites* and small *Trimerus*. These same genera characterize most all of the upper Rochester Burleigh Hill Member and represent the most tolerant of forms. Most all echinoderms fade out into deeper facies with the exception of widely scattered, long-stemmed *Dendrocrinus* and *Dimerocrinites*.

Silty beds tend to show a diversity of well-preserved trace fossils, but body fossils are generally absent. The middle part of the Lewiston C submember is nearly barren of fossils and with very low species richness; the total diversity over about 4 meters of section is only about 10 species. The near barren nature of Lewiston C in most locations probably reflects strongly stressed conditions of soft substrate, high turbidity, low light and perhaps low oxygen and/or elevated salinity conditions.

Interestingly, the faunal transition seen in the Lewiston B-C boundary deepening is closely mirrored in the C to D submember shallowing transition. Particularly notable is the return of elements of the *Homocrinus* fauna, including *Homocrinus parvus*, *Macrostylocrinus* and *Ichthyocrinus*, the ophiuroid *Protaster* and the rare edrioasteroid *Hemicystites*. Oddly, however, the flexible, *Asaphocrinus*, a relatively common form in the *Homocrinus* beds, is rare or absent in the upper transition but its ecological role may have been filled by *Lecanocrinus*, which is very rare in the lower Lewiston. The trilobite *Arctinurus* reappears, but is associated with more abundant *Calymene*. Clumps of well-preserved *Caryocrinites* reappear in the C-D, as in the B-C transition.

The upper portion of unit D and Lewiston E bryozoan beds display a distinctive abrupt increase in faunal diversity with more than 90 species recorded in the 1.5 meters thickness of this unit. The fauna is very similar but not identical to that of Lewiston B carrying most of the same bryozoans and brachiopods, although with somewhat higher diversity. Notably absent or very rare in D-E submembers are the tiny brachiopods *Dicoelosia* and *Skenidioides*.

However, this may in part reflect a bias because these small forms are known primarily from washings of disaggregated shales. To date, similar washings have not been obtained from the upper Lewiston. Other distinctive differences that do not simply reflect bias include the absence of *Anastrophia* and especially of calceocrinid crinoids in the upper Lewiston. Three genera of such "slipper" crinoids are present and moderately common in the Lewiston B, *Calceocrinus chrysalis*, *Charactocrinus pustulosus*, and *Eobalysiocrinus typus*. None of these crinoids have been found in the D or E units. The reasons for these differences are not known. However, in general, the similarities between the two units are striking and it appears that the same or very similar environment and biota migrated back into the region of present-day Niagara Escarpment outcrop belt from shallower areas to the north, where the organisms had retreated during the deepening recorded in unit C.

In addition to the broad B-C-D-E deepening-shallowing cycle, smaller, meter-scale cycles are also present in the Lewiston B and D successions. This is well illustrated in the data of the Caleb quarry (Figure 5). Each cycle commences with a thin bed or series of stacked beds of skeletal debris or pavement of shells (e.g. units 13, 18-19, 25-26, in part) these beds may also show a slight enrichment in bryozoans and cystoids and other echinoderms. These shelly beds have moderately elevated diversity. They are overlain by thicker intervals of sparsely fossiliferous mudstone, typically with a few thin calcisiltites (e.g., 1-17, 21-23, 26). Similar half-meter scale cycles of bryozoan rich and sparse mudstone occur in the Lewiston B. Together, these couplets of shelly and sparse sediments appear to reflect alternations of sediment starved conditions during which thin shell beds built up. Enhanced shell production and diversity may have been promoted by taphonomic feedback in which the development of shelly pavements permitted colonization of additional forms that required hard substrate for settlement. The cause of these periods of low influx of muddy sediments is not known with certainty; they may record periods of climatic drying during which less sediment was washed off from mountainous source areas. Alternatively, these may be times of minor sea level rise. As noted above, base level rise can cause sediment to be sequestered in nearshore areas. These smaller scale cycles were superimposed upon the general deepening or shallow trends of the larger Lewiston cycle.

Summary and Concluding Remarks

The extraordinary fossil assemblages excavated from the Caleb Quarry near Middleport, NY serve to highlight the richness of middle Silurian invertebrate animal life. These spectacularly preserved fossil assemblages occur in the middle Lewiston Member, famed Rochester Shale formation, the first formally named rock unit in North America and a widespread unit of gray mudstones and thin limestones of middle Silurian age (early Wenlock Epoch; Sheinwoodian Age), roughly 432 million years old. These exposures reveal rare glimpses of communities that inhabited a muddy Silurian seafloor beneath about 20 to 50 meters of normal marine water in the southern Subtropics, perhaps 20 degrees south of the paleoequator of Laurentia (ancestral North America). The organisms, including rare small corals and enigmatic conulariids, both probably tentacle bearing polyps, filter feeding brachiopods and bryozoans, elevated suspension feeding crinoids and cystoids, scavenging or predatory trilobites and predatory swimming cephalopods, lived together in loosely structured communities, interacting to varying extents (Figure 6).

In fact, these benthic organisms formed a general gradient of associations of decreasing diversity southward along a gently deepening seafloor or ramp. Shallower water areas to the north were inhabited by thickets of ramose (twig-like) and fenestrate (lacy) bryozoans with diverse associated brachiopods, less common attached bivalves, and stalked echinoderms, including especially small crinoids, cystoids and the uniquely abundant coronoid echinoderm *Stephanocrinus*. The trilobites were relatively diverse and dominated by *Bumastus*. Gastropods, including the platyceratids scavenged for food, crawling on the seafloor, or in some cases, attaching themselves over the anal vents of crinoid and cystoid hosts for free meals.

The primary predators of the day were represented not by fish as in modern marine communities, but by swimming nautiloid cephalopods, distant relatives of today's *Nautilus* with conical shells up to a meter or more long. At times of relatively lowered sea level these bryozoan thicket communities migrated southward into the study area of present day Niagara County.

The dense bryozoan patches faded southward into deeper water, where local outlying colonies provided substrates for the relatively long stemmed cystoid *Caryocrinites ornatus*, that occurred in clusters around bryozoans, and a few crinoids, but the primary organisms were the brachiopods *Striispirifer* and a few thin-shelled strophomenids, which formed local clusters and pavements on the muddy seafloor. Locally, brushy dendroid graptolites formed filter-feeding colonies somewhat analogous to the fenestrate bryozoans in shallower water. Trilobites, including *Arctinurus*, *Calymene*, *Dalmanites* and *Trimerus*, were relatively abundant and sometimes aggregated in groupings of several dozen individuals. These animals, lacking jaws, were probably soft-prey carnivores and scavengers adapted to furrowing into the muddy seafloor for worms and organic detritus. Their clusters may record mating aggregations, although they were in part very locally transported and oriented by basin-flowing gradient currents. During the relative deepening recorded by the Lewiston C submember, which occupies a majority of the Caleb Quarry section, the bryozoan thickets migrated northward and were replaced by these less diverse assemblages; however, the bryozoan dominated communities returned to this area tens of thousands of years later during a shallowing period recorded in the Lewiston D and E submembers.

Still further basinward, bottom waters became less well oxygenated and the unstable soft seafloor supported only sparse benthic life; epifaunal attached organisms became very rare. The primary remaining organisms were a few small flat shelled brachiopods, rare long stemmed crinoids in rare local patches, the trilobites *Dalmanites* and small *Trimerus* and rare ophiuroids. Deepest parts of the Rochester basin were seemingly nearly barren of life with the exception of soft-bodied animals, which produced the small branching feeding burrows of *Chondrites*. These deepest parts of the section are represented by the majority of the Lewiston C submember and again in the upper Rochester or Burleigh Hill Member. However, nearly all of the Rochester is barren dark gray, silty calcareous shale in the south end of Niagara Gorge, which provides a window into the deeper parts of the basin.

It is not entirely clear why these deeper areas remained so barren, but this pattern seems typical of the middle Silurian shales in eastern North America, including the nearly age-equivalent Massie Shale and the somewhat younger Waldron Shale in the North American mid-continent. Presumably a combination of low oxygen (though not anoxia), sediment instability and turbidity made these deeper areas largely uninhabitable.

Muds and silts of the Rochester Shale were ultimately derived from erosion of uplifted "Salinic" mountain belts in the tectonically active or orogenic areas, caused by ongoing collisions of the eastern margin of Laurentia to the east. The sediments were locally deposited as pulses associated with storm-created gradient currents mainly flowing from the north-northeast. At times, plumes and/or bottom flows of flocculated muds blanketed offshore areas disrupting, locally transporting, and exterminating seafloor communities and preserving their skeletal remains intact. Thin, shell rich limestones were formed by a combination of storm processing and interludes of sediment starvation, perhaps associated with minor episodes of sea level rise in relatively shallow water.

During the time interval represented by the 8 meters (26 feet) of strata at the Caleb Quarry, certainly tens to a few hundred thousands of years, there were minor climatic and sea level oscillations that produced cycles of sedimentation. Overall, the Lewiston B, C, and D-E submembers record a prolonged cycle, perhaps 400,000 years, involving fairly abrupt deepening (B to C) and gradual shallowing of the epicontinental sea with a water depth change of perhaps 20 to 30 meters. The cause of such sea level oscillation is uncertain but may reflect glacially induced rise (during melting of ice) and fall. The rise and fall of sea level was paralleled by migration of benthic seafloor organisms, which apparently tracked their favored environments.

Thus, the fossil beds near Middleport give significant and, at times, very clear insights into life and depositional environments on a muddy sea floor during a key time of transition, when the very first life forms – tiny psilophyte plants and myriapod (millipedes, centipedes) animals, were just emerging on land and just prior to a time when jawed fishes became an important part of the marine ecosystem. Here, hosts of typical middle Paleozoic marine animals lived on a subtropical muddy seafloor and died, sometimes dramatically during the backwashes of major Tropical storms, thriving locally and retreating in response to changing climates and major and minor changes in relative water depth.

Perhaps the broadest story these fossils tell is one of relative stability in the face of substantial environmental change. As with many Paleozoic assemblages, there is little evidence for evolution of the many dozens of species of organisms during the hundreds of thousands of years recorded in the Rochester Shale. A few species may have gone extinct during the course of this time and a very few may have immigrated into the local area, but the majority of the species remained in relative stasis: a stable Silurian "dynasty." Rather than changing, these organisms primarily responded to environmental change by tracking their preferred environments. More rapid restructuring of communities and evolution may eventually have accompanied the changes that were associated with deposition of the Lockport Group, but, in part, this may record an artifact of poor preservation in these dolomitized rocks. As more data emerges, it is apparent that a majority of Rochester Shale species probably persisted longer until the greatly increased salinity and/or shallowing associated with a transition to the Salina Group ultimately exterminated a majority of the long ranging species and ushered in the new "dynasties" of the later Silurian and the Devonian Period.

Acknowledgments

I greatly appreciate the input of numerous past students including James Eckert, Bea Yea Lin Eckert, William Goodman, Steve LoDuca, Wendy Taylor and Denis Tetreault, for their work on stratigraphy and paleontology of the Rochester Shale and related Silurian units. Other people who have helped and contributed along the way include Craig Clement, George McIntosh (Rochester Museum and Science Center), George Sanders, Beverly Seyler and Mark Pierce. This paper benefitted from careful editing and insights by Michael Lask and David Meyer. My research was supported by grants from the donors to the American Chemical Society, Petroleum Research Fund and NSF Grant EAR 0518511. This is a contribution to the International Geoscience Programme (IGCP) Project No. 591 – *The Early to Middle Paleozoic Revolution*.

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Figure 6 – facing page

Reconstruction of Rochester Shale seafloor depositional environment for transitional community type, slightly deeper than shallowest bryozoan thicket assemblages. Note local patches of *Fenestella* (far left), *Chilotrypa* (center) and *Hallopora* (far right) bryozoan colonies provide attachment substrates for the cystoid *Caryocrinites* (right); note small coral *Favosites parasiticus*, attached to the column of specimen on the far right, and the crinoid *Macrostylocrinus* (left); note the attached commensal gastropod, *Naticonema*. Smaller crinoids (*Homocrinus*) near center of view are attached to small shell fragments. Small solitary rugose corals (*Enterolasma*), the brachiopods *Striispirifer*, *Atrypa*, and *Leptaena*, and the ophiuroid (brittle star) *Protaster*, are scattered on the seabed. At the center, the trilobite *Dalmanites* scuttles along the seafloor and the predatory nautiloid cephalopod *Dawsonoceras* has captured a platyceratid gastropod. Note burrowing by sediment-feeding worms and a bivalve into the storm deposited, hummocky cross-laminated siltstone in the slice of sediment at base of view.

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This illustration is part of a mural showing three different Silurian environments. The mural is on display at the Giants Rib Discovery Centre in the beautiful Dundas Valley Conservation Area in Southern Ontario, Canada

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Figure 6