

Official Publication of the Mid-America Paleontology Society Volume 36 No. 2 Date: April, 2013



# THE DEVONIAN

A LOVE OF FOSSILS BRINGS US TOGETHER

# M.A.P.S. Digest--EXPO XXXV Edition

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## Preface

The editors wish to thank the contributors for responding to the Call for Papers in such a timely manner. The papers represent a wide range of Devonian related topics contributed by our members and others. The editors would like to especially thank Dr. Paula M. Mikkelsen of PRI for her efforts in providing reprints of *American Paleontologist* articles and for encouraging various authors to supply original papers. We would also like to thank Brian J. Witzke for delivering the keynote address.

## **About the Cover**

The cover image illustrates a Devonian seafloor preserved in the Hunsrück Slate Lagerstätte exposed at Bundenbach, Germany. Starfish include: (back to front) *Furcaster palaeozoicus, Loriolaster mirabilis, Bundenbachia beneckei*, and *Encrinaster sp.* Crinoids include (left to right): *Parisangulocrinus zeaeformis, Codiacrinus schultzei, Calycanthocrinus sp.*, and *Hapalocrinus sp.* Also pictured are sponges, a conulariid, and a trilobite (*Chotecops sp.*). (Original artwork © Rob Sula used with permission.)

## Iowa City, Iowa April 5, 6, & 7, 2013

## John Catalani and Chris Cozart, Editors

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## A Brief Introduction to the Devonian Period John A. Catalani

#### Background

The Devonian Period (approximately 415-359 million years ago) was one of the most significant time periods in Earth's history (Fig. 1). At this time, Laurentia was in the southern hemisphere and both physical and biological processes were operating in overdrive. The Acadian Orogenic phase of the Caledonian Orogeny deposited one of the most significant clastic wedges (Catskill Delta Complex) as well as contributing to the on-going uplift of the Appalachian Mountains. Biologically, the Devonian finally witnessed the dominance of vertebrates, fish, as well as the first true forests. Additionally, due to aggressive collecting, the story of the evolution of specialized fish and tetrapods and possibly, although this is by no means a certainty, the first appearance of true amphibians during the Devonian has become increasingly better understood.



**Fig. 1.** Chart outlining the stages of the Devonian Period, and its relation to other geologic periods, as well as the sea-level curve and glacial intervals. PD = present-day. (From Haq and Schutter 2008, Fig. 2.)

## **Acadian Orogenic Event**

During the Devonian, the Acadian Orogen was responsible for the deposition of one of the largest clastic wedges ever formed--the Catskill Delta Complex. Recently, the long (nearly 200 million years, Cambrian through Devonian) sequence of events that closed the Iapetus Ocean and initiated the formation of the northern Appalachian Mountains has been termed the Caledonian Orogeny. Therefore, in this interpretation it can be reasoned that the "Caledonian Orogeny encompasses a series of orogenic events or phases, each of which has a defining set of time-space characteristics" (McKerrow *et al.* 2000, p. 1149). This process involved various tectonic (subduction and collision) events such as arc-arc and arc-continent during the earlier Taconic Orogen and continent-continent during the later Acadian Orogen involving the "continental margins of Laurentia, Baltica and Avalonia bounding the Iapetus Ocean" (p. 1150). These events affected what are now known as the Northern Appalachians, Greenland, the British Islands, and Scandinavia among others.

Thus, during the Caledonian Orogeny, the Iapetus Ocean closed as the continental fragments of Laurentia and Baltica and the Avalon Terrane collided (Figs. 2 through 4). Separating this newly coalesced continent from Gondwana was the Rheic Ocean destined itself to be closed as these two continents approached each other and finally collided during the Alleghenian Orogeny resulting in the Southern Appalachians.



Fig. 2. Early Devonian paleogeography. (Modified from Ron Blakey http://jan.ucc.nau.edu/~rcb7)



Fig. 3. Late Devonian paleogeography. (Modified from Ron Blakey http://jan.ucc.nau.edu/~rcb7)



**Fig. 4.** A: Geologic setting after the Taconic Orogen and before the onset of the Acadian Orogen. B: Geologic setting of the Acadian Orogen when Avalonia collided with Laurentia. (Modified from Lynn S. Fichter http://csmres.jmu.edu/geollab/vageol/vahist/index.html) The progradational clastic wedge known as the Catskill Delta Complex formed as the Acadian Mountains (essentially the Northern Appalachians) eroded and deposited westward-thinning black shales. These Upper Devonian shales resulted from anoxic sediments and are on display in the gorges of the Finger Lakes District of upstate New York. At Taughannock Falls State Park north of Ithaca, NY, Taughannock Creek has cut a gorge over 60 meters deep through the shales and sandstones of the Genesee Group (Fig. 5).



**Fig. 5.** Thick Upper Devonian clastics of the Geneseo, Sherburne, and Ithaca Formations of the Genesee Group as seen at the upper Taughannock Falls gorge near Ithaca, New York. (Photograph by author.)

## **Devonian Climates and Sea Levels**

Devonian climates fluctuated throughout the period. In the Early Devonian, hot and dry, almost arid conditions were experienced everywhere and extensive evaporite deposits (mainly gypsum and salt) resulted, many of which are mined today. Shallow seas covering some of the continental fragments were temperate in nature. The Middle Devonian experienced shallow and warm seas worldwide. During the Late Devonian, however, glaciers advanced on the southern land masses severely cooling the climate.

Sea levels fluctuated slowly throughout the period. Sea level fell slightly beginning in the Late Silurian resulting in a lowstand at the beginning of the Devonian then rose to a highstand near the Givetian/Frasnian boundary and then fell gradually but consistently to the end of the period with

a conspicuous lowstand near the Devonian/Carboniferous boundary (see Fig. 1). These sea-level curves also revealed that the large-scale fluctuations were composed of many small-scale sedimentary cycles as a result of orbital forcing as well as eustatic and tectonic processes.

## **Devonian Life**

The Devonian Period was witness to monumental evolutionary events including the first trees and forests and the evolution of tetrapods from lobe-finned fish.



**Fig.6.** Two types of Devonian trees--see text for descriptions. Solid triangles indicate permanent structures. (From Meyer-Berthaud and Decombeix 2007, Figure 2.)

Vascular plants, which had invaded the land by the Late Silurian, were fairly small during the Early Devonian, rarely exceeding one meter in height, and were composed of plants that reproduced by spores. In the transition from water to land, plants had to adapt by evolving a waxy coating (cutin) to prevent evaporation, vascular tissues to transport water and provide rigidity, leaves with openings (stomata) for gas exchange, and roots to stabilize the stalk and take in water and nutrients. During the Devonian, land plants experienced rapid evolution and by the Late Devonian had produced large trees. One type of tree was composed of a permanent trunk, replaceable crown-concentrated branches and a limited root system. By the latest Devonian, however, more modern-looking trees, such as the 30 m tall *Archaeopteris*, had evolved that were composed of wood and possessed not only an extensive root system but also permanent branches occupying the entire trunk with leaves at their periphery (Fig. 6). Additionally, seed-bearing plants evolved during the latest Devonian. True

forests, based on assemblages collected at the famous Gilboa quarry in New York State, were present by at least the late Middle Devonian and Devonian coals are mined in many countries.

In the sea, large coral reefs (Fig. 7) developed that became the home for a variety of other animals and brachiopods became incredibly diverse. Most importantly a new group of cephalopods, the ammonoids, evolved from bactritid ancestors and lived beside their much older cousins the nautiloids. The only Devonian ammonoid order was the Goniatitida, the goniatites. Although their morphologies varied, the shells of most goniatites were small, relatively smooth, and involutely coiled similar to today's *Nautilus*. In addition, it appears that, based on a deep hyponomic sinus, the goniatites were good swimmers.



**Fig. 7.** University of Iowa Museum of Natural History diorama depicting a coral reef from the Devonian of Iowa. (Modified from Museum of Natural History photograph 8B3-0003, © The University of Iowa Museum of Natural History.)

Although it is the evolution of tetrapods that is of prime interest when studying the Devonian, vertebrates were not the first animals to venture onto dry land--various insects and other arthropods preceded vertebrates.

The Devonian is often called the "Age of Fishes" because fish evolved into many forms during this time. Although placoderms, primitive armored jawed fish, produced the largest predators of the time such as the 10-12 m long *Dunkleosteus*, it is the appearance of modern fish groups that was the most significant development. By at least the Middle Devonian both cartilaginous (sharks and rays) and bony (ray-finned and lobe-finned) fish had evolved. Sharks were amazingly diverse and bizarre in terms of body morphology. However, by far the most significant group was the lobe-finned fish that were the ancestors of tetrapods. Of the three groups of lobe-finned fish (lungfish, coelacanths, and crossopterygians), it was the fresh-water crossopterygians, such as *Eusthenopteron*,

that led to the first tetrapods. The traditional explanation that we were told in school was that airgulping lobe-finned fish, mainly *Eusthenopteron* with bones articulated in their pectoral fins, crawled from pond to pond during droughts in the Devonian thus strengthening their developing "legs". The result was a tetrapod, *Ichthyostega* was always mentioned, which was fully adapted to life on land. Problem was that at the time transitional forms beyond *Eusthenopteron* had not yet been discovered and *Ichthyostega* was viewed at the time as a more-or-less fully-functional land-living tetrapod. Fortunately, continued collecting turned up a number of "transitional" or stem-group forms that displayed morphologic characteristics increasingly more tetrapod-like filling out our assessment of the evolution of land-living vertebrates.

A very brief description of several of these intermediate forms (Fig. 8) will serve to illustrate some of the morphological changes that occurred during the fish-to-tetrapod transition. Besides *Eusthenopteron*, there were several fish present in the Late Devonian that displayed increasingly tetrapod-like structures. One of these fish was *Panderichthys* found in late Givetian or early Frasnian rocks of the Lode Formation of Latvia. The pelvic fin of *Panderichthys* was more primitive and smaller than its pectoral fin indicating that it was the pectoral fins that first began to change from a fin to a true limb. Locomotion along the shallow-water stream or lake bottom or even on land was feasible for *Panderichthys* and would have been facilitated mainly by the pectoral fins, similar to the method of locomotion on land undertaken by the extant "walking catfish", in contrast to true land-tetrapods which rely primarily on the hindlimbs.



**Fig. 8.** Cladogram of some of the stem-group fish/tetrapod fossils described in text. sp = spiracular opening. (From Clack 2007, Fig. 1.)

Possibly the most celebrated stem-group individual found recently is *Tiktaalik roseae* found in early Frasnian rocks of Ellesmere Island. *Tiktaalik* possessed several significant tetrapod-like derived features. These features included a flattened skull and elongated snout, eyes located on the top of the skull, wider spiracular opening and expanded spiracular chamber indicating more advanced respiratory abilities, and pectoral fins with articulated bones more advanced than in *Eusthenopteron* but still retaining fish-type fin rays. Additionally, the loss of extrascapular bones meant that the shoulder of *Tiktaalik* was not firmly attached to the skull--*Tiktaalik* was the first vertebrate that possessed a flexible neck. These features endowed *Tiktaalik* with a greater range in motion of the shoulder and wrist joints thus facilitating increased flexibility and a more upright stance to lift and support the body above the bottom as well as to lift its head above water to gulp air. It may even have been possible for *Tiktaalik* to make brief forays onto land to, say, avoid predators. *Tiktaalik* has been placed in the "morphological gap" between *Panderichthys* and *Acanthostega*.

The three critters described above can be referred to as tetrapod-like fish. However, in the latest Devonian, the Famennian, several fish-like tetrapods evolved. The first of these, *Ventastega curonica*, was found in late Famennian rocks of western Latvia. Although structures in the skull, such as a shovel-shaped snout and large eye holes positioned at the top of the skull, gave it an early-tetrapod shape, morphometric analysis showed that the proportions of the skull were more fish-like. *Ventastega* also possessed structures, such as large spiracular openings, that were at first used to facilitate air-breathing and were eventually instrumental in the development of the vertebrate middle-ear. The lower jaw had a tetrapod-like structure but retained fish-like features, such as coronoid fangs. The morphology of clavicle and pelvic structures were also tetrapod-like and *Ventastega* probably possessed limbs with digits and would, therefore, be classified as a true tetrapod. Thus, the suite of characters possessed by *Ventastega* is what one would expect in a transitional animal that is positioned between *Tiktaalik* and *Acanthostega*.

The two most famous stem-group tetrapods are *Acanthostega* and *Ichthyostega* both from the Late Famennian of East Greenland and known from extensive, well-preserved material. These two taxa had much in common such as backward-directed hindlimbs shaped more like paddles for swimming than legs for walking, fish-like tails that facilitated movement in water, and multi-digit limbs--eight digits on the limbs of Acanthostega and seven digits on the limbs of Ichthyostega. They were contemporaries in space and time but inhabited different environments--Acanthostega was almost exclusively aquatic while Ichthyostega was at least partially terrestrial but, as recent evidence suggests, both in a woodland habitat. Several structural limitations confined Acanthostega to the water including internal gills, wrist and ankle joints incapable of bearing weight on land, and primitive pectoral structures. However, the forelimbs of Acanthostega probably both aided the animal in its movement on stream/lake bottoms and assisted it in lifting its head out of stagnant, poorly-oxygenated water to gulp air. The developing and strengthening limbs, which we now believe evolved while these animals were confined to a water environment, allowed the early tetrapods to move more efficiently on lake or stream bottoms before venturing out onto land. Recent (Pierce et al. 2012) three-dimensional reconstructions of the limb joints of Ichthyostega indicate a lack of mobility that, along with a rigid thorax "due to large overlapping ribs" (p. 524), would have severely restricted its movement on land.

Finally, there is *Tulerpeton* known from well-preserved but fragmentary remains of the

shoulder, pectoral and pelvic limbs, and some skull elements collected in Late Famennian rocks from Russia. The limbs of *Tulerpeton* bore six digits each and its pectoral girdle was more robust than that of other Devonian tetrapods but, as with *Acanthostega* and *Ichthyostega*, the large hindlimbs were more paddle-like than foot-like. *Tulerpeton* may have relied more on air for breathing than water since gill-supporting structures were absent and therefore it probably lacked internal gills.

Although some of these animals have at various times been touted as the first true amphibian, it appears that distinction must be reserved for some Early Carboniferous form such as *Casineria* from Viséan rocks of Scotland. Be that as it may, the discovery of numerous fish/tetrapod forms forced us to alter our concept of evolutionary transformations from a traditional view of "missing links" as individual species or forms that link two well-known animal groups to a more realistic and holistic view that involves a suite of transitional forms--members of a continuum that delineate an evolutionary trend often resulting in a lifestyle change such as the water-to-land transition. Additionally, analysis of the derived features possessed by these intermediates illustrate both the substantial morphologic diversity they possessed and the view that most tetrapod-like structures evolved in the water and not on land as had been previously assumed.

#### **Bioevents and Extinctions**

The Devonian Period was punctuated by over a dozen biodiversity crises and extinctions termed bioevents. Three of these bioevents--Taghanic Biocrisis, Kellwasser Events, Hangenberg Event--were major biodiversity crises (Fig. 9).



**Fig. 9.** Late Devonian series of extinction events that resulted in the collapse of reef communities. (From Wood 2004, Text-fig 2.)



**Fig. 10.** Diagrammatic stratigraphic column of the rock units involved in the Taghanic Event of the northern Appalachian Basin as exposed in the gorges of upstate New York. (From Zambito 2011, Chapter 1, Figure 3.)

The Taghanic Event or Biocrisis began in the late mid-Devonian (Givetian) and was recorded in the rocks of the Hamilton, Tully, and Genesee Groups (Fig. 10). This event was a protracted event that began in the Late Givetian and may have lasted until the Frasnian-Famennian (F-F) extinction. As outlined by Zambito (2011, p. 4), the Taghanic Biocrisis can be resolved into three pulses:

- 1. invasion by the equatorial Tully Fauna and near total replacement of the endemic Hamilton Fauna;
- 2. return of the Hamilton Fauna and total replacement of the Tully Fauna; and
- 3. invasion of the cosmopolitan Genesee Fauna and total replacement of the Hamilton Fauna.

These events were facilitated and accompanied by several physical factors including global warming, spread of arid climatic conditions, burial of organic carbon, and dysoxia of epicontinental seas. However, the most significant factor was a global rise in sea levels (the Taghanic Onlap) regionally associated with the Acadian Orogen that overflowed the Transcontinental Arch linking formerly isolated basins and allowing invasions by equatorial cosmopolitan faunas resulting in the disappearance of provinciality. Taxa most affected by this biocrisis include corals, trilobites, brachiopods, and ammonoids.

The Frasnian-Famennian (F-F) boundary extinction is considered one of the so-called "Big Five" extinction events and resulted in an overall 57% extinction at the generic level. The collapse of reef communities continued and was most severe during the F-F event (60-65% extinction rate). Although they are major centers of marine biodiversity, reef communities "are particularly susceptible to the factors that cause mass extinction, and that recovery occurs more slowly than in other communities" (Wood 2004, p. 417).



**Fig. 11.** Spindle diagrams illustrating the decline in ammonoid diversity resulting from the F-F Boundary (A) and End-Devonian (B) biocrises. (From House 1999, Figure 2.4.)

The F-F Boundary Event consisted of two intervals: the Lower and Upper Kellwasser Events named after black limestone horizons in Germany (Fig. 9). During the Lower event, sea levels continued to rise from the Taghanic Onlap but that was followed by a drastic fall in sea levels. Similarly, the Upper event saw an initial rise in sea levels followed by an even more drastic fall that offlapped the Transcontinental Arch and exposed carbonate platforms thus decimating those ecosystems. The F-F Event was somewhat protracted over 1-2 million years and displayed a stepwise extinction pattern. Along with the continued collapse of the coral/stromatoporoid reefs, brachiopods and ammonoids were severely affected (Fig. 11A).

There has recently been some discussion whether or not the F-F Event can be called a true mass extinction. Stigall (2012, p. 4) argues that F-F extinction rates were no higher than background rates and that "an anomalously low rate of *speciation*, the origination of new species, was the primary cause of this decline in biodiversity". Be that as it may, the resulting impoverished Famennian fauna was one of low diversity.

The final Devonian bioevent occurred just before the Devonian/Lower Carboniferous boundary. This event has been called the Hangenberg Event named after the Hangenberg black shales in Germany. The Hangenberg represents the final event in the fluctuating environments of the Devonian. The generic extinction level was approximately 45% and included the total extinction of stromatoporoids and placoderm fishes as well as one of the most severe ammonoid bottlenecks in Earth history (Fig. 11B). Based on the level of vertebrate extinctions (more than 50% for marine and nonmarine vertebrates), the Lower Carboniferous tetrapod fossil-record hiatus known as Romer's Gap "emerges as a postextinction trough--a lull in abundance and diversity that can last for millions of years after such an event" (Sallan and Coates 2010, p. 10134).

Many causal factors have been proposed for the last two bioevents and include comet showers (timing is a bit off, though), organic carbon burial and drawdown of atmospheric  $CO_2$ cooling the planet, warming of oceans resulting in dysoxia, species invasion, and reduced speciation events. However, the most reasonable explanation for the fluctuating sea levels that were at the heart of these events is southern-hemisphere (and possibly one or more episodes centered on the Appalachians) glacial/interglacial episodes that alternately lowered sea levels and exposed shelf areas and then raised sea levels drowning shallow-water ecosystems. Some of these glaciations appear to have been as extensive as the more recent Pleistocene glacial episodes. And the cause of these glacial episodes was the same as for the Pleistocene: orbital forcing (Milankovitch cycles), particularly the 100,000 year eccentricity (circularity of Earth's orbit) cycle. Whatever the causes of these events, the dawn of the Lower Carboniferous saw a decimated fauna of low diversity.

## **Further Reading**

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## **Appendix I: Representative Devonian Invertebrate Fossils**



## Ammonoids from the Devonian of Iowa

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#### Introduction

Ammonoid cephalopods had their origins in the Devonian Period, quickly becoming an important component of mid-Paleozoic through Mesozoic marine faunas. With the focus of this year's Expo 35 being the Devonian, and with the venue change to Iowa, it seemed reasonable to pen an article updating some of the recently gleaned information on Iowa's Devonian ammonoid fossil record. The purpose of this article is to list the ammonoid genera and species present in the Iowa Devonian and to tie them into the proper stratigraphic intervals or standard ammonoid zones where possible.

Though sparse, discoveries over the past several decades have shown that ammonoids from Iowa's Devonian rocks are not as rare as once thought. In fact, ammonoids are encountered with some frequency if one knows exactly where to look. Iowa's Devonian rock record has three principal ammonoid producing intervals (see Figure 1). Previous works on Iowa's Devonian ammonoids (e.g. Miller, 1936; Fenton & Fenton, 1924) have become quite dated in respect to zonal correlations. More recent works (e.g. Baker, Glenister, & Levorson 1986; Hanson & Preslicka, 1996; Preslicka, Newsom, Blume & Rocca, 2010) focused on or mentioned ammonoids from a single formation and did not attempt to provide a complete ammonoid species list for the entire Iowa Devonian.

Currently known ammonoid species from the Devonian of Iowa, from oldest to youngest, include:

Little Cedai	Formation
Lowe	r Solon Member
	Tornoceras (Tornoceras) iowaense Miller 1936
Lime Creek	Formation
"Ama	ana Beds"
	Manticoceras regulare Fenton & Fenton 1924
	Sphaeromanticoceras rhynchostomum (Clarke 1899)

Tornoceras (Tornoceras) uniangulare (Conrad, 1842) Cerro Gordo Member Manticoceras regulare Fenton & Fenton 1924 Owen Member Crickites lindneri (Glenister 1958) Sphaeromanticoceras rhynchostomum? (Clarke 1899)

### **Maple Mill Formation**

English River Siltstone Member *Cymaclymenia striata* (Münster 1832) *Cyrtoclymenia strigata* House 1962 *Imitoceras opimum* (White & Whitfield 1862)

## Middle Devonian - Givetian Stage Cedar Valley Group, Little Cedar Formation

#### Lower Solon Member

Iowa's oldest known ammonoid species is *Tornoceras (Tornoceras) iowaense* Miller 1936. Miller described this species from the two specimens known to him at the time, and the age of the rocks yielding this fossil were miss-correlated as well. Recent discoveries by the Black Hawk Gem & Mineral Society (BHGMS) in east-central Iowa have recovered over one hundred specimens of this ammonoid (see Plate 1), contained in the most diverse Devonian cephalopod fauna, containing at least 13 species (~12 nautiloid, 1 ammonoid), known in the state. The BHGMS is presently working with the University of Iowa Geoscience Repository on a series of articles describing this unique cephalopod fauna.

T.(T.) iowaense is known to occur only in the Lower Solon Member (see Figure 1), and thus would potentially be of use as a guide fossil were it not for its limited geographic range - all known specimens are from a three county area in east-central Iowa. T.(T.) iowaense is also of limited correlation use in the worldwide ammonoid zonation, as it is an endemic - that is, a local species - it is not known to occur outside of Iowa.

T.(T.) iowaense occurs with conodonts of the Middle Varcus Zone, and as such, correlates to the Maenioceras Stufe, MD-II-D (see Figure 2) of the standard ammonoid zonation of New York (House & Kirchgasser 2008).

T.(T.) iowaense is the only ammonoid known from the entire Cedar Valley Group, which encompasses four formations, each comprising a major transgressive-regressive cycle (Witzke et al, 1989). The absence of other (younger) ammonoid genera is somewhat puzzling, given that the remaining Cedar Valley sequence is generally quite fossiliferous. It seems likely that a unique set of environmental circumstances led to the presence of T.(T.) iowaense in the Lower Solon Member. Paleozoic ammonoids were known to prefer deeper water offshore environments, and much of the remaining Cedar Valley interval was deposited on a relatively shallow water carbonate platform perhaps too shallow to attract ammonoids. There are a few specimens of  $T_{\cdot}(T_{\cdot})$  iowaense which hint at the possibility of a sexual dimorph - that is shells of males and females which are differing sizes at maturity. Recognition of dimorphism requires examination of large collections of well preserved adult specimens that have retained mature modifications (Davis, Furnish, and Glenister, 1969).

### Upper Devonian - Frasnian Stage Lime Creek Formation

#### "Amana Beds"

Ammonoids have been collected from the Lime Creek Formation of northern Iowa for well over a century (Miller 1936). However, most of the specimens from the type area of the Formation are fragmentary and rather poorly preserved. During the past few decades, strata producing well preserved ammonoids were discovered in east-central Iowa, and are known informally as the "Amana Beds" of the Lime Creek Formation.

The "Amana Beds" are interbedded shales and limestones which reach a thickness of up to 200' in well logs in east central Iowa. However, only the top ten feet or so are exposed at the surface at the two main exposures, and the rocks are not very resistant and weather over quickly. One of these is a highway roadcut which can only be viewed for a short time after the road is regraded. The other exposure is a creek cut on private land, which provides productive exposures only during wet cycles when the creek is actively cleaning off the exposures.

However, thanks to road reconstruction in the 1980's and the flood of '93 leading to more collecting in the 1990's, the most abundant and best preserved ammonoid fauna from the Devonian of Iowa was assembled from these exposures (see Plates 2-5). That is not saying much of course, considering only three genera and species are represented in the "Amana Beds" outcrops and another one (possibly two) different species (see Plates 6 & 7) in other exposures of the Lime Creek Formation to the north. Still, one of them, *Sphaeromanticoceras rhynchostomum* (Clarke, 1899) (see Plate 4) has a worldwide distribution and allows direct correlation of the "Amana Beds" to the Manticoceras Stufe, UD-I-J Neomanticoceras Geozone (see Figure 2).

The "Amana Beds" fauna also include the largest and best preserved specimens of the previously poorly known *Manticoceras regulare* Fenton and Fenton 1924 (see Plate 2). This species is the most commonly encountered ammonoid in the "Amana Beds", but appears to be endemic to Iowa, and therefore of limited stratigraphic use beyond the state's borders. *M. regulare* also hints at possibly being dimorphic (see Plates 2&3), although more specimens which retain mature modifications will be needed to verify this.

The "Amana Beds" have also yielded a single specimen of *Tornoceras (Tornoceras) uniangulare* (see Plate 5) which is a long ranging species and of little use stratigraphically.

The exposed portion of the creek outcrop of the "Amana Beds" is entirely contained within a single conodont zone, that of *Palmatolepis foliacea* which indicates Zone #12 of the Frasnian Montagne Noire conodont zonation (Klapper 1989). Flooding in the late 1990's revealed that the "Amana Beds" also likely contain the lower Kellwasser Event near the exposure top (see Figure 3).

This may prove that some portion of the "Amana Beds" actually correlate with the lower Owen Member of the Lime Creek Formation type area, as opposed to the Cerro Gordo member, which was the previously assumed lateral equivalent.

#### **Cerro Gordo Member**

The Cerro Gordo Member has produced rare fragmentary specimens of *Manticoceras regulare* Fenton and Fenton in northern Iowa since the time of Calvin (Miller 1936). These specimens pale in comparison both in numbers and quality of preservation with those specimens of *M. regulare* known from the "Amana Beds" to the south. One possible explanation for this discrepancy is that *M. regulare* may have clustered in the sea in the "Amana Beds" area, and the battered shell fragments found to the north in the Rockford area represent drift shells from dead or dying animals.

#### **Owen Member**

The Owen Member of north-central Iowa has produced specimens of two ammonoid genera, *Crickites lindneri* (Glenister 1958) and *Sphaeromanticoceras rhynchostomum*? (Clarke 1899) (see Plates 6 & 7). The problem lies in the fact that the precise stratigraphic position of the ammonoid specimens within the rocks of the Owen Member is not known. The Owen Member is now known to contain the two Kellwasser Events (see Figs. 1 & 2) within its strata. These are two closely spaced major transgressive pulses which culminated in an important extinction event that marks the Frasnian-Famennian Stage boundary.

*Crickites lindneri* is known from New York state only after the first Kellwasser event but prior to the second (House & Kirchgasser, 2008 p 79). *S. rhynchostomum* is not known to range that high in the New York section. There are several possible explanations for this discrepancy. The Owen Member specimen in question could be misidentified and perhaps could properly belong to *S. aff. rickardi* which does occur after the first Kellwasser event and co-occurs with *C. lindneri* in New York state (House & Kirchgasser 2008, p 79). Another possibility is that the *S. rhynchostomum*? specimen was found from Owen strata below the Lower Kellwasser event interval and is therefore older than the *C. lindneri* specimens.

The only solution to this problem will be to find in-situ ammonoid specimens in the Owen Member, and note their position relative to the Kellwasser Events. This will allow proper correlation with the "Amana Beds" to the south as well as to worldwide ammonoid geozones.

## Upper Devonian - Famennian Maple Mill Formation

#### **English River Siltstone Member**

This interval yields a potentially important fauna of ammonoids, albeit one that is not particularly well preserved. The specimens from this level are often fragmentary and are poorly cemented siltstone molds, frequently without sutural preservation which makes identification difficult. Many times the only preserved sutures will be along the edge where the original shell happened to have broken along a suture line prior to burial and fossilization. Exposures of the English River Member occur mainly in two areas of far southeast Iowa, along the English and Mississippi Rivers.

*Cyrtoclymenia strigata* House 1962 is the most common ammonoid encountered in the English River Member, and produces the largest known ammonoid specimens (diameter up to 25cm) from the Iowa Devonian. Fragments of this species are known to the authors from both English River Member outcrop areas (see Plate 8). This species is characterized by its rapidly expanding shell whorl height, and its relatively small umbilicus.

House (1962) also listed *Cymaclymenia striata* and *Imitoceras opimum* as being found in the English River Member along the Mississippi River (see Plates 9 & 10). *Imitoceras* is a long ranging genus, and is of little stratigraphic use. *Cymaclymenia* is of potentially more interest as its occurrence is worldwide, and its presence may indicate that the English River specimens belong to the Wocklumeria Stufe UD-VI-E, Cymaclymenia Geozone.

Ammonoids from the English River Member are potentially important as the New York section does not include specimens from this time interval (House & Kirchgasser, 2008). The English River Member provides a glimpse into faunas from some of the youngest Devonian rocks known in the North American Midcontinent area. Only one younger formation, the Louisiana Limestone, lies below the Devonian-Mississippian boundary.

### Conclusions

Ammonoids from the Devonian of Iowa, while not common, are not as rare as was once assumed. The purpose of this article was to summarize what genera and species are currently known and to try to tie this information into the modern ammonoid zonations.

Further collecting is much needed at all three of Iowa's Devonian ammonoid producing levels. More specimens which retain mature modifications are needed to verify or disprove whether the endemic to Iowa species *Tornoceras (Tornoceras) iowaense* and *Manticoceras regulare* are dimorphic in nature.

More careful collecting will be especially important in the Owen Member and English River Member intervals, whose contained ammonoid faunas are of greatest stratigraphic interest and may be able to shed some light on the Late Devonian end Frasnian and end Famennian ammonoid extinction events.

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**Figure 1. p. 24.** (Modified from Figure 3 of Day 2006.) Stratigraphic and biostratigraphic framework for the Middle-Late Devonian (late Eifelian- Famennian) strata of the Iowa Basin.

Abbreviations for Ammonoid Occurrence column:

T.I. = Tornoceras (Tornoceras) iowaense T.U. = Tornoceras (Tornoceras) Uniangulare S.R. = Sphaeromanticoceras rhynchostomum M.R. = Manticoceras regulare S.R? = Sphaeromanticoceras rhynchostomum? C.L. = Crickites lindneri I.O. = Imitoceras opimum Cym.S. = Cymaclymenia striata Cyr.S. = Cyrtoclymenia strigata.

Colored arrows point to approximate level of known occurrences: Lower (Red) = Little Cedar Formation; Middle (Green) = Lime Creek Fm; Upper (Blue) = Maple Mill Fm.

**Figure 2. p. 25.** (Modified from House & Kirchgasser 2008, Figure 20.) Diagram illustrating the evolution of Devonian ammonoid families. The width of the bars corresponds to the number of genera at particular times as indicated by the scale. Also indicated are the named environmental stress events. (Colored) arrows/bars mark approximate levels of Iowa Devonian ammonoid occurrences: Lower (Red) = Little Cedar Formation; Middle (Green) = Lime Creek Fm; Upper (Blue) = Maple Mill Fm.

## Figure 1

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Figure 2





**Figure 3.** Exposure of upper portion of the "Amana Beds" of the Lime Creek Formation (Upper Devonian - Frasnian) in east-central Iowa. Highest in-situ occurrences of *Manticoceras regulare* and *Sphaeromanticoceras rhynchostomum* are in Unit #6. Hammer head (arrows) is at possible Lower Kellwasser Event (black shale bed at base of Unit 9). Shelly benthic fossils are common in the layers up to that boundary. Above the hammer head no shelly benthic fossils are known, only ammonoid aptychi and conodonts (Hanson & Preslicka 1996). The most likely explanation for this sudden faunal and lithographic change is a transgressive event (sea level rise).



**Plate 1.** *Tornoceras (Tornoceras) iowaense*, the oldest known ammonoid from Iowa's rock record. This is the only ammonoid species known from the entire Cedar Valley Group (Late Middle and Early Upper Devonian). Recent discoveries by members of the Black Hawk Gem & Mineral Society have recovered over a hundred specimens of this rare species. Specimen found and prepared by T. Blume.



**Plate 2.** *Manticoceras regulare* (SUI #62376 diameter 16.5cm) from the Lime Creek Formation in east-central Iowa. Fragments of this species have been found near Rockford, IA for over a century, but the specimens from the east-central Iowa area tend to be much more complete and better preserved. Note the crowding of the last few septa, indicating this is a mature individual. This specimen may represent a macroconch (female). Specimen found by J. Preslicka & Douglas Hanson. Photo by D. Hanson.



**Plate 3.** *M. regulare* (SUI #62349) from the Lime Creek Formation of East-Central Iowa. This specimen may represent a microconch (male). It retains septa crowding at a diameter of 12.5cm, and is noticeably thinner as well. Specimen found by J. Preslicka & D. Hanson.



**Plate 4.** Specimens of *Sphaeromanticoceras rhynchostomum* from the Lime Creek Formation in east-central Iowa. Left - (SUI # 62369) Complete whorl, entirely phragmocone (no body chamber), showing small umbilicus. Right - (SUI #62368) Compressed fragment, with suture marks emphasized in black ink. Specimens found by J. Preslicka & Douglas Hanson. Photos by D. Hanson.



**Plate 5.** *Tornoceras (Tornoceras) uniangulare* (SUI #54333), from the "Amana Beds" of the Lime Creek Formation. This is a long ranging genus in the Upper Devonian. Specimen found by C.H. Belanski.



**Plate 6.** Sphaeromanticoceras rhynchostomum? (SUI #50157) from the Owen Member of north-central Iowa. Precise stratigraphic position within the Owen Mb. relative to the Kellwasser events is not known. Specimen found by Calvin O. Levorson.



**Plate 7.** *Crickites lindneri*, (plaster cast of SUI #31835) from the Owen Member of the Lime Creek Formation of north-central Iowa. This species has a very limited range in the New York ammonoid succession, and could be an important marker species in Iowa. Specimen found by Calvin O. Levorson.



**Plate 8.** *Cyrtoclymenia strigata*, a potentially very important guide fossil from the English River Siltstone Member of the Maple Mill Formation. Left - Holotype specimen (SUI #8041) which was designated by House (1962), diameter ~25cm, from exposures along the Mississippi River. Right - Specimen from exposures along the English River, diameter ~22.0cm, found by J. Preslicka & D. Hanson.



**Plate 9.** *Imitoceras opimum* (SUI #46916) from the English River Siltstone of southeast Iowa. Red arrow points to umbilicus of specimen, note caliper for scale. Specimen found by William M. Furnish.



**Plate 10.** *Cymaclymenia striata* (SUI #9627) from the Upper Devonian of Morocco. This same species occurs in the English River Siltstone of Iowa, according to House (1962). Specimen found by Brian F. Glenister.

## Fossil Lagerstätten of New York, II. The Cephalopods of the Cherry Valley Limestone

### Thomas E. Whiteley and Gerald J. Kloc

New York State is filled with exceptional fossil deposits, or "Lagerstätten" (Whiteley, 1998). The Cherry Valley Limestone represents a rarity among these deposits and in the New York Devonian in general; it is a rich concentration of cephalopods. Although these spectacular fossils had been known since the mid-nineteenth century, they were given their most careful study by the colorful cephalopod expert Rousseau Flower in the 1930s. The Cherry Valley limestone is known across the state, but the cephalopod-rich zone was originally reported by Flower (1936) from about Stockbridge in the east to Union Springs in the west with the highest concentrations around Manlius, just southeast of Syracuse. The cephalopods are both nautiloid and ammonoid with at least 27 species in all represented (Flower, 1936, 1938). Some of these are locally abundant while others are described from as few as one specimen. Cephalopods are members of the phylum Mollusca and as their name, "head-foot," indicates, all of the external functions of the animal such as breathing, eating, sight, and movement are carried on with at one end while the other, at least in Paleozoic cephalopods, remains tucked away in a shell. The shell grows with the animal showing regular growth rings on the exterior. The shell is divided into chambers by internal septa which are interconnected by a tube, the siphuncle. The cephalopod lives in an expanded area or living chamber with the tentacled head end out the front and the back end narrowed into a thin organ, the siphon, which penetrates into the siphuncle. With the siphon the cephalopod was able to regulate its buoyancy by the use of partial gas filling of the chambers. The shape of cephalopods varied from a straight, taped cone (orthocone) to fattened cones (brevicone) to a tightly coiled shape (advolute) and just about everything in between.

Most of the nautiloid species (22), reported by Flower, in the Cherry Valley Limestone are straight orthocones and brevicones although a few loosely and tightly coiled species are represented. The five represented ammonoids include one form, *Lobobactrites*, which is straight while the others are tightly coiled in a plane. The ammonoids, except the *Lobobactrites*, are all goniatitic meaning the septa are fluted but not in the complex manner of later ammonoids (not all experts agree that bactritids are ammonoids). Ammonoids are distinguished from nautiloids by the position of the siphuncle, which in ammonoids is on the ventral margin. In most post-Paleozoic ammonoids the fluting of the septa is very complex. The septa are only observed however, where the external shell or its record is missing.

Of the varieties of cephalopods listed by Flower, only two are considered abundant. The straight orthocone nautiloid *Striaceras typum* and the ammonoid *Agoniatites vanuxemi* (Figure 1). Flower recognized a number of slightly different morphologies for *S. typum*, which he called the alpha, beta, gamma, delta, and epsilon variants. These morphologies might have been recognized as different species but for the observation that by looking at a large number of specimens one could observe a continual gradation between the different shapes. Most of the Cherry Valley cephalopods are not found in the shales above and below in the lower Marcellus. This does not mean that they were not present but that any record would not be preserved in the slowly accumulating dark shales.



**Figure 1.** The Middle Devonian ammonoid *Agoniatites vanuxemi* from the Cherry Valley Limestone of New York (from Hall, 1879).

For the most common ammonoid, *Agoniatites vanuxemi*, the largest known specimen is 300 mm (11.8 inches) in diameter (Hall, 1879). A slab of Cherry Valley Limestone from the New York State Museum figured by Miller (1938) measures 1.6 by 2 meters (62 by 79 inches) and has on its surface at least 30 coiled cephalopods (listed as *Agoniatites vanuxemi*) and at least 23 straight cephalopods. This slab was found was near Manlius probably during highway construction. The Cherry Valley Limestone is well exposed in the Seneca Stone Quarry southeast of Waterloo and

cephalopods are easily found in the limestone. (The Seneca Stone Quarry is private and permission must be obtained to collect there.)

Rickard (1952) reported a localized concentration of cephalopods in an exposure at Schoharie, New York. Rickard additionally reported that 32 cephalopod species are known from the Cherry Valley. Five more were added since the earlier work of Flower. During field work one of us (GJK) found concentrations of cephalopods in the east at Engleville and in the west at Phelps. At Phelps, it was believed that the cephalopod rich zone was in the lower layer. The characteristic fauna is usually found in the lower part of the upper layer, when it is divided. Flower also mentioned that where the beds separate and the cephalopods stand out from the hard layer, they are highly eroded, suggesting erosion on the sea floor of the exposed material. Flower correctly assumed that the buried portions had to be rapidly buried.

Flower (1936) stated that the Cherry Valley Limestone is a dark limestone found between the dark shales of the Union Spring Member below and the Chittenango Shale above. These three members constitute the base of the Marcellus Formation that overlies the Onondaga Limestone. Flower also reported that the Cherry Valley is never more that 1 meter (3 feet) in thickness and in some areas appears to have an upper and lower part. Rickard reported the thickness as 5 feet at the type location and it has been observed to vary from 1 to 3 meters (3 to 10 feet) at Honeoye Falls. The Cherry Valley thickens in the east, with lithology changing to contain significant amount of calcareous shale.

A more current description of the Cherry Valley Limestone was given by Linsley (1994). The Cherry Valley is a shelly limestone containing large numbers of *Styliolina fissurella*, a small conical fossil of uncertain affinities. The limestone is divided into three layers, two massive limestones on the top and bottom separated by a nodular limestone with shaley partings (Rickard, 1952). The contacts between these layers are gradational. The Cherry Valley Limestone, for the most part, is interpreted to be a slow accumulation of sediment on an otherwise sediment starved marine platform (Griffing and Ver Straeten, 1991) during a time of sea level rise. Because the slow accumulation of sediment is not conducive to good fossil preservation the presence of concentrations of well preserved cephalopods demand additional explanation.

Any time one finds unusually well preserved fossils, it is safe to assume they were rapidly buried by some sort of event. And as the most common events during the Paleozoic were storms, storms must have caused currents which churned the loose sediment, trapping and burying the cephalopods (C. Brett, private communication). The second factor that explains the erosion of the unburied fossils is that the shells of cephalopods were composed of aragonite. Aragonite is a form of calcium carbonate, which is more readily dissolved than the more stable form, calcite. Even the buried shell material is no longer present but survives as molds within the limestone. Shell material exposed on the surface of the bed would quickly dissolve, reducing the chances that any record would survive.

The Cherry Valley Limestone contains unusual concentrations of common and rare cephalopods over a very large area covering at least from south of the Albany area in the east to Honeoye Falls in the west. These concentrations are the result of rapid burial in storm churned limey muds in more than one event. Although some of these concentrations appear to be localized, this may be more the result of whether good exposures are available than the presence or absence of concentrations of cephalopods.

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## On The Trail Of Devonian Goniatite Cephalopods in New York State

#### William Kirchgasser

In the grand sweep of Earth history, no group of organisms (or time or place) is necessarily more significant than any other. Certainly, however, some groups stand out. The reign of dinosaurs on the Mesozoic landscape, for example, holds special fascination. Their extinction some 65 million years ago coincided with the rise of modern mammal groups, including our primate ancestors. That same extinction event also terminated a group that gets less press but is no less fascinating: the ammonites. The name "ammonite" comes from the similarity of their planispiral coil (coiled in a plane like a rope on a deck) to a ram's horn, the symbol of the Egyptian god Ammon. Those in the Lower Jurassic rocks around Whitby in northern England were said to be serpents turned into stone by the prayers of the seventh century abbess St. Hilda. By the end of the eighteenth century, the ammonites had been compared to the modern chambered-shelled *Nautilus* and thus recognized as members of the molluscan group of predatory swimmers, the Class Cephalopoda (Subclass Ammonoidea). The myriad patterns of shell form and ornament and the intricate folding of the chamber partitions (the sutures) in ammonids, which are key features for recognizing genera and species, are among the most beautiful geometric designs in the organic world.

By the early nineteenth century, it was realized that the ammonite species in rock sections like the Lias (Lower Jurassic) at Whitby changed every few feet and always in the same order (whether in the Lias of Yorkshire, elsewhere in England, or equivalent rocks in Germany or faraway California). Thus began the use of biostratigraphy – the subdivision and time-keeping of events in geological time. The biostratigraphic utility of ammonoids has been one of the reasons so many people have studied them over the past two centuries. The most ancient ancestors of the Mesozoic ammonoids are the more simply sutured but equally interesting group called the goniatites, whose fossil record is well displayed in the Devonian age rocks of New York State. The basic anatomy of a Devonian goniatite is illustrated in Figure 1.

#### The Devonian Period and its Goniatites

By any measure, the Devonian Period (roughly 418 to 462 million years ago) was a pivotal stage in Earth history. Plate tectonic movements assembled the puzzle-pieces of the Pangaea supercontinent (which were later to drift apart into the familiar island continents of today). What is now New York State was in tropical latitudes. The Atlantic Ocean did not exist. Western Europe and northwestern Africa were separated by a mountain range, a distance about the width of New England. The core remnants of these mountains are now granite hills in the uplands of New Hampshire, Massachusetts, and Maine. Sediments shed from the mountains formed the great Catskill Delta, which built westward into a depression, known as the Appalachian Basin, at the margin of a vast inland sea whose offshore, deeper waters were the habitat of goniatite cephalopods.

The Devonian is subdivided into three parts or series (Lower, Middle and Upper, with numerous finer divisions known as stages and zones). These divisions were originally based on fossil sequences in Europe, mainly of goniatites. Devonian goniatites evolved rapidly and spread globally from evolutionary centers in the Old World. Some sixty biostratigraphic zones (known as
"genozones") are now recognized internationally. These zones average less than one million years in duration, allowing a high degree of precision in dating Devonian rocks.



**Figure 1.** Basic anatomy of a goniatite shell. From *Treatise on Invertebrate Paleontology*, Vol. L (University of Kansas Press), 1957.

Most genera and virtually all species of goniatites were short-lived, and therefore are restricted to one or a few zones. The pattern of goniatite evolution (and ammonoid evolution in general) is like a series of relay races with extinctions and innovations marking responses to relatively short intervals of severe environmental change (across stage boundaries), particularly the spread of low-oxygen conditions (black-shale facies) associated with global-scale sea-level rises. The variety of shell forms and suture patterns in goniatites were probably adaptations for various habitat depths, swimming speeds, and feeding strategies (Figure 2).



**Figure 2.** The variety of form in Devonian ammonoids. Wavy line at the bottom of each shell is the diagnostic trace of the sutures, with the arrow marking the outer edge of the shell. From House, *Atlas of Palaeobiogeography* (Elsevier), 1973.

#### **Roadmap to New York Goniatites**

The Devonian rocks in New York State are laid out like a stack of books, gently tilted southward from a line just south of the Erie Canal and New York State Thruway to the boundary with Pennsylvania. They extend from the Catskill Mountains (where they are mostly sandy terrestrial deposits) in the east to Lake Erie (where they are mostly off-shore marine shales) in the west. The subtle southward inclination of the rocks may not be apparent in roadcuts of south-bound roads like Interstate 81 south of Syracuse or 1390 south of Rochester, but the regional dip can clearly be seen along the sides of the deep north-south trending glacial troughs of the Finger Lakes, as well as the cliffs along the shore of Lake Erie south of Buffalo.

The goniatites described here illustrate various features of this diverse group. Each is an important guide fossil to an interval within the Devonian, not just in New York but elsewhere in the world as well. One can follow their trail with a roadmap by noting the geographic names of the goniatite-bearing formations and the localities of collection, the details of which are in the figure captions. The species are described in stratigraphic order and the route will take us south (upsection) and west, following the westward shift of the offshore goniatite-bearing rocks through time.

*Agoniatites vanuxemi*—Before the New York State Thruway was built in the 1960s, U. S. Rte. 20 was the automotive gateway to the west from Albany to Buffalo, and it remains the best highway for observing goniatite localities in the State. Near Cherry Valley, in Otsego County, there is a prominent ledge of limestone, within black shales above the prominent chert-bearing Onondaga Limestone (Formation), visible and accessible along a side-road parallel to the highway. Scramble to the top bed of the Cherry Valley Limestone and with a little searching you will come upon the coiled shells of *Agoniatites vanuxemi*. *Agoniatites* is recognized by a suture with a prominent

backwardly domed fold (or lobe) centered on the flanks. Visualize backing your right hand, thumb down, into the body chamber of the shell. Your extended fingers represent the arms or tentacles for grasping prey and just below your knuckles would be the mouth, surrounded by a horny beak for shell crushing. The subtle indentation of the last growth line (at the aperture) would be in the line of sight of the left eye of the animal. Your thumb near the shell margin represents the funnel through which jets of water propelled the animal, although much more slowly than the shell-less modern squids. Near your wrist would be the end of the fleshy tube (the siphuncle) that extended back through the chambers to the start of the shell, and was the organ for regulating (by gas and water exchange) the buoyancy of the animal in the water. Its marginal position is characteristic of most ammonoids whereas it is central in nautiloids, including modern *Nautilus*.

Agoniatites probably lived just above the sea bottom at a depth of about 30 meters (ca. 100 feet). The black shale interval that includes the appearance of Agoniatites in the Cherry Valley correlates with a major change in the world's oceans and the appearance and disappearance of many forms of marine life, an event called the Kacak Event (after a succession of rocks in the Czech Republic near Prague). Sea levels rose, creating deeper water in some ocean basins. Circulation was much slower in these basins, leading to low-oxygen conditions. Occasionally, this low-oxygen water rose to the surface, with catastrophic effects. The cephalopod graveyard at the top of the Cherry Valley Limestone records one such event – a mass killing of animals unable to escape suffocation, probably during an upwelling of deep, anoxic waters. The large Agoniatites in the left foreground is nearly a foot in diameter; the shells to its left are nautiloids. This dining-room-rugsized slab from Schoharie Valley is in the collection of the New York State Museum in Albany.

*Tornoceras uniangulare*—The black shales of the lower Hamilton Group, just above the Cherry Valley Limestone, mark the first appearance in New York of the cosmopolitan *Tornoceras*, a long-ranging genus with species in most subsequent goniatite faunas. The closed umbilicus (center or axis of the coil) and prominent rounded lobe near the margin are characteristic (the forwardly projecting folds are called saddles). The shell form is clearly that of a swimmer. The ubiquitous and recurrent *Tornoceras* probably lived in depths down to 146 meters (ca. 480 feet).

*Pharciceras amplexum*—The Tully Limestone (Formation), named for exposures around the village of Tully, south of Syracuse, in Onondaga County, is the last major limestone layer in the New York Devonian. Its shelly fauna of corals and brachiopods and many other groups records another global-scale event (known as the "Taghanic Event") in which earlier fossil associations (the Hamilton Group faunas) were replaced. This turnover is again associated with a worldwide rise in sea level, which in New York begins in the upper Tully and continues in the overlying black Geneseo Shale In the transition, the goniatites nearly became extinct worldwide (*Tornoceras* survived!). The replacing fauna included this species of the cosmopolitan, multi-lobed genus *Pharciceras*, known in New York from just a single horizon in the upper Tully (Figure 3). The most spectacular exposure of the Taghanic Event units in New York is at Taughannock Falls State Park on the western side of Cayuga Lake.

**Ponticeras perlatum**—The top of the black Geneseo Shale and overlying Lodi Limestone (Genesee Group), mark the appearance of large ammonoids with broadly rounded lateral saddles and lobes belonging to *Ponticeras perlatum*, the last Middle Devonian goniatite known in New

York. These specimens are from the Lodi Limestone near the villages of Lodi and Ovid, near Seneca Lake. Impressions of *Ponticeras* occur in the surrounding dark Genesee Group shales at many localities around Cayuga Lake.



**Figure 3.** *Pharciceras amplexum.* Tully Limestone, Tully, Onondaga County, New York. Below the shell is a trace of the suture and to the right is a cross-section through the shell.

*Koenenites styliophilus*—The signature goniatites in dark shales of the Penn Yan and West River Formations (Genesee Group) of the Upper Devonian are species of the genus *Koenenites*, which is distinguished by an additional lobe on the umbilical side of the pointed lateral lobe. This specimen is from a block of the Genundewa Limestone from Rt. 20, Bethany Center, Genesee County. The recrystalized specimens are badly weathered, but fine specimens still turn up here and throughout the region in fresher exposures where the Genundewa caps waterfalls. The Genundewa is named for exposures below Ge-nun-de-wa or Bare Hill at the side of Canandaigua Lake, said to be the legendary birthplace of the Seneca Nation. *Manticoceras sinuosum*—This genus and species, a textbook example of a Devonian goniatite (Figure 1), repeats the shell-form and probable water-depth habitat (ca. 30 meters) of *Agoniatites*. As shown by this specimen from the Cashaqua Shale (Sonyea Group) near Naples, Ontario County, however, the suture in *Manticoceras* develops a large, asymmetrical lateral saddle and pointed lateral lobe (Figure 4). *Manticoceras, Tornoceras,* and *Cheiloceras* are among the dominant genera of the Devonian, and are represented by several lineages and hundreds of species.



**Figure 4.** *Manticoceras sinuosum.* Cashaqua Shale, Conklin Gully near Naples, Ontario County, New York.

**Probeloceras lutheri**—At the center of the coil of this species the larval shell, called the ammonitella, is visible. *Probeloceras lutheri* was probably a drifter rather than a swimmer, living and feeding in surface waters. This specimen has been replaced by the mineral pyrite, or fool's gold and came from Eighteen mile Creek near Buffalo. *Probeloceras lutheri* and another probable drifter in the highest Cashaqua (*Prochorites alveolatus*) are known elsewhere only in Western Australia, where they occur in the same order, a distribution suggesting a western, probably trans-Arctic (but tropical), seaway connection with Australia.

*Cheiloceras amblylobum*—The upper Hanover Shale (West Falls Group) and black Dunkirk Shale (Canadaway Group) record another major Devonian turnover event, this one called the Kellwasser Event (named for localities in the Harz Mountains of Germany), which occurs at the boundary between the last two subdivisions of the Devonian, the Frasnian-Famennian stages. This boundary is commonly recognized as one of the "big five" mass extinctions of the last 550 million years. No Frasnian ammonoids survived the extinction except a few offshoot tornocerid lineages which gave rise to all later groups, including the cosmopolitan genus *Cheiloceras*. Goniatites are exceedingly rare in the highest parts of the New York Devonian during the Famennian Stage. Evidently their habitats continued to shift westward with the progressive infilling by the Catskill Delta and consequent shutting-off of potential migratory routes. *Cheiloceras amblylobum* (Figure 5), an index species from Germany, occurs in New York in a single bed in the Gowanda Shale (Canadaway Group), the highest known goniatite bed in the State.



**Figure 5.** *Cheiloceras amblylobum.* Gowanda Shale, Corell's Point, Lake Erie, Chautauqua County, New York.

*Maeneceras aff. acutolaterale*—This is the highest known goniatite species in the New York Devonian (although there are some seventeen international goniatite divisions still to go to the

top of the Devonian; only two of these are represented in the Appalachian Basin, one in Pennsylvania and one in Ohio near Cleveland). It is referred to as *M*. "aff." *acutolaterale*, meaning that it has "affinities with" this species but may not actually belong to it. It is known from this single specimen collected in the Ellicott Shale (Conneaut Group) near Summerdale, Chautauqua County. The precise horizon at the site may never be known. The specimen may be an isolated stray (postmortem drifter), as the rocks in this remote corner of southwestern New York are thick sections of mostly barren sandstone and conglomerate (nearshore shelf facies), the goniatite habitat having shifted out-of-state.

#### Epilogue

Although nineteenth century paleontologists discovered most of the common goniatite species in New York, new and rare forms continue to be found, adding refinement to the international zonation. There are still many puzzles. The rarity of the Middle Devonian *Maeneoceras* (known from a single species in the upper Hamilton Group), is surprising as this is a diverse and common genus in Morocco, an area connected to New York at times via the Afro-Appalachian seaway link. True *Beloceras* would also be expected to occur, given the species-level links with Australian faunas (where it is common) lower and higher in the succession. Too many New York species are known from one or only a few and often poor specimens. Richer and better-preserved fossil faunas are needed to advance our understanding of the paleobiology of the group. You need not be a trained paleontologist to join the search. The methods and pleasures are similar to birding but the technique is to look down, not up.

Each spring, weathering and erosion yield a new crop of rocks and fossils to the creek sides and roadcut debris across the State. Given the vastness of the Devonian terrane and the countless streams and crisscrossing roads, it is safe to say the best specimens and faunas are still to be found. Imagine the graveyard of *Agoniatites* at the top of the Cherry Valley projected underground beneath several counties and appreciate the fossil treasures hidden beneath the Appalachian Plateau. In your travels, should you stumble upon a flat, coiled shell, look for the telltale suture line of the goniatite.

#### **Further Reading**

I have borrowed freely from the writing of my colleagues, especially the late Michael House of Weymouth, England, and Thomas Becker, Milnster University, Germany. The habitat comments come from a paper by G. E. G. Westermann in the book *Ammonoid Paleobiology* (Landman, Tanabe and Davis, editors; 2000, Plenum Press). Locality details and illustration credits can be found in House and Kirchgasser (in press, *Bulletins of American Paleontology*) and references therein. The general literature on goniatites is vast and includes many web sites such as Goniat. Thanks to Kim Coleman for the design and arrangement of the illustrations.

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# Heliophyllum, New York's Classic Devonian Coral

#### James E. Sorauf and William A. Oliver, Jr.



**Cover.** Heliophyllum halli confluens (Hall), collected near Avon, New York, prepared and donated by Gerry Kloc of Rochester, New York. U. S. National Museum #13587. Reprinted from the cover of American Paleontologist, 10(4), November 2002.

The genus *Heliophyllum* includes the most characteristic corals of the eastern North American Middle Devonian faunas. These are also fossils that most collectors can identify due to their distinctive form (bar-like carinae forming ridges on the radiating corallite septa, to be precise) (Figure 1). For more than thirty years, we have been studying these beautiful fossils. This work had several aims in addition to simply getting to understand this group of corals and see modifications that they had undergone on the Middle Devonian sea floor. One such aim was to explore variation within fossil species, because we know that modern corals vary widely in morphology among individuals, both regionally and within localized populations. Numerous fossil species are based on very small samples, but we had large numbers of corals to work with, permitting more accurate analysis of variation. A second major aim of our work has been to clarify the zoological nomenclature of these classic corals so that we could feel confident that we were in fact dealing with a rational taxonomic system analogous to that of enlightened modern workers dealing with living corals, although we do not have the benefits of soft tissue biology to aid us.

This project began, in a sense, during the early career of Bill Oliver, whose Master's thesis at Cornell University focused on Middle Devonian coral beds in central New York (1951). Since this time, first as a faculty member at Brown University and then as a member of the United States Geological Survey, Bill continued his interest in the Devonian corals of New York State and throughout eastern North America, eventually in much of the world. Jim Sorauf, trained at the University of Kansas, came to New York State as a young faculty member at Harpur College (Binghamton University), having been introduced to Upper Devonian corals in Belgium. We



**Figure 1.** *Heliophyllum halli halli.* These transverse and longitudinal thin section views illustrate the typical form of solitary specimens of the species from New York, with numerous structures (radial septa and crossbar septal carinae in the transverse and the numerous small blister-like dissepiments shown at the right). Diameter of lower section, approximately 6.9 cm.

became friends through meetings and field trips, eventually agreeing that it would be of mutual benefit to work together on a problem that would require additional time together in the field and laboratory, lead to better understanding of Devonian biostratigraphy, and above all, resolve a major problem concerning New York corals. Thus, we have worked together on this project since 1969, often putting *Heliophyllum* aside while pursuing other projects. Each of us researched other topics, and served in nonresearch professional roles, giving the "*Heliophyllum* project" our concentrated attention for short periods of time only until the past year. The project has led to a series of papers by one or

both of us on *Heliophyllum*; colonial forms seen in the Onondaga Limestone (1974), skeletal microstructure (1976), biogeographic distribution (1977), relationships with Spanish corals (1988), branching colonial species (1994), relationships between colonial forms (1997), paleoecology and paleobiology (2001), and finally, the expanded work, definitive to date, on the *Heliophyllum halli* species complex (2002).

#### **The Corals**

*Heliophyllum* from Middle Devonian strata of New York are recognized as the *Heliophyllum halli* species group. What are these names and what is their significance? The "*Heliophyllum halli* species group" (Table 1) is a group of closely related species, most prominent of which is the common *H. halli*. This name was first proposed by Milne-Edwards and Haime in 1850, thus they are also authors of the type subspecies, *H. halli halli*. This subspecies includes as synonyms six species names of other authors, ten subspecies or variety names, and ten "formae" (of Wells), the last having no official status in nomenclature (nor intended to by Wells). The greatest number of, and most widespread *Heliophyllum* specimens belong to the type subspecies (Figure 1), which occurs throughout the Hamilton Group and Tully Limestone, most commonly in coral beds. This group of corals provided a large sample of greatly varying morphology, from which we described assemblages (which we call populations) from ten stratigraphic positions, containing forms invariably present that are intermediate between individual types that can appear strikingly different in small samples. Thus, each of our populations contains a broad range of morphology, as is characteristic of living coral populations.

**Table 1.** Nomenclature of *Heliophyllum halli* species group taxa from the Middle Devonian, Givetian, strata of New York State.

Species included in Genus *Heliophyllum* Hall - *H. halli* species group:

H. halli Milne-Edwards and Haime, 1850
H. halli halli Milne-Edwards and Haime, 1850
H. halli confluens (Hall, 1877)
H. halli belfonense Oliver and Sorauf, 2002
H. halli joshuense Oliver and Sorauf, 2002
H. delicatum Oliver and Sorauf, 1994
H. stewani Oliver and Sorauf, 1994
H. cribellum Oliver and Sorauf, 2002

*Heliophyllum* can be either colonial or solitary. There are three colonial subspecies shown in Table 1, the best known is *H. halli confluens* (Hall, 1877). Each of these colonial forms are seen to be generally similar to accompanying solitary individuals of the species, save for their colonial peculiarities and some additional, more subtle differences. (These are variations in the internal structure of the septa and just as important, septal carinae, the crossbar-like septal structures characterizing the genus; Figure 2.) Each occurs within only one of our ten populations of the Hamilton beds, *H. halli confluens* only within the Jaycox Member of the Ludlowville Formation. *Heliophyllum halli bellonense* contains massive colonial corals superficially similar to *H. halli confluens*, but with a delicate skeleton (easily deformed), and also resembling solitary corals that occur with it. The latter only occurs in the Bellona coral bed of the Tully Limestone. *Heliophyllum halli joshuense* is another group of massive colonial corals recognizable as separate because of peculiarities in the wall between individuals in the colonies, and being limited to the Joshua coral bed in central New York.



**Figure 2.** *Heliophyllum halli confluens* Wells. This specimen is of a small colony, a triplet. The parent, shown to the left in this view of a transverse thin section, strongly resembles the solitary subspecies. Overall length approximately 12.6 cm.

One branching species of the genus that we recognized eight years ago, *Heliophyllum delicatum*, was assigned to *H. proliferum* by James Hall in 1877, but this species deserves recognition as separate because of its different morphology (with very delicate skeleton) and limited stratigraphic range, only occurring in the Deep Run Shale. *Heliophyllum stewarti* to date has only been found in central Ohio.

In our most recent work we also recognize one new species of solitary corals belonging to *Heliophyllum, H. cribellum.* This form had not been previously named, but is recognizable by its uniformly small size, and by its outer area complicated by the presence of structures which give this area an "interwoven" appearance, thus is named using the Latin word for sieve, *cribrum.* It is known only from the Centerfield Limestone. Specimens were not recognized as a separate species until we studied abundant material from several of these populations, instead they had been regarded as juveniles of the larger species, *Heliophyllum halli.* 

Biogeography of these corals is noteworthy because corals are among the most provincial of marine animals, and the Middle Devonian world itself was remarkably provincial (meaning different areas of the world had different kinds of organisms). Three marine biogeographic realms are recognized for the Devonian earth. New York was in the Eastern Americas Realm, as opposed to Eurasian and Southern Hemisphere realms. *Heliophyllum halli*, as it lived in this marine basin, was the same species recognized in present-day Venezuela, Michigan, and Indiana, at the Falls of the Ohio River, and Hudson Bay Lowlands. Numerous other species of *Heliophyllum* are described from these places, but many of these will probably be recognized eventually as synonyms of *H. halli. Heliophyllum halli* is one of the most common corals of the Eastern Americas Realm. A second aspect to occurrence of *Heliophyllum halli* is the recognition of the genus and species in the Eastern Hemisphere. Occurrences in Spain and Morocco are accepted, but numerous others are questionable. This illustrates some "leakiness" at the eastern border of the Eastern Americas Realm, but provinciality of these faunas is marked, and the genus was not widespread outside of this realm.

#### **Coral Morphology**

Our analysis of taxonomic and systematic units is based on well-defined populations of *Heliophyllum* from ten stratigraphic levels. Examining the stratigraphic position of these populations of the entire Hamilton Group, the relative east-west position of coral beds is seen to shift westward with time.

The shape of the coral skeleton itself (the corallum) at least partly reflects ecological conditions. The upper surface of the corallum provided a cup-like shelter (Figure 3) and a place of attachment of the animal or polyp. Some polyps distended themselves (by filling with seawater) to shed fine sediment, here the clay settling in the Hamilton sea. In *Heliophyllum halli*, two characters are especially important, shape and carination. A flat, platy form, seen as one growth extreme, indicates rapid increase in diameter, with slow rates of sedimentation to provide a flat base to resist overturning. *Heliophyllum* commonly shows an arched or reflexed peripheral platform, which may have helped polyps to distend. Straight individuals can occasionally be found in a vertical growth position, partly encased by sediments. Right angle bends (Figure 4) are common and indicate toppling of corals, with rapid recovery, thus avoiding smothering (Figure 3). In many solitary forms,

root-like extensions of the basal skeleton helped attach corals to hard substrate, holding them in a nearly upright position.



**Figure 3.** *Heliophyllum/um halli halli* Milne-Edwards and Haime. Longitudinal thin section view of a specimen which has fallen onto sediment and recovered by growing differentially upwards (at the left side). Overall length approximately 15.0 cm.

Among the most easily recognized features of *Heliophyllum* are the septal carinae, which are flange-like elevations on the sides and tops of septa. They are fundamental parts of the septa and have the same or comparable structure. Each carina is formed by one or more rod-like

structures (trabeculae). Within each septum, the carinae projected above and inward from the septum to form a toothed septal margin. Based on their shape, carinae are described as "yard-arm," "zig-zag," or "irregular." In *Heliophyllum*, straight carinae extending across the septum (yard-arm) are the most characteristic but combinations of various types in a single coral are common. The attachment of the polyp to its skeletal upper surface was probably facilitated by these structures.



**Figure 4.** *Heliophyllum halli halli* Milne-Edwards and Haime. These are two views of a solitary coral which shows a bend in its early history, at the base, and a slow diminution of size in the last stages of life, at the top. Overall height approximately 5.5 cm.

We earlier (1976) described several types of carinae in Hamilton *Heliophyllum*, based on a simple form or more complex branching of the trabeculae. We confirm the usefulness of study of skeletal structure to help in recognizing groups within *H. halli*. However, more variation and less clear boundaries between types are seen in the larger collections now at hand. Well-developed yard-arm carinae, especially if thin, almost always reflect simple trabeculae, while more complex forms are more irregular (Figure 2). To summarize, most *Heliophyllum* are solitary, but branching forms

and massive colonies with and without walls between individual corallites occur. Most of the colonial forms are recognized as species or subspecies. *Heliophyllum halli* is very unusual among species of the Rugosa in this characteristic, of including both solitary and colonial forms.

#### Acknowledgments

A project that extends over a long period of time, as this study has, depends on numerous people. Over this period we benefitted greatly from the help of William Pinckney of the U.S. Geological Survey who made several thousand museum-quality thin sections of the myriad specimens that we located in the field or museum. Additional thin sections were prepared by Richard Jacyna at Binghamton. David Tuttle of Binghamton University processed or took most of the photos for our publications on *Heliophyllum*, with additional photos provided by Pinckney and by Keith Moore of the U.S. Geological Survey. Coral studies such as these would not have been possible without this support and assistance, available at both the U.S. Geological Survey and at Binghamton University. These conditions are rare or nonexistent at most institutions at present and for the foreseeable future.

The geological and paleontological content of this work also benefitted greatly from our association with J. W. Wells, from the field enthusiasm and stratigraphic work of Gordon Baird and Carleton Brett and more recently that of Charles Ver Straeten and David Griffing.

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# Calceocrinids of the Devonian and Early Mississippian Thomas Williams

# Introduction

James Hall in 1852 first distinguishes a fragmented dorsal cup of a crinoid from the Middle Silurian of New York that he called *Calceocrinus* and eventually classified as an Inadunate Disparid Calceocrinid crinoid. Hall would go on to collect other Calceocrinids including several complete specimens. Ulrich in 1886 introduced three new genera that he named: *Cremacrinus, Dolatocrinus* and *Heliesocrinus* from the Ordovician of Minnesota. This began the work on Calceocrinoids which would later be continued by Bather 1893, Jaeckel 1918, Goldring 1923, Springer 1926 and many others. Moore in 1962 would publish the Revision of Calceocrinidae putting together a comprehensive work bringing together all of the previous work (Moore 1962). Calceocrinoids relatives go possibly as far back as the Lower Ordovician but are defiantly present in the Middle Ordovician and lasted into the early Permian. (Moore 1962, Ausich 1999) Calceocrinids as a Taxonomic family have one of the longest tenures of all crinoids lasting 230 million years. This tenure may have been due to an unusual life style of living along the sea floor (Boyarko 2007). Ancestral relatives such as *Deltacrinus* (Ulrich 1886) and *Synchirocrinus* bear a real striking resemblance to *Halysiocrinus* (Ulrich 1886) and direct ancestry as shown by their taxonomic structure.

Inadunate crinoids as a whole originated in the lower Ordovician period and evolved in many different directions and some survived at least into the Triassic period. Somewhere, between what has been currently confirmed to the origins of *Halysiocrinus*, *Cunctocrinus* and other confirmed genera from specimens from the Devonian period with *Halysiocrinus* lasting into the Mississippian period when it disappears from the fossil record to reappear briefly in the Permian of Russia. Calceocrinidae as shown by Ausich were well represented in the Ordovician and Silurian periods but began to decrease in numbers during the Devonian and early Mississippian. A definite gap exists in the fossil record with no confirmed reporting from the end of the early Mississippian to the early Permian in Russia. There are nine genera with 58 confirmed species of Calceocrinidae with eleven occurring in the Ordovician, thirty on the Silurian, decreasing to eight in the Devonian and nine in the Mississippian as reported by Moore 1962. Kesling and Sigler have added one more genus and species from the Silica shale of Ohio. Calceocrinidae are well represented in both North America and Europe during the Devonian including the unusual *Senariocrinus* found in the Hunsrück slate of Germany (Moore 1962 and Hess *et al.* 1999).

Currently the classification scheme for Inadunates and Halysiocrinus is listed below but may very well change based upon new research.

Crinodea (Miller 1821)
Inadunata (Wachsmuth & Springer 1885)
Disparida (Moore & Laudon 1943)
Calceocrinacea (Meek & Worthen 1869)
Calceocrinacea (Meek & Worthen 1869)
Halysiocrinus (Ulrich 1886)
Deltacrinus (Ulrich 1886)

Genus:	Synchirocrinus (Jaeckel 1918)
Genus:	Cunctocrinus (Kesling and Sigler 1969)
Genus:	Senariocrinus (Schmidt 1934)

Future research by Ausich and others may reorganize crinoids as a whole with Inadunates potentially undergoing the most significant changes. Ausich presented at Expo in his talk and his Expo 31 article, the likely potentially that, "Inadunata is not a natural evolutionary group of taxa. Therefore, the tax Inadunata may be eliminated, and the Disparids and Cladids, which are closely related, are elevated to the subclass status (Ausich 2009). Significance of this is the evolutionary development of crinoids from their origins in the lower Paleozoic but potentially through modern crinoids still alive today. During the Ordovician, Disparids were extremely important in the mix of fauna, but declined in importance after the Silurian. More recent research on Ordovician crinoids as for possible origins of subclass, articulate crinoids which are currently post Paleozoic crinoids but whose true origin is not yet understood (Ausich 2009).

Extinctions play an important role in crinoid evolution with the Ordovician extinction being the second most devastating in geologic history. Disparids and Calceocrinids suffered greatly from this extinction but survived to become contributors to the fauna's of the Silurian though Lower Mississippian time periods. Crinoid preservation in the fossil record does show after the Ordovician extinction overall, Disparids were far fewer in numbers allowing Cladids and Camerates to take a greater role in the fauna. Disparids and Calceocrinids in particular would recover in the Silurian with Calceocrinids reaching their height in the number of species in the Silurian but would decrease after this with time (Ausich 1986). Camerates would have their day becoming dominate forms in the Devonian and Lower Mississippian but, by the early Pennsylvanian they too would severely decline in numbers and diversity.

Late Ordovician glaciations significantly lowered sea levels and definitely severely lowered sea levels. Lowering of sea levels especially if quickly occurring does not allow for species to adjust thus enhancing extinctions of groups of organisms that are more depth specific for survival. In simple terms loss of environment to survive in and one possible explanation to fewer numbers of Disparids favoring other groups that are better in extreme survival conditions. This extinction event and other factors related to it significantly affected how modern crinoids evolved and the eventual elimination of Disparids and possibly the extinction of Halysiocrinus sooner rather than later from the fossil record. Ausich has suggested that predation and the evolution of fenestrate bryozoans' had a major effect on Calceocrinids elimination that began in the Devonian (Ausich 1986). The Mississippian period too had its glacial events disrupting sea levels and perhaps again pushing Disparids and Halysiocrinus closer to complete elimination. Perhaps the predation effects and bryozoan competition was aided by the environmental factors of the Extinction events caused by environmental changes through the Devonian and Mississippian which were significant. Stress in the environment usually allows species more able to adapt an edge over their competition. Perhaps fenestrate bryozoans benefitted from these changes during Calceocrinid decline. The Pontiac Illinois fauna shows a definite preference for Cladids over Disparids with only one of this group represented in the fauna (Ausich 1986, 1999). Perhaps these sets of facts may be described by research of Lane who found interesting facts regarding crinoids and their environmental shifts. Lane found that Camerates dominated terrigenous and carbonate settings in the Silurian, however, by the Middle

Devonian Inadunates would come to dominate terrigenous areas. Calceocrinids were present in these environments and appeared to mirror the Inadunates in their sediment tolerance. However, after the early Mississippian Calceocrinids disappear from the fossil record until the early Permian.



Restoration of Cunctocrinus fortunatus.

**Figure 1.** Examples of Calceocrinids. (Modified from Moore 1962, Plates 1-3 and Figure 19 and from Kesling and Sigler 1969, Text-figs. 2 and 3.)



**Figure 2.** Typical calceocrinid in a non-feeding position. (Moore 1962, Figure 1.)

# **Description Calceocrinoids**

# Calceocrinoids and Halysiocrinus:

*Synchirocrinus* very closely resembles *Halysiocrinus* in appearance, but is different in more robust in appearance, however, a definite ancestor from the Middle Silurian from the Wenlock of Great Britain and the Beach River Formation of Tennessee. The Middle Silurian does appear to have been the pinnacle for the most species for Calceocrinidae which includes *Synchirocrinus*. Numbers of genus definitely appear to taper off after the middle Silurian but are well represented into the Middle Devonian (Ausich 1986).

Calceocrinoids in particularly *Halysiocrinus* for those of us collect crinoids has produced absolutely spectacular specimens at times particularly those found in the Borden Formation at Crawfordsville Indiana. However, with the exception of the Crawfordsville fauna *Halysiocrinus* is rare in occurrence to say the least, even at Crawfordsville this crinoid is uncommon and Disparids are not common at all in this fauna. Distinct possibilities of environmental change and competition have already taken its toll on this group. The entire Family Calceocrinidae has a geologic range possibly from the Lower Ordovician to the Lower Permian; however, *Halysiocrinus* only has been shown to exist from the middle Devonian through the Osagean of the Lower Mississippian (Ausich 1986, Moore 1978).

Moore in 1962 published a Revision of Calceocrinoids with a systematic description of this group. Inadunate crinoids generally have an aboral shaped cup with close sutured plates, fixed brachials and for the most part no interbrachials with anal plates are typically found in the aboral cup (See Figures 1, 2). Calceocrinoids crown is pendent or recumbent on the stem with good bilateral symmetry; however, sometimes this interesting form of bilateral symmetry is not perfect. *Halysiocrinus* (Ulrich 1886) overall has a slender crown to a moderately full girth not as robust as some of the Silurian Calceocrinidae. This comparison shows an evolutionary streamlining in the overall shape of the crown (Moore 1962, 1978, Van Sant 1964).

Arrangement of Calceocrinidae basal plates in the cup and their stem attachment and the structure of the radial circlet basal plates and the nature of reticulinear hinge arrangement. This feature and the asymmetrical disposed basals and the higher part of the cup composed of radial plates makes this group extremely different other crinoids. The basal circlet of the cup is typically formed by three or four plates in a triangular shape (See Figure 3). Devonian *Senariocrinus* basal plates may actually fuse into what appears to be a single triangular plate. This does not appear to be the case with most of the Calceocrinidae which has posed some problems in classification.

*Cremacrinus* from the Silurian and Devonian *Senariocrinus* differ from most Calceocrinidae with the apparent fusion and arrangement of radial plates. Calceocrinidae radial and super radial plate configuration does vary between genera. In most cases of Calceocrinidae the differences in the radial plates is one of the determining changes through time could be any factors in classification however, questions remain as to evolutionary decisions. Why the radial and super radial plate design changes could be related to structural orientation of the entire crown, environmental other factors not yet understood. Despite the changes through time with the arrangement of radial plates in Calceocrinidae the plane of bilateral symmetry did not change as shown by Moore thus differentiating them from other crinoids in structure of other crinoids (Moore 1962, 1978).





The cup has large lateral radial plates that adjoin each other between the infer radial, super radial, of the median radial plate as do other Disparids. Infer radials of B and C rays adjoin the stem impression and are beneath the super radial of B and C rays. Basal circlet plate along the medial element hinge is low (accurate plate). E Ray plate of *Halysiocrinus* is perfectly symmetrical. Super radial and infer radial plates separated well by the adjoined lateral radial plates which support curved main axils (Figure 3).

Arms of *Halysiocrinus* either isotomonously or heterotomously branch in the E Ray that and are connected to the large radial plates that do mirror each other. This feature against has extreme importance in classification of its evolutionary features. Bifurcation may or may not occur from the medial arm from the E super radial and when it does it may be multiple. Generally arms of the lateral rays are invariably multiple (see Figures 1 and 2). Calceocrinidae generally possess a group of brachials that exist as axillaries and are identified as the main axil. Arms attached to the main axil are termed axil arms with these arms continue to branch out forming the primaxil and the secondaxil arms. *Halysiocrinus* has a bifurcation of the medial arm as well as the shape and bifurcation of the axil arm. These features of the arms can vary a bit among the identified species. Arms can be pinnulate or non-pinnulate of the different species identified (Moore 1962).

Anal tube arrangement is typically an elongate segmented structure that is believed to be a modified arm probably the C-Ray. This appendage extends to the top of the crown and is typically as long as any of the other arms or slightly greater in length. The plates of this structure are normally

uniserial a bit more massive and have a generally concentric shape. This adaptation appears to be the, "...sole appendage borne the radial plate to which it is joined" (Moore 1962). Again some difference in *Cremacrinus* and *Senariocrinus* utilize the super radial of the C-Ray, however, other genus, "it is a fused super radial formed by a lateral union of the B- and C super radial" sometimes called a subanal plate (Moore 1962).

## Paleoecology

Crinoids known as "passive suspension filter feeders" require a specific set of combined factors to survive that include: open marine conditions, a reasonably high oxygen level, and sufficient water current to pass food particles for survival. Substrate selection does appear important in the appearance of Calceocrinoids. Calceocrinids liked shallow seas surviving on carbonate platforms with clastic sediments deposited into their living environment. Calceocrinids in the fossil record have been found in shale and limestone sequences, carbonate dominated sequences and shale's. During the Silurian period Calceocrinids have been found to be present in the Brownsport Formation of Tennessee and Rochester shale of New York. This shows a diverse type of sediment that Calceocrinids were capable of tolerating during this time. During the Silurian Calceocrinoids were found in considerably more environments than the Ordovician showing an increase in environmental diversity. Carbonate shelf's Reef Bioherms and off shore siliciclastics are the most popular habitats for Calceocrinoids. Preferred Devonian period environment shows a similar preference but with again carbonate shelf's the most popular occurrence. Mixed carbonate siliciclastic shelf's and deep siliciclastic prodelta environments became more prominent occurrences which does shows a gradual shift in occurrence, but used in the Silurian time. Devonian period shows a similar diversity in sediment tolerance a shown by their presence in the Moscow Shale of New York and the Oriskany Sandstone of Maryland.

Lower Devonian Manlius and Coeymans formation of central New York reveals a favorable paleo-environment for crinoids with shallow lagoons and shoals. Varied limestone deposition occurs in the Manlius and Coeymans including fine grained, crinoidal, cherty, ribbon bedding, thick bedded with some storm deposits limestones and shaly dolomite. Crinoids in this area seem to prefer the interface deposits between the two formations. The shoal environments of the Coeymans limestone shows deposition of skeletal material deposited under high energy conditions in an off shore shoal. This is a contrast to the Manlius facies showing "platy ribbon-bedded facies" indicating a more quiet water lagoon. Both facies have good quantities of crinoids with the best areas occurring between the inter-bedded areas of the two formations. Storm episodes may have been recorded by the presence of fine carbonate silts which probably disrupted crinoid beds particularly in the lagoon systems (Hess *et al.* 1999).

The Hunsrück Slate Lower Devonian in age was deposited in a number of off shore basins in a down wrapping basin reaching thicknesses up to 4000 meters. Sediment sources appear to be clays and silts deposited from streams and later turned to slate through metamorphism of the Variscan mountain building event. Several different depositional environments exist, however, fossil deposition occur in the inter-channel areas with a well oxygenated bottom. The sediments were compressed to one tenth of its original thickness not unusual for this type of geologic process. Bedding planes and most other sedimentation features have been destroyed as well as many fossils not lying along cleavage planes of the slate (Hess *et al.* 1999). What is unusual is the preservation of

the fossil at all since metamorphism tends to destroy fossils, perhaps the pyritization helped preserve the fossils. Landslide type deposits, tempersite events, turbidity and density currents quickly buried specimens with high iron levels in the sediment making these burials anoxic and promoting pyritization. Even tangles of crinoid stems acted as traps for starfish, trilobites and other organisms found preserved sideways indicates rapid burial of specimens and sticky mud. These conditions give us this unusual gorgeous preservation of fossils not commonly known (Hess *et al.* 1999).

Windom shale deposits of the middle Devonian represents an off shore mud bottom shallow marine environment. These deposits however, were not favorable to rugose corals perhaps do to larger amounts of sediment and perhaps not favorable to Calceocrinoids as well do to large amounts of sediment. The Windom shale depositional environment appears to favor camerate crinoids on stems able to elevate themselves off the substrate limiting the effects of sediment.

Middle Devonian deposits of both Arkona and Sylvania Ohio Silica Shale's are both classified as mudstones with thin skeletal limestone lenses. Crinoids tend to be found on the top of these skeletal limestone lenses that are interfaces of the limestone and the mudstones. Spectacular crinoid specimens are sometimes found in these areas of the interface (Hess *et al.* 1999). A similar situation was observed by the author in the Birdsong Formation of Tennessee when a Calceocrinoid was found on a highly fossilized limestone that was previously covered by thick green shale.

During the Mississippian period *Halysiocrinus* becomes the only remaining example found in a decrease environment types. *Halysiocrinus* is found in the Borden the ramp carbonate banks, mudstones and shales in off shore deeper siliciclastic prodelta environments as well as the carbonate ramp platforms of the Burlington formation (Boyarko 2007, Ausich 1986).

Histograms prepared by Boyarko of plotting environments vs. frequency show the preference of Calceocrinoids of preferred environments through the Paleozoic. Overall, Calceocrinids seem to prefer Carbonate shelves, deep subsidence ramps and deep siliciclastic platforms; however, there is a shift back forth through time in the types of environments preferred. Ordovician environments Calceocrinoids prefer carbonate shelf's and deep sub tidal ramps. The Calceocrinids of the Silurian and Devonian have the greatest diversity in environment types with crinoids such as Halysiocrinus being more selective preferring carbonate ramps and deep siliciclastic prodeltaic environments. What this shows is a narrow environment selection in the Ordovician, expansion in the Silurian and Devonian and again more selective environment selection in the Mississippian of the single genus *Halysiocrinus* (Boyarko 2007).

#### Life Style

Actual living positions of this group of crinoids has been widely discussed from it having an upright stem dropping downward to various living positions resting on the bottom. Discussed six varied life style modes which include an upright mode described as the dropper either open or closed arms. This model has been dismissed as it would be inefficient as does not allow the organism efficient feeding and may have made more susceptible to current variations. In addition this life style does play into the more interesting hinge structure that exist that actually allows the organism the ability to spread its arms out for efficient filter feeding structure which would be

perpendicular to the current. A life style referred to as the kite does involve the crinoid being lifted off the bottom utilizing the current to help it lift itself off the bottom. This mode of life might possibly make any Calceocrinidae more dependent upon the current than normal and would require the crinoid to expose its ambulacral groves to the current. Also this mode of life style would require the organism ability to survive high current environments to stay aloft and would require more light more fragile arms to produce a hydrodynamic lift. In other words the overall weight of the crinoid would need to be light enough for normal currents to simply lift it off the substrate. Baumiller in 1992 concluded that this form of living could not happen under normal living conditions. However, the possibility of using the kite method of repositioning itself in response to current changes, dislodgement, or as a crawling method to improve its feeding position. This does appear to be a response possible for Calceocrinids (Boyarko 2007). This mode of life as well as the drooping life styles may have posed a risk to arms being broken off in the current causing the organism to lose food sources from lack of feeding structures (Boyarko 2007, Ausich 1986).

Other modes of life involve Calceocrinids living on the bottom in different include two versions of what is called the runner model and the weather vane model. All three of these models involve the stem lying along the bottom with the crinoid in a parallel position to the current. The position of the crown would be held vertical or horizontal along the stem column. When the crinoid was feeding the hinge would open up spreading the arms out in a fan structure. Some discussion still potentially remains as to the ambulacral grooves protected or facing the current directly. Third substrate method of living called the weather vane method which suggests the crinoid had the flexibility at the hold fast to adjust itself to the current. It seems potentially logical to assume that Calceocrinids may have had the ability to reorient themselves somewhat to their surrounding conditions allowing more flexibility in the attachment between the holdfast in the stem more than likely could have existed. Therefore the weather vane mode of life style is not very probable, if the stem was stressed in such a fashion they would have probably broke off at the holdfast (Boyarko 2007, Ausich 1986).

Typically discussed living style of *Halysiocrinus* and other Calceocrinids has concluded that made it a crinoid that rested upon the sediment using its holdfast and stem to stabilize and secure itself. Possibly the stem acted as an additional anchoring tool but also allowed it some position adjustment in the sediment (Ausich 1999). Orientation of the crinoid logic and observation of modern crinoids suggest that the crow would orient itself with the aboral side of the arms facing the current allowing for maximum spreading of its arms using it bilateral symmetry and hinge structure for feeding (see Figures 1 and 6-9). This also allows the crinoid to protect itself better and orient itself against being ripped out of the substrate or torn off of its attachment (Boyarko 2007, Ausich 1986).

Disparid Calceocrinids with their well developed "bilateral recumbent design" had a well developed hinge allowed them to spread out their arms for feeding just above the substrate as opposed to lying directly on the substrate (see Figure 4 and 6-9). Ability for elevation off the substrate would allow more advanced forms of Calceocrinids the ability to increase feeding opportunity but use the substrate from high current protection. This mode of living is referred to as the preferred runner mode of life. However, this dependence on the sediment would also pose some

risks from high levels of sediment intrusion quickly burying them and predation from organisms such as starfish and gastropods (Ausich 1986).



**Figure 4.** Typical calceocrinid in a feeding position. (From Hess et al. 1999, Fig. 29.)

More primitive relatives of *Halysiocrinus* such as *Senariocrinus* (see Figure 1) of the Hunsrück slate Bundenbach Germany suggested that they might simply have planted their stems directly into the mud with the main calyx of the crinoid resting in the mud then spreading its arms above the substrate (see Figure 1) (Hess *et al.* 1999). Schmidt presented the thought that *Senariocrinus* was a floating, free-living crinoid using the stem only for temporary attachment and free-floating swimming. It is more likely this more primitive Calceocrinid lived similarly to *Halysiocrinus* on the sediment using it stem as an anchor (Ausich 1999). Some Middle Ordovician Calceocrinid specimens from the Bromide and other formations have extremely short stemmed specimens in which the arms are actually longer than the stem suggesting that stem was simply stuck down loosely into the mud or found attach to other objects. Both of these attachment strategies appear to have been effective modes of life style as other Calceocrinids would use this approach as a lifestyle mode (Boyarko 2007). Calceocrinids represented from the Silurian period preferring shallow water carbonate platforms and reef bioherms with clastic sediment deposition. These are more classic types of crinoid living environments.

Middle Devonian Silica Shale deposit in northern Ohio had the single know Calceocrinid representative *Cunctocrinus fortunatus* survived here in relatively shallow but quiet seas featuring shale deposition. Overall, the silica shale deposits fauna is extremely diverse in invertebrate and vertebrate fauna as listed by Kesling and Chilman 1975. This fauna, based on diversity, suggests a rich well oxygenated environment with plenty of nutrients available. Echinoderms, including blastoids, are a significant part of the fauna and most of the crinoids found in the Silica shale are typically Camerates. However, cladids, and flexible crinoids are present in higher numbers as shown by a faunal description of the Silica Shale (Kesling 1975). If one looks at the fauna, it shows echinoderms either capable of movement (starfish) or able to get plenty of elevation off the substrate. Calceocrinids, similar to *Cunctocrinus*, also appear to have preferred runner lifestyle on or near the substrate (Kesling 1975 and 1969).

Calceocrinids have also been found in the Lower Devonian Birdsong formation of central Tennessee. The Birdsong can be up to sixty feet thick and is alternating layers of limestone and shale's with a rich variable fauna. The shale deposit was part of the Ross shelf of a shallow warm sea only a few hundred feet deep. A Calceocriniod specimen was found on a limestone surface in a quarry near Holiday Tennessee shown as photograph (see Figure 6).

Crawfordsville crinoids of the Borden off shore deltaic environment had a definite tiered community that recognized three stratified zones with Inadunates such as Halysiocrinus being a, "nonpelmatozoans" resting on the bottom. The overall community was believed to have been, "...a shallow water community with a muddy but well aerated bottom." This would help explain why Halysiocrinus did thrive in the Borden and why many well preserved specimens have been recovered (see Figures 4 and 6-9) (Van Sant and Lane 1964). Halvsiocrinus is also found in the Mississippian rocks of the Keokuk Burlington limestones in Illinois and Iowa. The numbers of complete specimens of Halysiocrinus are fewer but complete specimens are found so one could assume that well aerated bottoms existed in this environment as well. Specimens from the Borden did attain a reasonable size indicating that conditions in this environment were favorable (see Figures 6-9). Halysiocrinus however, is the only genus of Calceocrinus present at this time suggesting that predation and increased competition from fenestrate bryozoans was taking its toll on this entire group. Elimination of the previous existing substrates of the Burlington and Borden environments to a substrate not as favorable to Halysiocrinus possibly favored Cladids and other forms of crinoid's proliferation. These other forms may have been simply able to choke them out of space.

The Keokuk Burlington would later be chocked off by sediments from the Appalachian Mountains continuing their rise pushing sediment east to west in large clastic deposits. Crinoids of the Burlington, Borden, Warsaw Ft. Payne, and New Providence shale represents a flourishing crinoid facies with matching fauna. Limestones composed almost entirely of crinoidal debris such as the Burlington shows just how many crinoids were present in these carbonate seas. Crinoids in these formations just listed flourished through the end of the Osagean and Halysiocrinus appears to have become a dead end at this time as did many other Disparids in these areas, however Halysiocrinus was found in the Lower Permian of Russia. This presents the questions did they go actually go absent in North America or no remains found to this point. Deposits in Europe may answer this question as to what actually happened. Other Crinoid groups would manage to survive this and explode in the Chesterian such as Inadunate cladids crinoids. Geologic history and change always repeats itself as plate tectonics slowly but surely changes continental environments. Mississippian environments would continue to extremely favorable for crinoids to flourish, however, as Africa continues its push into North America more changes on depositional environments would continue to occur. Cladids and Camerates crinoids both show examples very capable of living reveal Chesterian time substrates with Cladids becoming more dominant as time progresses.

Perhaps these traits which make its structure unique may have made its downfall as well. By the early Mississippian, *Halysiocrinus* was on the decline and was far from consistently present in the fauna. Borden formation specimens may have presented a substrate more favorable for a slight but brief reemergence, but this genus was not able to expand its dominance (Moore 1962).





Structure of Calceocrinidae and its life style make it extremely one of the most interesting crinoids to have existed. Calceocrinidae, primitive evolutionary beginnings regarding its unique bilateral symmetry of this crinoid tracks back to the Ordovician beginnings of this group. A strange form of bilateral symmetry along the E-BC plane has been attained, "… in a plane other than that coinciding with the anterior posterior axis of the theca (see Figures 1-4) (Moore 1978). This feature shows, "successive steps in evolution of the symmetry are clearly recognizable and its derivation from an ancestral Homocrinid stock" (Moore 1962).

*Halysiocrinus* numerous axil arms support large not dominant beta ramules which links it to *Synchirocrinus* as its best possible ancestor. However, links to *Deltacrinus* of the Silurian exist from the aboral cup similarities (see Figure 5) (Van Sant 1964). These two characteristics help Halysiocrinus the last of this group link back to the Silurian and it's evolutionary beginnings and thus defining a very long existence for the this genus (Ausich 1986).

#### Conclusion

In conclusion, Calceocrinids, such as *Halysiocrinus*, were able to bounce back from adversity in the Silurian and Devonian to be significant contributors to the fauna. The early and middle Devonian saw Calceocrinoids as significant but their decline had already begun from environmental factors including possible predation they could not adapt to. In the early Mississippian *Halysiocrinus* was the last genus but it was fairly well represented in numbers were reported nine total species reported. However, at least to this point in North America past the early Mississippian Calceocrinoid in the fossil record are absent. Specimens shown in Figures 6-9 display the manner in which the hinge was attached allowing individuals to open up along the ocean bottom as shown in Figure 4. One example of Calceocrinoid is known from the early Permian of Russia. So where are the rest of the specimens or at least the traces, they must be hiding somewhere in the fossil record. Calceocrinids as a Family were very successful for most of the Paleozoic Era but it appears the extremely unique mode of lifestyle and structure that allowed them to be successful perhaps eventually led to their downfall.

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(Fossil specimens photographed by John Catalani.)



**Figure 6.** Calceocrinid from the Devonian Birdsong Formation, Holiday, Tennessee.

**Figure 7.** *Halysiocrinus nodosus* from the Mississippian Edwardsville Formation, Crawfordsville, Indiana.



**Figure 8.** *Halysiocrinus nodosus* from the Mississippian Edwardsville Formation, Crawfordsville, Indiana.

**Figure 9.** *Halysiocrinus nodosus* from the Mississippian Edwardsville Formation, Crawfordsville, Indiana.

# Interaction among Devonian Sea Life Preserved in the Jeffersonville and Sellersburg Limestone, Clark County, Indiana and Jefferson and Oldham Counties, Kentucky

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# Introduction

Survival on Earth has been dependent on other life since the first one-celled organism digested another one. A walk through the woods reveals numerous examples of interdependence – from shelf fungi attached to a tree to poison ivy vines clinging to the bark. Peel the bark of a dying try and you will see numerous arthropods that call the tree their home. The common word for these interactions is *symbiosis*.

So how does this relate to fossils? Numerous examples are found through the fossil record. The author will review observations, based on specimens, of how different types of organisms interacted with one another during the Middle Devonian in the Jeffersonville and Sellersburg Limestones. Observations and interpretations will be summarized with a look at whether there is evidence of mutualism, commensalism or parasitism, as well as organisms simply being used as a convenient substrate. The Devonian ecosystem is similar to what is found in south Florida or the Bahamas – a shallow marine environment.

## **Symbiosis Preserved**

Fossils often show evidence of relationships with other organisms living or dead. A basic understanding of modern marine life processes / interaction is helpful to make inferences 390 million years ago. With Devonian fossils, the evidence is found in the skeletal remains. A study of epizoans on *Paraspirifer bownockeri* was published in 1980 (Sparks, et al), but a comprehensive review of the interaction of all Devonian fossils has not been done. Symbiosis between and with soft-bodied organisms is rarely preserved in limestone strata. Many of the fossils collected by the writer are silicified and show extraordinary external detail. Quartz replacement makes the investigation of detailed internal structure impossible because specimens are often hollow.

Evidence of parasitism – where one organism benefits at the expense of another, is pretty rare. The best *possible* example is a tube-like worm *Gitonia coralophyli* (Hall & Clark) that grew *between* the septa of solitary rugose corals (**figure 1A, B**). Did it harm the coral? There is little evidence of physical damage to the coral's structure. Did it compete for food? Again, while it is possible the soft part of *Gitonia* could have "wormed" its way into the gut of the coral polyp, evidence is lacking. Multiple *Gitonia* in a single rugose coral is not unusual.

Borings in stromatoporoids by soft-bodied organisms are very common in the Jeffersonville

Limestone (**figures 2 & 3**). Evidence indicates that, 1) organisms of various sizes penetrated the colonies or, 2) there were different species that bored. Were they burrowing worms or sponges? A more thorough study in non-silicified specimens through thin-sections would be necessary to make that determination. Were the stromatoporoids already dead when the boring occurred, or was it the result of some form of parasitism? Some show evidence of being tumbled by ocean currents before burial, and the boring could have been done at that time. Further studies are needed to draw any definite conclusions.

Easily confused with borings in stromatoporoids is the presence of certain types of tabulate and rugose corals. Auloporid corals including *Aulocystis*, *Aulopora* and *Romingeria* are often associated with stromatoporoids. When everything but the polyp aperture is hidden within the stromatoporoid, it is virtually impossible to determine the genus or species (**figure 4**). Examples where the colony is at least partially exposed are common enough to establish a relationship (**figure 5**). These are likely to be examples of commensalism rather than mutualism, because there is little evidence the stromatoporoid was harmed.

The tabulate coral *Syringopora* (typically *S. hisingeri* Billings) is found symbiotically within stromatoporoids. This would likely be an example of commensalism, because there is no evidence that the stromatoporoid was affected negatively.

Narrow (ceratoid) rugose corals like *Acinophyllum* and some heliophyllids are found in the stromatoporoids like the auloporids. They are distinguishable by the septa which tabulates lack. As is the case with tabulates, it is very difficult to identify to species level of rugose corals obscured by the stromatoporoid (**figure 6**).

# Dead or Alive: Fossils as substrate - or what came first?

One of the most commonly observed interactions in the fossil record is the case where one organism uses another as a surface on which to grow. Anything large enough for a planktonic juvenile to settle on and grow / reproduce can serve as a substrate. It is a matter of observation to determine if the substrate was living or dead at the time a second organism settled on it. Some creatures are dependent on other forms of life – they can be parasitic, symbiotic, commensal, etc. Most marine invertebrates have a larval plankton phase. Once mature, coral and some cephalopods can grow to be *much, much* larger after a few decades.

**Stromatoporoids** were a colonial organism in the Phylum Porifera that was widely distributed in the Devonian. Their calcified skeletal structure often exceeds a meter in length. The largest fossil at the Falls of the Ohio is minimally 45 m (~150 feet) in length along a bedding plane! Their abundance allowed them to have many types of interactions with other invertebrates. They served as substrate and encrusted organisms partially or completely, depending on the relative size of both (**figure 7A & B**).

**Tabulate Corals**, like *Favosites*, were also commonly employed as substrates, though the polyps with their cnematocysts likely kept encrusting organisms at bay until a large part of the colony was dead (**figure 8A**). Like modern scleractinian corals, once deceased, they were utilized

by other organisms almost immediately, especially where the seafloor was covered in lime-mud. Devonian corals grew in the same forms found in modern corals – particularly mound-shaped and in fronds that were staghorn or palmate shaped. When corals were flipped over, they became a suitable substrate (**Figure 8 B, C**).

**Rugose Corals** include "horn" corals and colonial forms like "pipe organ" and Petoskey stones. The variety of shapes is very diverse, as was their use as substrate. As with tabulates, the polyps of rugose corals probably would attack (and consume, if larval) any potential organism wanting to settle on their upper surface. Within colonies, individual corallites might die leaving space for another organism to settle. The sides of some species provided ample room for colonization, although generally only a small fraction of horn corals are found to be used as a substrate. Tabulate corals are found on rugose corals (**figure 9A, B**), though it is more common to find other rugosans attached – particularly juveniles or small colonial forms (**figure 9C, D**). Inarticulate brachiopods such as *Petrocrania* are uncommon. Finding colonial rugose corals like *Eridophyllum* are only rarely found as substrates for brachiopods and other smaller organisms (**figure 9E**).

**Brachiopods** had a variety in both form and external shell ornamentation. Some were smooth or covered with fine ribs, others were imbricated or were coarsely ribbed and some were covered in spines that kept organisms from settling on them while living. Encrusting organisms might disrupt the water current affecting the quantity and quality of plankton they required for nourishment. It was in their best interest to keep potentially deleterious larvae from settling onto their shells. The concave sulcus was the most common place for organisms (i.e. other brachiopods, *Cornulites*, etc.) to attach while the brachiopod was living (**Figure 10A, B**). Bryozoans could colonize a brachiopod unobtrusively for some time, growing over much of the shell. Once dead, the colony could expand over the commissure and continue growth on the opposite side.

**Gastropods** had the advantage of being mobile, but that didn't keep them from being used as a substrate by small organisms. Once dead, colonizing forms like bryozoans, corals or sponges could completely cover the shell (**figure 7, 11**).

**Bivalves** were often partially or completely buried in sediment, preventing a colonizing organism from causing too much difficulty. However, once the clam was dead, it was "fair game." Pectens did not bury themselves extensively, so they would have the same "problems" of colonizing larvae as brachiopods, but are uncommon so interactions have not yet been observed. The most common fossil interactions are among the elongate clams, like *Modiomorphia concentrica* (Conrad), frequently encrusted by *Aulocystis transitorius* Stumm. It is a fair common bivalve in the Sellersburg Limestone (**figure 12**). Such interactions are rarely noted in the Jeffersonville Limestone where mollusks (excepting *Hippocardia* and *Pseudaviculopecten*) are almost always found as internal casts.

**Bryozoans** grew in colony forms similar to tabulate corals (mounds, branching), though the zooids were much smaller than coral polyps. Order Trepostomata, Cystoporata, Cryptostomata, Fenestrata and Hederellida are represented, the latter exclusively encrusting (**figure 13A**). Devonian examples of bryozoan serving as substrate are much rarer than in the Ordovician. An example of an

inarticulate brachiopod attached to a frond of a fenestrate bryozoan was collected (**figure 13B**). It was probably on a living colony because it grew to be rather larger. *Aulocystis* on branching bryozoans have been observed in the Speed Limestone.

**Crinoids** were not commonly found as a substrate. The column was used occasionally, but the calyx was rarely noted serving that purpose. After death, the calyx would disarticulate relatively quickly - flexible and cladids faster than the camerates (W. Ausich, personal comm.). The camerate crinoid *Dolatocrinus* was used by *Aulocystis frutecosa* (Davis) encrusting at the base of the calyx where the column attached (**figure 14**). The column was present since the coral surrounds, rather than covers, the attachment point. This indicates the crinoid was probably living when the *Aulocystis* settled.

Crinoid holdfasts occur as button-like forms which are preferential to stromatoporoids and tabulate corals (**figure 15A**) or, more rarely, crinoid columns were wrapped around branching tabulate coral or draped across (and later covered by) stromatoporoids (**figure 15B**). The symbiotic relation was likely commensalism, except for the few coral polyps that *may* have been covered by the column. Crinoids with multi-cirri or coiled rope-like holdfasts preferred a soft sediments substrate.

Substrate or Primary:	STR	TC	RC	WOR		BIV	GAS	BCH	BRY	CRI	UI
Stromatoporoids or Sponges	A	C	A				C			C	A*
Tabulate corals	C	C	U	U		C		R	R	U	
Rugose Corals	C	С	C	U					C		
Bivalves											
Gastropods	C	C		R							
Brachiopods			R	R				C	R		
Bryozoans								А			
Crinoids		U	U								R
Unidentified fossils											
A = Abundant C = Common U – Uncommon R = Rare (single example found) Empty = Not observed * Possible sponge or worm borings						S T R W B C B B C U	TR = StiC = TabC = RugVOR = VIV = BivGAS = GaCH = BiCH = BiCH = BiCH = CriII = Unic	romatop ulate Co gose Corr Vorm valve astropod rachiopo ryozoan noid lentified	oroid or ral al d	sponge	

 Table 1 Review of Symbiosis by Strata

**Table 1** plots the substrate on the X-axis and the type of fossil that settles on the Y-axis. There are numerous examples of a larger organism serving as a substrate for a smaller one, but there are also examples of organisms settling on fragments (i.e., **figure 8A**; or small horn coral attached to a section of crinoid column that eventually grew to cover it). There are certain organisms (such as worms) that are never observed serving as a substrate. Others are sufficiently rare, to not show any interaction. These tend to be the highly mobile organisms like trilobites and cephalopods. (**Note** that on **Table 1**, bivalves commonly serve as a substrate for tabulate corals, specifically *Aulocystis transitorius* Stumm on *Modiomorphia concentrica* (Conrad). Specimens of corals serving as substrate for bivalves are not observed, so the grid space is empty.)

#### **Fossils and Stratigraphy**

Evidence of symbiosis in the Devonian is commonly observed in specimens of fossils collected in the Jeffersonville, Speed, and Sellersburg Limestone. Conditions indicate a well-oxygenated, fairly shallow marine environment (Greb, et al, 1993; Powell, 1970; Perkins, 1963). True reefs did not form, but corals and stromatoporoids bioherms were abundant in the lower part of the Jeffersonville (partly Emsian and partly Eifelian age). Corals are also abundant in the Beechwood Member (Givetian age) of the Sellersburg Limestone (sometimes called the North Vernon Formation,) is a crinoidal limestone.

The Jeffersonville Limestone is very rich in faunas that show biological interactions. Examples can be found in abundance on the fossil beds at the Falls of the Ohio State Park and wherever the limestone weathers out silicified fossils – construction sites, road cuts, and limestone quarries.

In the Speed Limestone which occurs only in Clark County, Indiana, the small rugose *Bordenia knappi* Hall and tabulate *Aulocystis transitorius* Stumm are common, and both depended on other organisms for substrates on which to grow. *Bordenia* eventually lost its substrate (fenestrate bryozoans fragments were most common), but was able to stand upright on its own. *A. transitorius* was an encruster by nature and obligated to stay attached to its substrate – commonly bivalves and brachiopods.

The Silver Creek member of the Sellersburg Limestone is argillaceous, indicating clay sediment mixed with the calcium mud. This contains the lowest diversity in the rock area and consequently few interactions. Those are typically *Aulocystis transitorius* Stumm on *Spinocyrtia granulosa* (Hall). It is almost never found on the abundant *Pseudoatrypa* sp. which was probably covered with flat spines. *Modiomorphia concentrica* (Conrad) are commonly covered by the auloporid coral. Other bivalves are rarely observed encrusted.

*Protoleptostrophia perplana* (Conrad) brachiopods, commonly found in the Silver Creek member are often encrusted by bryozoans (type uncertain) and the inarticulate brachiopod *Petrocrania hamiltonae* (Hall). The worm *Cornulites* sp. is uncommonly observed.

The Beechwood Member of the Sellersburg Limestone contains numerous corals,

stromatoporids and echinoderms. Preserved interactions of these faunas are common, particularly the rugose corals that seemed to attach to almost anything hard. Crinoid columns are often found weaving between and under stromatoporoids and *Favosites* corals. *Aulocystis frutecosa* (Davis) has been found attached to the branching tabulate *Thamnoptychia alternans* (Rominger), spiriferid brachiopods, crinoids, and in colonies without any apparent hard substrate.

## Conclusion

With the collection or documentation of abundant Middle Devonian fossils in the area around the Falls of the Ohio in the field where the Jeffersonville, Speed and Sellersburg Limestone outcrops, it is possible to record the interaction of species. Instances of direct interaction of living organisms as well as those that used dead organisms as substrate can be made with these observations. Some are noted through borings and other traces, while others deposited an exoskeleton. Continued collecting and close examination of in situ fossils may add additional knowledge of the interaction, particular of the less commonly preserved species.

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# Figures



Figure 1A. *Gitonia coralophyli* (Hall & Clark) in *Heliophyllum venatum* Hall.



Figure 2. Stromatoporoid with borings.



**Figure 4.** Unidentified auloporid symbiotic with a stromatoporoid.



**Figure1B.** *Gitonia coralophyli* (Hall & Clark) in *Heliophyllum* sp.



Figure 3. Stromatoporoid showing the internal.



**Figure 5.** *Romingeria* intergrown with a stromatoporoid.



Figure 6. Rugose corals in stromatoporoid.



**Figure 7A.** *Turbinopsis shumardi* (DeVerneuil) mold in stromatoporoid.





**Figure 8A.** *Striatopora bellistriata* Greene substrate for *Prismatophyllum truncata* (Stewart).

**Figure 7B.** *Turbinopsis* completely encrusted by a stromatoporoid.



**Figure 8B.** Aulocystis (?) procumbens (Davis) encrusting Favosites turbinatus Billings. This is a post-death encrustation because the *Favosites* would have been oriented with the point upward.



**Figure 8C.** Inarticulate brachiopod *Petrocrania* sp. on the underside of tabulate coral *Favosites turbinatus* Billings.



**Figure 9A.** Chonostegites tabulatus (Edwards & Haime) encrusting a horn coral. This was most likely after the horn coral's death since it completely encloses it.



**Figure 9B.** Alveolites winchellana (Miller) encrusting Prismatophyllum conjunctum (Davis).



**Figure 9C.** *Prismatophyllum* that grew on a horn coral while it was in growth position. It probably was not alive since the polyp would have attacked it.



**Figure 9D.** Juvenile horn coral attached to the side of *Enallophrentis duplicata* (Hall) that was deceased at the time (growing perpendicular).



**Figure 9E.** Brachiopod *Pentagonia peersi* (Cozzens) sits atop *Eridophyllum archaici* was Billings, probably in growth position.



**Figure 10A.** Spinocyrtia granulosa (Hall) with Cyrtina hamiltonensis (Hall) and Devonochonetes coronatus (Conrad) in the sulcus.



**Figure 10B.** *Cornulites* sp. on *Alatiformia verrucosa* (Hall) in the sulcus.


**Figure 11A.** *Favosites turbinatus* Billings grew over the gastropod *Palaeozygopleura*. The aragonite shell eventually dissolved away leaving a mold.



Figure 11B. *Murchisonia* sp.? encrusted by a stromatoporoid.



**Figure 12.** *Modiomorphia concentrica* (Conrad), encrusted by *Aulocystis transitorius* Stumm.



**Figure 13B.** Inarticulate brachiopod *Lindstroemella* sp. attached to fenestrate bryozoan.

**Figure 13A.** *Spinocyrtia granulosa* (Hall) encrusted by *Hederella* sp.



**Figure 14.** *Aulocystis frutectosa* (Davis) encrusting the base of a *Dolatocrinus* sp. calyx. (Right, inside of crinoid.)



Figure 15A. Crinoid holdfast attached to a stromatoporoid.



**Figure 15B.** Crinoid column serving as a holdfast attached to *Striatopora bellistriata* Greene.

## Long Before Cayuga's Waters: The Spectacular Devonian Geology and Paleontology of the Ithaca, New York Region

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## Introduction

"Central New York State" is an area of approximately 9,000 square miles (ca 23,300 sq km), covering parts of 15 counties around the 11 Finger Lakes, roughly bounded by a polygon with corners at the cities of Syracuse, Rochester, Corning, and Binghamton, with Ithaca approximately at the center (Figure 1). Besides being known for wine, dairy cows, and lots of institutions of higher education, the region is justly famous among geologists and paleontologists for its excellent and accessible exposures of Devonian-aged rocks filled with abundant, diverse, and well-preserved marine fossils. These rocks were some of the first in North America to be seriously studied in the early nineteenth century, and formed the basis for much of what became our "textbook" understanding of many topics in geology and paleontology, including ancient deltas, shallow marine sedimentary environments, and life in Devonian seas (Wells, 1963a; Aldrich, 2000). The Devonian of New York is simply one of the most complete and fossiliferous sequences of middle Paleozoic strata in the world (see Brett, 1986:1).

he geology of central New York also provides an excellent natural laboratory for investigating global and regional Earth processes of the past, including changes in climate, sea level, and mountain-building, and the response of life to those changes (Brett, 1986; Brett et al., 1991, 2011). The Pleistocene and Holocene glacial erosion of the region has, furthermore, excavated the Devonian geology into conspicuous relief, giving the region its characteristic topography of lakes, gorges, and gently rolling hills (Allmon and Ross, 2007) (Figure 2). As if all this were not enough, the recent (and highly controversial) development of natural gas resources in the Middle Devonian Marcellus Shale in Pennsylvania and New York has also demonstrated that this geology still has much to teach us, not least about both fossil fuels and the challenges involved in its exploitation (Cronin, 2013; Ross and Cronin, 2013).

The Devonian fossils of central New York are also noteworthy because they have served as the "type examples" of several path-breaking paleontological studies. In 1963, for example, Cornell professor John Wells used growth lines on Devonian corals (such as Figure 7A) from central New York to demonstrate that the number of days in the year has decreased over the past 360 million years (because tidal friction has slowed the Earth's rotation as it moves around the sun), an idea that up until that time had been only theoretical (Wells, 1963b). The trilobite *Phacops rana* (now called *Eldredgeops rana* [Figure 9B]) from New York's Middle Devonian Hamilton Group was one of the original examples of the evolutionary model of punctuated equilibrium proposed by Niles Eldredge

and Stephen Jay Gould (Eldredge and Gould, 1972); this model postulates that much of evolution occurs rapidly, associated with geographic isolation of small populations, followed by prolonged periods-up to millions of years- of little to no change, which Eldredge and Gould termed "stasis". Fossil assemblages from the Hamilton Group later formed the basis for the related idea of coordinated stasis (Brett et al., 1996; Zambito et al., 2012), which posits that not only do most evolving lineages of species not change their form over time, but multiple lineages tend to remain static in concert with each other, and then turn over abruptly and *en masse*.

Yet central New York's Devonian paleontological riches are not as well-known as they should be outside of professional circles, even within the region itself. Beyond serious collectors, curious rural kids, and observant farmers, most of the general public, and even many teachers and other educators, are regrettably unaware that they live among some of the most impressive and accessible paleontological resources in the world. There are, for example, few books for general readers or collectors that might facilitate appreciation or identification (but see Whiteley et al., 2002 for a conspicuous exception). The most recent book covering multiple major taxonomic groups (Linsley, 1994) is unfortunately long out of print (although it is available online [www.museumoftheearth.org/files/pubtext/Linsley\_1994.pdf], and a revised print version is in preparation).

We cannot, in this short paper, do justice to the paleontological riches of the Devonian of central New York. Our goal is merely to introduce them and provide some suggestions for sources of further information and exploration.

### **Geological Background**

Following the breakup of the early supercontinent known as Rodinia in the late Precambrian (ca. 600 million years ago), the area that is now central New York was most likely positioned in a shallow sea around the margin of the ancient continent that geologists call Laurentia (most of which would someday become eastern North America) (Isachsen et al., 1992). Although Cambrian rocks are not exposed at the surface in central New York, they crop out in northern New York state, on the periphery of the Adirondacks (Whiteley et al., 2002; Landing, 2007).

By the Ordovician, the eastern margins of Laurentia were becoming continuously deformed through collisions with one or more volcanic island arcs (for a modern analog, think Japan or the islands in the Banda and Timor regions of Indonesia), collectively forming the Taconic Orogeny (named for the Taconic Mountains in eastern New York and western New England). As with the Cambrian, no Ordovician strata are exposed in central New York, but outcrops occur around the margins of the Adirondacks (Whiteley et al., 2002; Landing, 2012).

The mountains that formed during the Taconic Orogeny were largely eroded during subsequent uplift during the Early Silurian period, and areas of clastic (sand and mud) deposition were gradually transformed into areas of shallow water carbonate (limestone) deposition, which included reefs. Subsequently, the climate grew more arid and an arm of deltaic sedimentation cut off flow into the basin, leading to a disparity between evaporation and water input rate, creating extensive salt deposits which are still mined beneath the region today. Spectacular Silurian fossils

can be found in north-central and western New York, including eurypterids, trilobites, corals, and echinoderms (Isachsen et al., 1992; Whiteley et al., 2002; Landing, 2007).

By the Late Silurian, eastern Laurentia had collided with yet another landmass, a microcontinent known as Acadia (think modern Madagascar). The resulting Acadian Orogeny was responsible for most of the Devonian sedimentary rocks of central New York. What is now the Finger Lakes region was located in a sagging (geologists say "subsiding") basin behind the mountain belt that was being uplifted in the (then) southeast, building what are sometimes referred to as the Acadian highlands or mountains (Figures 3,4). This basin (usually referred to as the "Appalachian Basin") resulted from a combination of crustal thickening associated with the mountain-building and further subsidence caused by the weight of the accumulating sand, silt, and mud eroding from those mountains (Ettensohn, 1985) (Figure 3). These sediments eventually became the Devonian strata exposed today in central New York.

Global sea level in the Devonian fluctuated greatly but overall was higher than at present, and much of what is now eastern North America – including the region northwestward of the Acadian Orogeny -- was covered by shallow sea (Brett et al., 2011). This mountain-building created a vast, northwestward-expanding wedge of sediment known as the Catskill Delta. The sediments in this delta varied based on their proximity to the mountains (Figure 4), from terrestrial to deep marine deposits (Isachsen et al., 1992). Closest to the mountains, riverine and shoreline deposits of sandstone and conglomerate formed. Farthest offshore (to the northwest), black muds accumulated and would eventually become organic-rich black shales (such as the Marcellus; Figures 5,6). Overall, the wearing down of the Acadian Mountains was probably accelerated by the fact that northeastern North America was then located in the subtropics, and this led to relatively high rates of erosion. In sum, the region between what are now Albany and Buffalo may have resembled the course of today's Ganges River in eastern India, from the Himalayas to the continental shelf in the Bay of Bengal.

Despite appearances, New York's Devonian strata are not strictly an example of "layer-cake geology", such as appears in many textbook diagrams. Rather, different types of sediments, deposited in different environments (collectively known as "facies") interfinger with each other. This is because of the changes in water depth associated with the westward building of the Catskill delta. Nearshore sediments are generally coarse-grained while offshore sediments are generally fine-grained (Figure 4). As sea level changes, sedimentary environments are said to "migrate" through time – for example, with rising sea level finer sediments are deposited where before coarser sediments were laid down -- and organisms likewise migrate, tracking their preferred environment. This may help explain why assemblages of organisms last so long; when they don't like the environment, they don't go extinct, they move, following their favored environment (Brett et al., 2007).

The rocks that formed from the sediments of the Catskill Delta today are found from the Hudson River Valley to Buffalo (Figure 1). An east-to-west drive along Rt. NY5/US20 from Albany to Buffalo will take you through or near outcrops of terrestrial redbeds to deep-water dark sediments. Only a portion of this giant wedge of sediment is visible in central New York. The bulk of these exposed strata are placed in the Middle Devonian Hamilton Group, Tully Limestone,

Geneseo Shale and several Upper Devonian units (Figure 6). Although sediments from subsequent periods, starting with the Carboniferous, were probably deposited above the Devonian beds, they have been erased from the region's geological record by post-Devonian erosion. The rocks of central New York are all nearly flat-lying, with only a very slight (about half a degree) dip to the south, which means that older rocks are exposed at the surface to the north and younger rocks to the south (Figure 1).

#### **The Hamilton Group**

The Middle Devonian Hamilton Group has long been known around the world for its abundant, diverse, and well-preserved fossils. The Hamilton consists of up to 2000 feet (600 m) of shale, siltstone, and limestone, and is divided into four main units: (from oldest to youngest) the Marcellus Shale, Skaneateles, Ludlowville, and the Moscow Formations (Figure 6). With one exception, only the upper part of the youngest formation, the Moscow, is visible around Ithaca. The exception is the upper part of the Ludlowville Formation. Because of that slight southern dip of all strata in central New York, strata of this age would not normally be exposed this far south. However, the presence of a gentle fold, called the Fir Tree Anticline, which was produced during another later episode of mountain-building, elevates the strata sufficiently high at its crest so that erosion has cut into older beds at a few places (for example, Taughannock Falls and on the opposite east side of Cayuga Lake at Ludlowville).

The Ludlowville Formation takes its name for fossil-rich shales exposed along Salmon Creek at Ludlowville, New York, about 10 miles north-east of Ithaca. Siltstones and sandstones of the Ivy Point Member are well exposed along a railroad cut at Portland Point slightly to the south. These beds are noted for diverse and abundant brachiopods including the concavo-convex *Tropidoleptus* (Figure 8C) the elongate "butterfly" brachiopod *Mucrospirifer* (one of the most characteristic Middle Devonian fossils; Figure 8E), the robust brachiopod *Spinocyrtia*, and various bivalves; the swirly, "rooster tail-like" trace fossil *Zoophycus* is also abundant (Figure 11C).

The Ludlowville is separated from the overlying Moscow Formation by a sharp contact of a thin fossiliferous limestone bed, the Tichenor Limestone (or lower Portland Point Member of older literature, also named for the railroad cut exposures). This limestone rarely exceeds two feet thick and is composed of crinoid columnals and contains fairly abundant large corals. It has been traced from Lake Erie to near Schoharie in eastern New York State (Baird, 1979), and probably represents reworked fossil skeletons during a rise in sea level following a major drop, which may have exposed much of central New York above sea level.

The uppermost Hamilton unit, the Windom Shale member of the Moscow Formation, is extremely fossiliferous, and contains abundant and diverse brachiopods and bivalves, and trilobites belonging to two species, with *Eldregeops rana* being by far the most abundant (Woodrow, 1988; Linsley, 1994). Brachiopods include *Ambocoelia, Pseudatrypa*, and *Mediospirifer* (Linsley, 1994). Altogether, more than 60 species of marine fossils are known from the Windom Shale in this area (Figures 7-11).

These animals lived in a variety of biological communities which inhabited distinct

environments. These environments differed in, for example, depth, sediment type, and current energy, and these conditions affected which species lived where (Figure 12).

Overall, the Hamilton Group rocks represent a shallowing of sea level through time, but within this trend are a number of depositional cycles resulting from the combined effects of changing rates of sediment accumulation, basin subsidence, and global (eustatic) sea level change (Brett et al., 2011). These factors created a range of environmental conditions throughout the Middle Devonian, ranging from moderately to strongly low-oxygen conditions (Figure 5).

## **Tully Limestone**

Overlying the Windom Shale is the Tully Limestone, the only carbonate rock exposed at the surface in the Ithaca area. It is a hard fine grained limestone that forms the caprock of the lower falls at Taughannock Falls and dozens of other waterfalls throughout central New York. The Tully is a fascinating and complex stratigraphic package, comprising as many as seven limestone units separated by unconformities (Heckel, 1973; Baird and Brett, 2008; Baird et al., 2012) (Figures 13,14). All of these units thin westward and are missing stratigraphically in some locations. Altogether the Tully spans perhaps about a half-million years. It probably represents an interval of overall low siliciclastic input, perhaps associated with a nearshore barrier, probably related to faulting, that trapped terrigenous sediment in eastern New York and kept it out of the central region (Ettensohn, 1985). In most localities, the Tully contains abundant fossils, including especially brachiopods and corals in some beds (Figure 15).

#### **Geneseo Shale**

Following deposition of the Tully, mountain-building activity caused major subsidence in the basin. Combined with a rise in global (eustatic) sea level at around the same time, the result was very deep water over much of south-central New York (Ettensohn 1985). This combination of environmental change at this time may have caused what is called the Taghanic Bioevent, which resulted in the disappearance of much of the diverse and abundant Middle Devonian fauna worldwide (Baird and Brett, 2008; Baird et al., 2012).

After this event, the now-deepened Appalachian Basin was the site of deposition of thick, dark gray-to-black shale almost devoid of benthic fossils. This is the Geneseo Shale, which lies unconformably on top of the Tully Limestone. The Geneseo was deposited in a deep, anoxic environment. It is approximately 200 feet (65 m) thick and beautifully exposed at Taughannock Falls just north of Ithaca (Figure 2A). At its top, the Geneseo grades into silty sandstones of the Sherburne, Renwick, and Ithaca Formations.

#### Ithaca Shale and Above

Overlying the Geneseo Shale is a series of coarser-grained rocks – siltstones and silty shales, with some thin limestones. From older to younger, these strata include the Sherburne, Renwick, and Ithaca formations (Figure 6). Since 1981, the boundary between the Middle Devonian (Givetian Stage) and Late Devonian (Frasnian Stage) in central New York (based on the stratigraphic

distribution of conodonts) has been placed at the contact between the Geneseo shale and the overlying Sherburne formation (Zambito et al., 2007, 2009) (Figure 6).

Deposition of these coarser sediments marks an increase in rate and volume of sedimentation and growth of the front of the Catskill Delta, resulting in shallowing water depths and more hospitable conditions for benthic animals. The Sherburne, Renwick, and Ithaca formations together consist of about 400 feet (120 m) of alternating finely-bedded silty shales and thicker resistant layers of siltstone. These beds probably accumulated through a long interval of storms and/or turbidite flows on the front of the Delta (Zambito et al., 2007, 2009).

A fascinating feature of the Ithaca Shale is the "recurrence" of species from the underlying Hamilton Group. Most of the diverse Hamilton fauna appears to have become globally extinct either at the end of deposition of the Moscow or within the deposition of the Tully (see Figure 6). Some, however, reappear after their apparent extinction in beds within the Ithaca Formation, before finally disappearing for good. This was first noticed in the late nineteenth century by Cornell paleontologist Henry Shaler Williams (1913). Although this phenomenon has recently been restudied (Zambito et al., 2007, 2009), the explanation for it remains unclear.

The fauna of the Ithaca Shale itself includes abundant brachiopods, nautiloids, and ammonoids (Zambito et al., 2007, 2009), and also *Plumalina*, a distinctive feather-shaped fossil that has recently been confidently identified as a hydroid (Muscente and Allmon, 2013) (Figure 7C).

### **Post-Devonian Geology**

Erosion has erased most of the geological activity that Tompkins County has experienced since the Devonian Period. During the Carboniferous Period (Mississippian and Pennsylvanian), with the eastern basin already filled with sediment, the shoreline moved past western New York. The Alleghenian Orogeny occurred as the result of North America's collision with Africa (Isachsen et al., 1992; Linsley 1994). This enormous collision, combined with others in the Urals and elsewhere, created the supercontinent Pangaea by the end of the Permian. The Alleghenian Orogeny dumped a new wedge of sediment well into the interior of North America. The compressive stresses of this collision created some broad, gentle folding, such as the Fir Tree anticline, and minor thrust faulting of the Devonian rocks in central New York.

By the Late Triassic to Early Jurassic periods, about 200 million years ago, Pangaea was just beginning to break apart. Rifting created basins in southeastern New York state and adjacent New England that were quickly filled with sediment. Although dinosaur bones cannot be found in New York -- since the strata containing their remains has been eroded -- trace fossils of dinosaurs, footprints of the small theropod dinosaur *Coelophysis* can be found in these Triassic basins. Exhibits of these footprints can be found in Ithaca's Museum of the Earth and in the New York State Museum in Albany.

The Pleistocene glaciation was responsible for carving the local topography of the Ithaca area. The latest glacial advance peaked around 21,000 years ago and finally retreated 11,000 years ago, leaving behind drumlins and moraines, which can be found northeast and south of Ithaca

respectively. Another result of continuous glacial advance and retreat are the Finger Lakes, which were originally ancient north-south river valleys that were deepened through glacial scouring. After the latest glacial retreat, the Finger Lakes were dammed by deposited glacial sediment; eventually, streams carved through these mounds of sediment to form the existing gorges and waterfalls. This downcutting has also exposed the prevalent right-angled jointing of the bedrock that was caused by tectonic stresses.

### Future Research in the New York Devonian

It is remarkable that, although geologists and paleontologists have been studying the rocks and fossils of the Devonian of New York for almost 200 years, there remains so much active research on them and still so much to learn. New species remain to be described, most lineages have not received detailed evolutionary study, and we are just beginning to learn the details of changes in sea level and climate as recorded in this amazing stack of strata. If there is this much still to discover in the geology of such a long-studied region, imagine what remains to be found everywhere else!

### To learn more

General references to the geology and fossils of the Devonian of central New York include Isachsen et al. (1992); Linsley (1994); Whiteley et al. (2002); and Allmon and Ross (2007). The Museum of the Earth in Ithaca has extensive permanent exhibits on the local geology and paleontology; see <u>www.museumoftheearth.org</u>.

#### Acknowledgments

We are grateful to John Catalani, Paula Mikkelsen, and Sally Vann for editorial assistance, Judith Nagel-Myers for help with illustrations, and Laurie Van Vleet and Alana Semple for permission to reproduce their photographs.

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## **Figure Captions**

- **Figure 1.** Map of New York State showing the outcrop area of Devonian-aged rocks. Dark gray (to the south) = Upper Devonian; black (in the middle) = Middle Devonian; white (narrow ribbon to the north) = Lower Devonian. This map assumes a flat topography and no folding of the rocks; older and younger layers actually outcrop in various locations due to topography (gorges, lakes) and minor folds. (Modified from Isachsen et al., 1992.)
- Figure 2. Some of the many gorges of the Ithaca area, in which are exposed Devonian rocks. A. Taughannock Falls. B. Ithaca Falls. C. Cascadilla Gorge. D. Buttermilk Falls upper gorge. E. Buttermilk Falls.
- Figure 3. Paleogeographic map of Laurentia in the Middle Devonian. Base map from <u>http://www2.nau.edu/rcb7/nam.html</u>.
- **Figure 4.** Cartoon cross-section of the Catskill Delta, which formed as a result of mountainbuilding (orogeny) in the Middle Devonian, showing the range of depositional environments from onshore to offshore (east to west). The Acadian Mountains are roughly equivalent to today's Catskill Mountains. (Modified from Isachsen et al., 1992.)
- Figure 5. The distribution of dissolved oxygen in the shallow sea that covered New York in the Devonian. A. Cartoon showing how life could still inhabit the water column, even if

there was little or no oxygen at the bottom. (From Brett et al., 1991.) **B.** Diagram showing the relationship of bottom oxygen levels with changes of sea level in the Devonian stratigraphic section. (Modified from Ettensohn, 1985.)

- Figure 6. Stratigraphic column for the Devonian of the Ithaca area. A. Simplified version, showing the names and relationships of the major units. B. A more realistic version, showing variation of the different units east to west across central New York. (From Brett et al., 2011.)
- Figure 7. Devonian sponges and cnidarians (corals and relatives) of the Ithaca area. A. Solitary rugose (horn) coral, *Siphonophrentis halli*. Ludlowville Formation, Middle Devonian. Scale bar = 10 cm. B. Tabulate coral, *Favosites* sp. Moscow Formation, Middle Devonian. Scale bar = 10 cm. C. Hydroid, *Plumalina plumaria*. Ithaca Formation, Upper Devonian. D. Glass sponge, *Uphantaenia* sp. Rock Stream Formation? Upper Devonian. Scale bar = 10 cm. E. Glass sponge, *Hydnoceras tuberosum*. Rock Stream Formation, Upper Devonian. Scale bar = 5 cm.
- Figure 8. Devonian brachiopods from the Ithaca area. All are from the Hamilton Group (Middle Devonian) unless otherwise noted. All scale bars = 10 mm. A. Rhipidomella penelope. B. Spinatrypa spinosa. C. Tropidoleptus sp. D. Mediospirifer audaculus. E. Mucrospirifer mucronatus. F. Brachiopod shell "hash". Ithaca Formation, Upper Devonian. G. Leiorhynchus sp. Ithaca Formation, Upper Devonian.
- Figure 9. Devonian trilobites and crinoids of the central New York. A. *Greenops boothi*. Windom Shale member of the Moscow Formation, upper Middle Devonian. Scale bar = 5 mm. B. *Eldregeops rana*. Windom Shale member of the Moscow Formation, upper Middle Devonian. Scale bar = 5 mm. C. *Dipleura dekayi*. Ludlowville Formation, upper Middle Devonian. Scale bar = 5 cm. D, E. Crinoid stem fragments. Ithaca Formation, Upper Devonian. Scale bars = 10 mm and 5 cm, respectively.
- Figure 10. Middle Devonian snails and clams of the Ithaca area. All Scale bars = 10 mm. A. Gastropod, *Diaphorostoma ventricosum*. D. Bivalve, *Vertumnia reproba*. C. Bivalve, *Orthonota undulata*. D. Bivalve, *Paneuka robusta*. E. Bivalve, *Grammysia sp*.
- Figure 11. Devonian nautiloid cephalopods and trace fossils of the Ithaca area. A. Spyroceras crolatum. Windom Shale member of the Moscow Formation, upper Middle Devonian. Scale bar = 10 mm. B. Unidentified. Ithaca Formation, Upper Devonian. C. Zoophycus. Windom Shale member of the Moscow Formation, upper Middle Devonian. Scale bar = 10 cm. D. Burrows and flute casts (marks made by moving water). Rock Stream Formation, Upper Devonian.
- Figure 12. Three restorations of typical Hamilton Group (Middle Devonian) fossil assemblages. A. *Tropidoleptus carinatus* assemblage. Typical of the Mottville Member of the lower Skaneateles Formation. B. Coral assemblage from the Pompey Member of the middle Skaneateles Formation. C. *Mucrospirifer mucronatus* assemblage. Typical of the

Skaneateles and Ludlowville formations. (All from Brower and Nye, 1991.)  $ATH = Athyris \ cora \ and \ A. \ spiriferoides; \ ATR = Psuedoatrypa \ sp. \ cf. \ devoniana; \ BRY = Bryozoan \ sp.; \ BEM = Bembexia \ sulcomarginata; \ CAM = Camarotoechia \ congregata; \ CHO = Devonochonetes \ sp; \ CRI = Crinoids; \ FEN = Fenestellid \ bryozoan; \ GLO = Glossites \ sp.; \ GRE = Greenops \ boothi; \ HET = Heterophrentis \ simplex; \ MOP = Modiella \ pygmaea; \ MOD = Midiomorpha \ sp.; \ MUC = Mucrospirifer \ mucronatus; \ NOB = Nuculites \ oblongatus; \ NYA = Nyassa \ arguta; \ PLE = Protoleptostrophia \ perplana; \ SGR = Spinocyrtia \ granulosa; \ SPH = Sphenotus \ sp.; \ TRO = Tropidoleptus \ carinatus \ .$ 

- Figure 13. Stratigraphic section of the Tully Limestone. (From Heckel, 1973.)
- Figure 14. Photo of the Tully Limestone at Lower Taughannock Falls, Taughannock Falls State Park, north of Ithaca.
- Figure 15. Generalized fossil succession in the Windom Shale and Tully Limestone. (From Baird et al., 2012.) a—Heliophyllumhalli; b—Spinatrypa spinosa; c—large bryozoans; d—Mediospirifer audaculus; e—Allanella tullius; f—Devonochonetes scitulus; g—Camarotoechia mesocostale; h—Emanuella praeumbona; i—Pustulatia (Vitulina) pustulosa; j—Tropidoleptus carinatus; k—Athyris spiriferoides; l—Mucrospirifer spiriferoides; m—Rhyssochonetes aurora; n—Emanuella subumbona; o—Schizophoria tulliensis; p—Tullypothyridina venustula; q—Echinocoelia ambocoeloides; r—Spinatrypa sp.; s—Pseudoatrypa devoniana; t—Ambocoelia umbonata; u—small rugosan; v—auloporids; w—Leptaena rhomboidalis; x—styliolines. Key conodonts include: 1—Icriodus latericrescens Latericrescens; 2—Polygnathus alveoposticus, 6—Icriodus difficilis; 7—Polygnathus beckmanni; 5—Polygnathus alveoposticus, 6—Icriodus latifossatus, 10—Polygnathus cristatus; 11—Polygnathus disparalvea. Key goniatites include: 1—Tornoceras (T.) cf. uniangulare; 2—Pharciceras Amplexum; 3—Tornoceras (T.) cf. arcuatum.





Figure 2











Figure 5A











Figure 7





Figure 9





Figure 11









Figure 15

# **Devonian Outliers of the Ozarks of Missouri**

### **Bruce L. Stinchcomb**

The Ozarks (or Ozark Uplift) since the mid 19<sup>th</sup> century has been recognized as an area of ancient (and seemingly unfossliferous) rocks of Precambrian, Cambrian and Lower Ordovician age (Branson, E. B. 1944). In the 1920's with the availability of the automobile accompanied by the building of a state road system to accompany it, detailed geologic mapping was more easily carried out (Dake, 1930, Bridge 1930). Much of this geologic mapping originated from Rolla Missouri where both the Missouri Geologic Survey and the Missouri School of Mines were located. Just north of Rolla were large masses of Mississippian age sandy chert capping conspicuous knobs north of town. Some of these chert boulders were full of fossils many of which were mollusks (Bridge J., 1917). Some of these knobs could be seen from the ridge chosen in 1926 for the fledgling Route 66 where it approached Rolla coming from the east-such remnants of once more widespread strata are known as outliers. These boulders also occurred at the edge of the plateau or escarpment on which Rolla itself is situated. In a ravine north of town at the western edge of this escarpment in 1921 was discovered a mass of quartzite which contained an abundance of not Mississippian but rather Devonian marine fossils (Bridge, J. and B. E. Charles, 1922, Stinchcomb 2008). This discovery was more surprising than were the Mississippian outliers as patches of Mississippian rock were known at the time scattered over other parts of the Ozarks, usually occurring on high ridges or forming the tops of knobs-hills which stood out because of their higher elevations compared to other Ozark hills. All of these outliers appeared to represent sediments deposited in ancient sinkholessinkholes or solution structures which formed over long periods of weathering and solution of underlying older Cambrian and Lower Ordovician strata. These "filled sinks", when later filled with sediment having offered a greater amount of cherty rock to defy erosion and weathering while surrounding carbonate rocks were worn down---the sink-hole-formed rock acting as a type of shield or cap preventing erosion as adjacent rocks were removed. The end result being that, what was once a low area (sinkhole), with time and uplift, became a high area (knob). When the Rolla Devonian outlier was discovered other similar Devonian outliers were unknown. With its abundance of fossils (which originally were considered Lower Devonian in age, Branson, 1922), it was thought to have been deposited in an extension of Lower Devonian seas which deposited rocks found at the eastern edge of the Ozarks in Ste Genevieve County. An arm of this sea was thought to have extended across the Ozarks and was that body of water in which the Rolla Devonian marine life lived.

As an undergraduate geology student at Rolla, the author discovered Devonian fossils in quartzite near the town of Owensville very much like those found years before at Rolla. He also found another locality for what appeared as Middle Devonian fossil coral impressions in Gasconade County. As both of these occurrences were about midway between the Rolla outlier and extensive fossiliferous Middle Devonian limestone (Callaway Limestone) found just north of the Missouri River, the depositional model for the (somewhat mysterious) Rolla quartzite made more sense with its being deposited in an arm of a seaway extending southward (in current geographic terms) to Rolla. The seaway which deposited the Callaway Limestone covered much of northern Missouri and extended northward into Iowa where its deposits are known as the Cedar Valley Limestone.

These Devonian outliers as well as Ozark outliers of other geologic ages have always been an interest of mine. Many of them are shown on the 1979 geological map of Missouri (but not on the 2002 edition). Besides the Devonian outliers mentioned above, there are numerous outliers of fossiliferous chert and limestone (especially chert) scattered over the Ozark Uplift. Others shown in pink on the 1979 geologic map of Missouri are sandstone and quartzite of the Lower Middle Ordovician St. Peter and Everton Formations. Puzzling outliers of both Middle Ordovician fossil bearing limestone and Mississippian (Meramecian) corals are also known to occur associated with the Decaturville Astroblem south of Lake of the Ozarks, a structure with lots of puzzling geological features. Probably the best known Ozark outlier (for its fossils) is the Chronister site, the locality of Missouri's only known dinosaur and also the site for Missouri's "official" state dinosaur *Hypselbema missourensis* (Gilmore and Steward, 1945 and Stinchcomb, 2009).

Although always being somewhat difficult to collect, obtaining good fossils from Missouri's outliers today it is much more difficult than it was in decades past. The Rolla Devonian and Mississippian outliers, once remote spots in the woods, today are now in people's backyards as the town has expanded. The most prolific Gasconade County Devonian locality is now in a second home development. The Missouri dinosaur site was until recently, being systematically worked but the protecting infrastructure of a large greenhouse was demolished from a winter ice storm which was followed in the spring by high winds—the site currently being full of mud and water. There undoubtedly are other fossil bearing outliers yet still undiscovered but these are not going to be easy to find. Those Ozark outlier collections which currently exist represent a record of one of the unique features of Ozark geology---they came through the hard work and perseverance of dedicated collectors.

On a different note regarding Devonian fossils in the Ozarks are the various "fish teeth" found in abundance locally in late Devonian sandstone (Bushberg and Sylamore Sandstones) which crop out at the edge of the uplift (Branson, E. B., 1944). Usually found in an abraded condition, these teeth are primarily of the placoderm genus *Ptychodus* sp. Unlike the Devonian fossils of the Ozark outliers they give support to the Devonian Period being referred to as the "Age of Fishes" as these teeth are about the only megafossils present (however these same sandstones can be rich in conodonts, the teeth-like microfossils found to be so useful in correlation of Paleozoic rocks). Devonian strata in the central and northeastern parts of Missouri have also yielded a rich fauna of placoderms (primarily teeth and bony armor) as well as the teeth and dorsal spines of shark-like fishes (Branson E. B. 1914)—but that is another story.

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## **Figure Captions**

1. Devonian and Mississippian outliers near Owensville in Gasconade County Missouri as shown on the 2003 geologic map of Missouri. These remnants of once more widespread strata are found throughout much of the Ozark Uplift of Missouri. Often they are found at the tops of high hills known as knobs or they are found at the topographically highest parts of ridges. Some (but not all) of these outliers are fossil bearing. The 1979 geologic map shows more of these outliers than does the 2003 map for reasons unknown to the author.

#### **Brachiopods**

2. *Schizophoria iowensis*. Internal molds in quartzite. The schizophrenic brachiopod! The brachial (top) part of this brachiopod (upper two rows), differs so much from the opposite valve that the Greek designation (schizo = dual) was used in its generic name. This is the same root as in schizophrenia which in psychiatry means two personalities. Devonian quartzite outlier northwest of Owensville Mo.

- 3. Another group of internal molds (steinkerns) of *Schizophoria iowensis*. Devonian quartzite outlier, eight miles northwest of Owensville Mo.
- 4. *Spirifer euryteines* Owen. A group of quartzite steinkerns of this distinctive brachiopod genus. Devonian quartzite outlier northwest of Owensville Mo.

## **Gastropods** (snails)

- 5. *Loxonema robustum* Hall. Internal molds (steinkerns) of a widespread Devonian gastropod. This is a common gastropod in the Lower Devonian Grand Tower Formation and one of the reasons why the Rolla outlier was thought to have been deposited in an extension of the lower Devonian seaway which would have come in from the east (present geographic coordinates) rather than from the north. Devonian quartzite outlier, Rolla, Mo.
- 6. *Bellerophon* sp. A planispiral gastropod (some paleontologists have suggested that some bellerophontids are actually monoplacophorans). Bellerophontids go back well into the Cambrian where they predate "normal" gastropods which, unlike bellerophontids, are not coiled in a plane. Devonian quartzite, northwest of Rolla, Mo.
- 7. *Euryzone lucina* Hall. Internal molds (steinkerns) in sandstone of this widespread Devonian gastropod. These came from sandstone of one of the Owensville Devonian outliers northwest of Owensville on Goerlisch Ridge. The sand which makes up the sandstone of these outliers is probably reworked from the Lower Middle Ordovician St. Peter Sandstone. This gastropod is indicative of the Middle Devonian and is not found in the Rolla area although it was locally common in the outliers northwest of Owensville.
- 8. *Hormotoma maia* Hall. A ubiquitous high spired gastropod found mostly from the Middle Ordovician thru the Lower Devonian. The presence of the genus *Hormotoma* was another reason why the Rolla outlier was considered lower rather than middle Devonian. Rolla quartzite outlier, Rolla, Mo.
- 9. Gastropod opercula impressions? Odd geologic occurrences like the Ozark Devonian outliers can sometimes yield or preserve organisms or parts of organisms normally not found as fossils. What are believed to be the "lids" or opercula of the above gastropods are found in the same sandstone beds as the above fossils.

## Cephalopods

10. *Gomphoceras* sp. Internal molds (steinkerns) of nautiloid cephalopods. This is another molluscan genus characteristic of the Lower Devonian but not (so much) the Middle part of the Period. The occurrence of this cephalopod in the Rolla outlier lent credence to its being connected to the Lower Devonian seaway in which the Grand Tower Formation to the east of Rolla was deposited rather than connected with the Middle Devonian (Cedar Valley) seaway to the north. (These are somewhat suggestive of the widely distributed Lower Devonian straight cephalopods from Morocco usually labeled as "Orthoceras").

11. *Nephritceras* sp. (left) A living chamber of this large coiled cephalopod from the Owensville Devonian outliers. To the right is a partial specimen of this genus from the Middle Devonian Callaway Limestone, Callaway County Mo. The Callaway Limestone correlates with the Cedar Valley Limestone of Iowa.

## Arthropoda---Trilobites

- 12. A trilobite head (or cephalon) of the genus *Proetus* in quartz sandstone. Sandstone, being grainy, doesn't preserve much detail in most fossils. Considering how coarse this sand is (probably reworked sand from the St. Peter Sandstone), preservation of this bulbous nose trilobite is fairly good. From one of the Owensville Mo. sandstone outliers.
- 13. Group of trilobite pygidia ("tails") and head (cephalon) preserved in sandstone. The Missouri Ozarks has a lot of fossil trilobites, genera and species often not found anywhere else. However, like these Devonian outlier specimens, they are rarely found complete. Owensville sandstone outlier, Gasconade County Mo.
- 14. Impression in quartzite of complete specimen of the trilobite *Proetus* sp. Devonian quartzite outlier, Rolla Mo.
- 15. Proetus sp. In sandstone from one of the Owensville outliers.
- 16. Proetus sp. Trilobite pygidia Owensville outlier.
- 17. Bridge's and Charles 1922 prediction and comment that more Devonian outliers would be found to the **south** of Rolla in the future. They weren't! More outliers were found to the **north** which connected the Rolla outlier with the Middle Devonian outcrops near the Missouri River at the northern part of the Ozark Uplift. Some of these connecting outliers were found by yours truly.

## Vertebrates-Placoderms

18. *Ptychodus calceolus* teeth. Various size and shaped teeth of this placoderm can be locally abundant in late Devonian sandstones (Sylamore and Bushberg sandstones) which surround much of the Ozark Uplift. These give credence to the Devonian as being the "**age of fishes**".

























Conclusions.—The presence of a Grand Tower outlier at Rolla indicates a much greater submergence of the Ozark upl ft during Onondaga time than has commonly been supposed. The nearest outcrops of the Grand Tower formation are at least 100 miles to the east. The St. Francois Mountains, the structural center of the uplift, are directly between the two exposures, and it is not believed that these were covered in Devonian time. In view of the thinning out of the Devonian to the north, it may be assumed that the Onondaga sea extended westward along the southern border of the St. Francois Mountains, and that it may have covered much of the southern portion of the uplift. Further field work may reveal other outliers, which will enable the boundaries of this sea to be traced more definitely. Figure 17

## The Marcellus Shale: Why Devonian Geology Matters Today

## Kelly E. Cronin

#### Introduction

Approximately 390 million years ago, about 30° south of the equator, a warm epicratonic sea spread northeast of the rising Acadian Mountain range. Small planktonic organisms lived, died, and settled to the bottom with mud and clay to form what would become the Marcellus Shale. Over the ensuing hundreds of millions of years, the heat and pressure of burial and tectonic movement transformed the organic matter in the Marcellus Shale into natural gas. The immense size of the Marcellus Shale makes it easily one of the largest natural gas resources in the world. An extraction technique developed in the 1990s that allowed recovery of natural gas from tight shales combined with rising natural gas prices and a hike in the estimates of gas recoverable from the Marcellus. The presence of natural gas, the technologies that are useful in its extraction, and some of the environmental issues that arise from extracting natural gas are all influenced by the geologic history of the Marcellus Shale.

#### **Marcellus Shale Geology**

The Marcellus Shale is the basal member of the Hamilton Group in the Middle Devonian. On the northeastern shore of the sea that deposited Marcellus Shale, near what is now Albany, New York, tectonic activity compressed the landscape and formed the Acadian mountain range. The deepest part of the sea was located in the eastern part of the basin, and it gradually became shallower to the west. The Acadian mountains experienced intense erosional forces, and stream activity carried the eroded sediment into the sea basin. Algae and other planktonic organisms inhabited the surface waters of the sea, and as they died they sank to the bottom of the basin and mixed with the sediment that flowed in from the mountain erosion. The Marcellus Shale was deposited over 2 to 4 million years (Ver Straeten, et al., 2011). The gas-bearing shale portions of the Marcellus are the older Union Springs shale and the younger Oatka Creek shale. Between these sections of shale is the Cherry Valley limestone. (Whiteley, et. al., 2002).

The total organic content of portions of the Marcellus Shale is high – from 1% to 17% by weight (Ver Straeten, et al., 2011). The concentration of organic matter in the shale is due sea level rise, which limited the distance sediment traveled into the basin, caused long periods of anoxia, and prevented seasonal mixing that otherwise would have oxygenated the sediment (Ver Straeten, et al., 2011). There was also increase in phosphorus and nitrogen which stimulated primary productivity, contributing to both anoxia, as primary producer populations exceeded the available oxygen, and direct input of organic matter as those organisms died and settled to the bottom (Ver Straeten, et al., 2011, Sageman et al., 2003). The organic matter did not decompose when it sank to the basin floor, and after burial it became the natural gas in the Marcellus Shale.

## The Fossil Fauna of the Marcellus Shale

Due to the lack of oxygen, most benthic organisms, like trilobites, clams, and coral, could

not survive well in the basin during much of Marcellus deposition, so the black shale portions of the Marcellus subgroup are fossil-poor relative to the rest of the Hamilton Group. Nonetheless there are fossils to be found there. There are occasionally bivalves and leiorhynchid brachiopods as well as pelagic organisms. Cephalopods include goniatites and nautiloids, both straight and coiled. There are also dacryoconarids and styliolininds (Ver Straeten, et al., 2011). See Figure 1.



**Figure 1.** These are fossils typical of the black shale sections of the Marcellus Shale. From: Brower, J. C., and O. B. Nye. 1991. Quantitative analysis of paleocommunities in the lower part of the Hamilton Group near Cazenovia, New York. New York State Museum Bulletin 469 pp. 37-73.

Parts of the Marcellus Shale are much more fossil rich because there were spans of time during which oxygen level increased. There are two distinct faunas, the lower "Stony Hollow Fauna" and the upper "Hamilton Fauna (Ver Straeten et al., 2011)." The Stony Hollow Fauna contains benthic animals like the brachiopods *Variatrypa arctica, Kayserella, Carinatrypa,* and *Pentamaerlla*, corals like *Guerichiphyllum*, and *Dechenella haldemanni* trilobites. The classic Hamilton Fauna, dominated by brachiopods and including rugose corals, bivalves, and gastropods, appears in the upper part of the Marcellus (Ver Straeten et. al., 1994; Whiteley et. al., 2002).

#### **The Marcellus Shale Post-Deposition**

The Marcellus Shale is the only member of the Hamilton group with commercial natural gas potential. Over time, more sediment was carried into the basin, burying the Marcellus deposits; water circulation in the sea also improved, creating a more oxygen-rich environment where decomposition could occur and where trilobites, coral, and other well-known Devonian fossil organisms could live.

Three geologic forces combined to create sets of natural fractures, or joints, throughout the Marcellus Shale. The first of the forces that created these joints was the formation of the natural gas itself. Burial of the Marcellus Shale sediment created immense heat and pressure. Over time, this heat and pressure broke the chemical bonds in the undecomposed organic matter, forming methane and other hydrocarbons. Pressure and temperature were high enough over time in the Marcellus Shale that, especially in the eastern portion of the play, the natural gas is entirely composed of methane. Some natural gas liquids can be found in the western part of the Marcellus, mostly under Ohio. The newly formed natural gas created pressure inside the shale, and as the gas expanded, it helped created natural fractures in the rock, also called joints. The formation of Pangaea and the Alleghanian Orogeny that occurred when the African Plate collided with the North American Plate further exacerbated the joint formation in the Marcellus.

The joints in the Marcellus Shale run in two separate, roughly parallel "sets" called J1 and J2. Joints in the J1 set run east-northeast throughout the Marcellus Shale. The J2 joint set runs generally north-northwest, cutting across the J1 joint set. Joints in the J1 joint set are spaced more closely together than joints in the J2 joint set. Joints in the J2 set are more likely to have healed, which means the joints have filled in with minerals and are no longer pathways for gas flow (Hill, et. al., 2002).

The third force that created joints in the Marcellus Shale is the decrease in pressure from the erosion of the overlying rocks. The Marcellus Shale has been buried by numerous other rock layers in the millions of years since its deposition. Some of these layers have eroded since the Alleghanian Orogeny ended. Much of the erosion was caused by the numerous glaciations that have sculpted the current landscape of the Northeast. These erosional forces brought the Marcellus Shale closer to the surface of the Earth, thereby decreasing the downward pressure provided by overlying rocks. As overlying weight that had compressed the ground was released, the J3 joint set was formed. They, too, run roughly parallel to each other, and are referred to as release joints and unloading joints (Hill et al., 2002). Release and unloading joints created by the various unloading of rock and ice are only present at or near Earth's surface, so J3 joints are not found at the depth of Marcellus Shale natural gas extraction, which happens at depths between 3,000 and 8,000 feet in Pennsylvania (Engelder et

al., 2009).

#### The Marcellus Today

Today, the Marcellus Shale underlies 54,000 square miles in parts of New York, Pennsylvania, West Virginia, Ohio, New Jersey, Maryland, Virginia, Kentucky, and Tennessee. It outcrops north of the Finger Lakes in New York, gradually becoming deeper and thicker to the south and east. Where it does outcrop, it is dark black in contrast to the surrounding limestone – evidence of the high organic content that formed the natural gas.

Of the states underlain by the Marcellus Shale, only Pennsylvania, Ohio, West Virginia, and New York contain economically recoverable natural gas. Of these states, all but New York are currently undergoing natural gas extraction using a combination of technologies called horizontal, high-volume slickwater hydraulic fracturing.

There is a considerable amount of natural gas in the Marcellus, but just how much is recoverable remains a matter of some debate. The estimate of the amount of gas has been rising for the last 30 years. Before the late 1980s, geologists estimated that the Marcellus Shale contained around .5 trillion standard cubic feet (scf) of natural gas. In 1988, that estimate was increased to 26.5 trillion scf, and in 2008, revised further to 50 trillion scf (Engelder and Lash, 2008). From there, still higher numbers have been put forward. Chesapeake Energy estimated that there is 363 trillion scf in 2008, and the Energy Information Administration increased it to 410 trillion in 2011, a number based partly on industry estimates. The final word seems to have come from the USGS, who in August 2011 estimated the amount of recoverable natural gas in the Marcellus to be 84 trillion scf. The EIA has since revised their own estimates down to this number (Cronin, 2011). For perspective, total US consumption of natural gas in 2011 was 24.4 trillion scf (EIA, 2012).

## **Natural Gas Extraction**

Part of the reason for the revised estimates was development of new ways to recover natural gas from shale. Horizontal drilling and hydraulic fracturing were developed separately as fossil fuel extraction technologies, but were combined for the first time commercially to develop the Barnett Shale in Texas.

#### Horizontal Drilling and Hydraulic Fracturing

Directional drilling, of which horizontal drilling is one type, allows wells to be drilled at various angles underground to reach fossil fuel sources that are not accessible from the surface directly above them. Horizontal drilling, starts with a vertical well bore which is then angled until it is oriented horizontally – in the Marcellus, it takes about 1,000 vertical feet for the well make the 90° turn. From there, the well can be drilled horizontally underground for thousands of feet. The first horizontal well ever drilled was drilled into the Antrim Shale – another Devonian shale – in Michigan in 1988 (Williams, 2011).

The Marcellus Shale is "tight," meaning it has very little pore space. This trapped the gas within the rock for hundreds of millions of years, but it also prevents the gas from flowing through the shale into the well bore and to the surface. To get around this problem, such tight source rocks are artificially cracked or fractured, by any of a variety of techniques, in order to stimulate well

#### production.

Fracturing source rock in order to increase gas well production has a long history. Beginning in the 1860's, the explosive nitroglycerin was used, sometimes illegally, to crack rocks in shallow wells. Since then, various fracturing fluids have been used to fracture rocks by hydrostatic pressure. In the past, fluids have included acid, acid combined with water, squeeze-cement, napalm and gasoline, and a variety of gelled fossil fuels (King and Morehouse, 1993). Water is the main fracture fluid in Marcellus wells in Pennsylvania, Ohio, and West Virginia. These fracturing fluids, when under high pressure, create or expand fractures in the rock. The fractures allow the gas to flow into the well and to the surface.

The large volume of water required for hydraulic fracturing and the chemicals added to the water to reduce its viscosity combine with horizontal drilling and hydraulic fracturing to give the process used to extract gas from the Marcellus – horizontal high-volume slickwater hydraulic fracturing – its name.

#### Drilling and Fracturing a Well

Drilling a well and recovering gas from the Marcellus Shale is a complicated process. Once the site has been chosen and prepared, the well is drilled. The drill bit must be lubricated with either air or fluid, both to ensure that the bit can be used smoothly, and to create pressure so that the sides of the newly created well bore do not collapse. As the well is being drilled, it is lined with steel casing. Casing prevents the collapse of the well bore and prevents drilling fluids and gas from escaping through the sides of the well. Steel casing is inserted into the drilled hole, cemented in place, and then the well is drilled deeper with a slightly smaller drill bit. Then another, slimmer casing is hung in the deeper well hole and cemented in place (King and Morehouse, 1993). The cement is pumped down the well inside the casing. When it reaches the bottom of the hole, it flows out and back up the space between the casing and the drilled well, the area called the annulus. Because casing lines the entirety of the well, it must have holes punctured into it in order for hydraulic fracturing to proceed and natural gas to have a pathway into the well. These holes are created by perforation guns that are positioned in the lateral – the horizontal part – of the well. The perforation gun shoots small projectiles, called shaped charges, directly into the casing. These charges punch through the steel casing and cement-filled annulus.

Hydraulic fracturing is a multi-step process that uses water mixed with a variety of chemicals to expand and create fractures in the Marcellus Shale, and as a delivery system for proppant, which holds open the fractures after the pressure from hydraulic fracturing is removed.

Because the laterals can reach several thousand feet in length, it is not possible to maintain the pressure needed to fracture the entire lateral at once (Arthur, et. al., 2008). Therefore, hydraulic fracturing happens in several stages, along only a portion of the lateral at one time. An average of 4.2 gallons of water is required to fracture a Marcellus Shale well. The primary determinant of this volume is the length of the lateral being fractured. It takes between 300,000 and 500,000 gallons of water to fracture each 500 feet of well bore (NYSDEC, 2011). Generally, acid is first pumped down the well to clear the well bore of excess cement so that the fracturing fluid can more easily reach the shale (Arthur et.al., 2009). Acid may also be used to etch the shale, making it easier to break apart.

The acid is followed by the fracture fluid. To be effective, the fluid must be viscous enough to hold and deliver proppant to the fractures rather than letting it settle to the bottom of the wellbore, but friction must be minimized to reduce the still considerable amount of force that must be exerted at the surface to maintain enough pressure in the well to fracture the shale. Gels are used to increase the viscosity, and friction reducers are added to minimize friction. At the temperature and pressures present at depth, these gels can break down, so other additives, called cross-linkers, are added. Cross-linkers maintain viscosity even as the heat increases at depth. Chemicals called breakers are added next to break down the gels and cross-linkers so that the proppant is released into the fractures. Breakers also increase the amount of fluid that will flow back out of a well after hydraulic fracturing (Arthur et. al., 2009)

Still other chemicals, called surfactants, reduce surface tension and, like breakers, increase the amount of fracture fluid recovered from the well (NYSDEC, 2011). If acid is used, it must be followed by a corrosion inhibitor in the fracture fluid so that the steel in the casing, tools, tubes, tanks, etc. are not damaged (Arthur et. al., 2009). The amount of corrosion inhibitor depends upon the type of casing used, and the temperatures at depth in the well. If temperatures are sufficiently high, another chemical called a booster, is added to allow the corrosion inhibitor to work effectively.

The gels added to drilling fluid are largely organic compounds, and provide an environment in which bacteria can thrive. Bacterial growth can clog fractures and produce metabolic byproducts that can corrode equipment. Chemicals that kill bacteria, called biocides, are therefore added to the fracture fluid to inhibit the growth of microorganisms (NYSDEC, 2011).

Salts are generally added to the fracture solution, to prevent clay in the target formation from swelling, migrating, and blocking fractures. Salts are also referred to as clay stabilizers in this context. A pH adjuster can also be used to regulate the acidity of the fluid at the correct level for the surfactants, crosslinkers, and friction reducers to interact properly (Coburn, 2011).

The fracturing fluid travels down the well bore to the section of the lateral being fractured. The lateral section has been perforated at regular intervals to allow the fluid to move between the well and the rock and the gas to flow back into the well bore. Here the fluid is forced under pressure through the perforations in the cement into the shale. Changes in pressure widen and lengthen existing fractures and create new fractures to be filled with fluid and proppant.

### Why the Geology Matters

The Marcellus Shale contains natural gas because of its geological history of deposition in an anoxic sea with enough undecomposed organic matter to transform into methane through the heat and pressure of hundreds of millions of years. Existing joint sets are the result of tectonic activity since the deposition of the shale, and provide conduits for natural gas to flow through to be extracted. Natural gas companies use the orientation of the joints to maximize the effectiveness of hydraulic fracturing when extracting natural gas by orienting the wells to intersect with as many of the natural fractures as possible (Chipperfield, 2008). The characteristics of shales determine the technology used to extract the natural gas. The geology of the Marcellus Shale makes it an attractive
prospect for the natural gas industry, but it also creates some problems. Many – though not all – of the environmental concerns that have been raised concerning gas drilling in the Marcellus Shale can find their root causes in its geologic history.

## Wastewater Disposal

Most of the water used to hydraulically fracture a well is not returned to the surface; only about 10% to 30% of it comes back up the well at all. The rest remains trapped in the Marcellus Shale (Engelder, 2012). The water that does return contains chemicals from the fracturing fluid as well as brine and naturally occurring radioactive material from the Marcellus Shale itself, all remnants from the shallow sea where the shale was deposited.

Uranium and thorium, both radioactive elements, preferentially adhere to clay and organic matter in sea water. When the clay sediments and dead planktonic organisms settled to the bottom of the sea, these elements settled with them. Uranium and thorium still occur in the Marcellus, along with their daughter products, radium-226 and radium-228, which are considered more hazardous in this context (NYSDEC, 2011). Radium is soluble in water, and it comes to the surface along with the flowback fluid after hydraulic fracturing and the produced water that flows out of the well for its entire productive life. Radium can combine with other elements and precipitate out of the fluid and onto pipes and equipment as scale.

Other leftovers from the ancient ocean include heavy metals and salts. Both occur in the produced water from natural gas extraction. Common heavy metals found in formation water in Marcellus Shale wastewater in Pennsylvania include lead, arsenic, barium, chromium, magnesium, manganese, strontium, and uranium. The salt content of produced water from the Marcellus Shale, salt left from millions of years of shallow oceans, can be extremely high, several times that of sea water (NYSDEC, 2011).

Disposal of this flowback and produced water is a primary environmental concern for gas drilling. Releasing it untreated into the environment would have disastrous consequences. One study performed in West Virginia, for example, found that when untreated hydraulic fracture fluid was spread over 0.20 hectare, almost all ground vegetation died within two days, trees started dropping foliage within 10 days, and 56% of the trees in that area were dead after two years (Moseley et. al., 2010). Efforts to treat this water in standard wastewater treatment plants for release back into surface water caused a serious spike in total dissolved solids in the Monongahela River in Pennsylvania. Though this was later attributed to a period of low flow in the river, it still highlights the care that must be taken with disposal of drilling wastewater (Charles, et al., 2012).

A second option for disposal of wastewater is the use of Class II disposal wells, also known as deep injection wells. Disposal wells make use of deep geological formations, often depleted oil and gas wells, to store large quantities of wastewater from fossil fuel extraction underground. If properly sited and executed, these wells should isolate their contents from both groundwater sources and other rock layers. Most of the around 28,000 disposal wells related to oil and gas operations are located in Texas, Oklahoma, Kansas, and California.

Perhaps the most important features of a deep injection well is that the fluid will stay in the formation into which it is being injected without migrating to other formations. Properly sited and executed, an underground injection well is currently the only disposal option that completely prevents wastewater from entering surface and groundwater. It is not without its risks, however. Underground injection wells involve pumping billions of gallons of fluid into rock formations, orders of magnitude more than hydraulically fractured wells for natural gas extraction. High pressures are sustained for weeks at a time for fluid injection, as opposed to days for hydraulic fracturing, and the well can be used over many years to dispose of the fluids. It is potentially hazardous because it means that injection wells have the potential to cause induced seismicity (human-caused earthquake activity). For example, seismic activity in Ohio and Texas has been linked to disposal of natural gas wastewater in injection wells. A study in Texas correlated the occurrence of a number of small earthquakes between 2009 and 2011 with certain injection wells used for fluid disposal from the Barnett Shale (Frohlich, 2012). A number of small earthquakes near Youngstown, Ohio were linked to an injection well there, which has since been shut down (ODNR, 2012). Most injection wells operate without detectable seismic incidents, but small earthquakes are a potential consequence of a well that is improperly sited.

Proper siting of an injection well hinges upon geology. Wastewater is injected into porous layers – often sandstone or limestone formations – that are isolated by impermeable formations. In order for injection wells to cause seismicity, they must have been sited near a fault that is already at near-failure stress. Furthermore, enough of the fluid in the injection well must be able to reach the fault that it causes slippage along it (ODNR, 2012). If these things can be avoided, disposal of wastewater in injection wells can be an effective way to remove it from the water cycle practically forever.

## Methane Migration

Methane migration into drinking water wells has also been an issue connected to natural gas drilling, and one that has its root in the geologic characteristics of the area. The Marcellus is by no means the only gas-bearing layer in the Appalachian Basin. Natural gas has been known to seep to the surface in this region for hundreds of years. In fact, the first record of a natural gas seep in New York was in what is now Ontario County, when Native Americans showed the area to French explorers in the 1660s (NYSERDA, 2007). Natural gas has been extracted from formations shallower than the Marcellus since the 1820s. Methane occurs naturally in the groundwater in New York, albeit usually in concentrations below EPA drinking water standards (Kappel et. al., 2012). Despite these things, the process of natural gas development in the Marcellus has the potential to – and, in fact has – contaminated private drinking water wells with methane.

In order for methane or other fluids to migrate from a formation and into a drinking water source, there must be a pathway to do so. Some concerns have been raised that hydraulic fracturing could increase the connectivity of the Marcellus Shale to the overlying layers, thus creating new pathways for groundwater contamination to occur. This is unlikely to occur for a number of reasons. First, the pressure created by the hydraulic fracturing is only active for hours or days, and the fractures that are created are held open only by proppant after the pressure is released. Otherwise, these fractures would close under the pressure exerted by the rocks around it and above it. Second, the rock layers above the Marcellus Shale, between it and drinking water sources, have different stiffness and stress characteristics, and fractures would not simply propagate straight up though them.

While hydraulic fractures are unlikely to propagate through many layers of rock to aquifers, there is actually evidence in Pennsylvania that brine from the Marcellus Shale has migrated through naturally occurring fracture networks that existed before gas drilling and into shallow groundwater in some areas. These areas, with possible pre-existing connections between the Marcellus Shale and groundwater might be at higher risk of methane migration from drilling (Warner, et. al., 2012).

Another way to create conduits through which methane can migrate is through the wells themselves. Groundwater contamination can occur when methane from the Marcellus Shale or shallower natural gas bearing formations migrates up an improperly constructed natural gas well and into a water source. Improper casing of wells or casing failures have contributed to contamination of groundwater in twice in Pennsylvania between 2008 and 2011as well as in Colorado and Wyoming (Considine et. al., 2012). The more publicized incident of groundwater contamination occurred in Dimmock, Pennsylvania. There, the contamination has been attributed to improperly cemented Marcellus wells that allowed methane to migrate up the wells and into groundwater (NYSDEC, 2011).

Oil and gas drilling has commonly occurred throughout NY for over a century, and some of these wells were improperly abandoned. At least 70,000 wells have been drilled in NYS and only 30,000 are accounted for by the DEC (Osborn et. al., 2011). When a well is no longer producing commercial quantities of oil or natural gas, a company abandons the well. Abandoning a well properly involves removing some of the casing and other surface equipment, plugging the well with cement so that it is no longer a conduit for fluids migrating from beneath the surface, and then reclaiming the surface. If wells are improperly abandoned, they can act as a connection between the surface and the depth of the well. In most cases, improperly abandoned wells are older and relatively shallow, but unaccounted-for, improperly abandoned wells could potentially connect a fracture network to a groundwater source.

The natural gas extraction opportunities and environmental issues discussed here are only the ones that pertain to the Devonian geology of the Marcellus Shale. The wellhead price of natural gas, as well as the proximity of the Marcellus Shale to major population centers in the Northeast combined to encourage drilling in this particular shale. Most risk analyses point to fluid spills at the surface as the greatest factor in potential surface and groundwater contamination from drilling rather than methane migration along improperly cased or plugged wells. Air pollution and habitat fragmentation issues are common to all fossil fuel extraction and most industrial processes, rather than only natural gas extraction from the Devonian. Nevertheless, enough of the characteristics of Marcellus drilling can be traced back to its geologic history, that Devonian geology is truly relevant today.

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