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THE ORDOVICIAN

A LOVE OF FOSSILS BRINGS US TOGETHER

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MID-AMERICA PALEONTOLOGY SOCIETY

A LOVE OF FOSSILS BRINGS US TOGETHER

Western Illinois University
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John Catalani and Chris Cozart, Editors

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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 Ordovician related topics contributed by our members, professionals, and our guest speaker, Robert C. Frey. We would also like to thank Robert C. Frey for delivering the keynote address.

ABOUT THE COVER

The cover photo is of a group of *Beloitoceras* cephalopods swimming near an upper Ordovician seafloor. Image provided by the Burpee Museum from their Diorama of an upper Ordovician sea floor from northern Illinois.

The Ordovician--An Introduction
John A. Catalani

Introduction

The Ordovician (approx. 489-443 million years ago), which started as a compromise to resolve a conflict of overlapping strata, is now recognized as the Geologic Period that witnessed the greatest increase in taxonomic diversity in the history of life on Earth. After decades of intense field work, radiometric dating, and lively discussion, a set of Global Stages have been defined and now serve as a standard for correlating Ordovician rocks around the world. As we shall see, the Ordovician Period is one of widespread epeiric (shallow cratonic) seas that fostered an incredible diversity of life that evolved in a warm, wet, mostly stable greenhouse climate punctuated by some of the most violent volcanic eruptions in Earth's history.

History of the Ordovician as a time Period

The story of the Ordovician Period begins with the establishment of British stratigraphic investigations and two giants in the history of geology: Sir Roderick Impey Murchison and Reverend Adam Sedgwick. The two began as friends and often collaborated in the field. One such collaboration resulted in the two erecting the Devonian System. In the 1830s, they worked together mapping the "transition" rocks, those lying between Devonian and primary rocks, in Wales. Murchison mapped the fossiliferous rocks in the south and worked his way north while Sedgwick, who preferred to map lithologies and rock strikes, began in the north and proceeded south. In 1835, they presented a joint paper at a Dublin conference that divided the "transition" rocks into two new systems. Murchison was responsible for the upper Silurian System (named for the Silures, a Welsh Borderland tribe) while Sedgwick proposed the lower Cambrian System (from Cambria, the old Roman name for Wales).

Unfortunately for the friendship, a more detailed survey in the 1840s revealed that certain rock layers were incorporated into both Systems. Conflict and controversy ensued as each refused to compromise. In addition, Murchison continued to add older rock layers to his Silurian System until he virtually assimilated Sedgwick's entire Cambrian.

Fortunately, as we shall see, Murchison divided his Silurian System into Upper and Lower units that, along with Sedgwick's Cambrian, provided a tri-unit division of the "transition" rocks (it was the Lower Silurian that was claimed by both men). Murchison and Sedgwick died in the 1870s but their followers carried on the dispute until Charles Lapworth provided a solution. In 1879, Lapworth used the tri-unit division to formulate a compromise--he placed the disputed Lower Silurian rocks into a new System he named the Ordovician (for the Ordovices, an ancient tribe in Wales). He rationalized this by using index fossils, primarily graptolites, to define the Ordovician strata and isolate these rocks from those of both the overlying Silurian and the underlying Cambrian Systems (see Fig. 1).

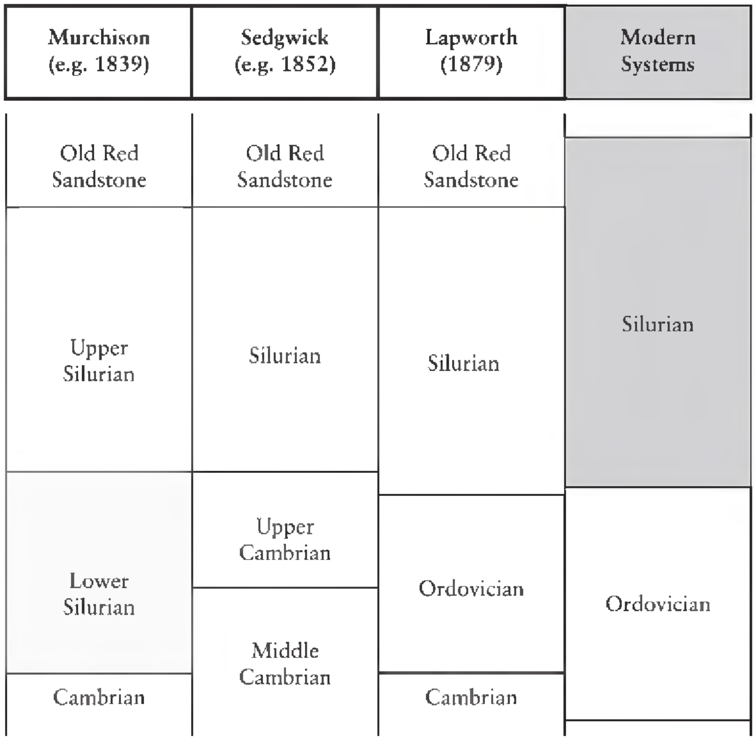


Fig. 1. Chart of Murchison's Silurian System, Sedgwick's Cambrian System, and Lapworth's compromise that resulted in the Ordovician System. (Modified from Fig. 1.1 in Palmer, D. *et al.*, 2000, British Silurian Stratigraphy.)

The Ordovician was accepted as a System by the British Survey in 1901 and by the United States Survey in 1903 but it was not until 1960 that the Ordovician Period was officially adopted by the International Geological Congress.

The Ordovician Today

Since the Ordovician was officially accepted as a Period of the geologic time scale, the classification and assignment of Ordovician stratigraphic units has undergone dramatic changes culminating in the Global Ordovician Chronostratigraphic Chart completed in 2007. In addition to the establishment of the global stages (names, boundary definitions, and type sections), many other units were reassigned and/or renamed thus altering how we now subdivide the Ordovician.

In the stratigraphic system used during the early and middle 1970s, the mid-west Ordovician was divided into three clearly defined Series based, of course, on the best information available at that time including fossils and rock correlations. The lowest (oldest) of these Series was termed the

Canadian. The Canadian is exposed in the limestones and cherts of Minnesota, Wisconsin, and Missouri. The fossils contained in these rocks are more similar to those of the Cambrian than to those found in rocks of the rest of the Ordovician, at least for the nautiloids. This is what prompted the late Rousseau Flower, at that time the world's foremost authority on nautiloids, to begin using "Canadian" unofficially as a System, comparable in rank to the Ordovician, in many of his publications. The middle Series was named the Champlainian and contained the mollusc-brachiopod rich dolostones and limestones well exposed in the eastern United States. In the mid-west, two fairly fossiliferous Champlainian groups of rocks are exposed--the lower Platteville Group (a formation in Wisconsin and Minnesota) and the upper Galena Group. At that time, the Platteville was assigned to the upper part of the Blackriveran Stage while the Galena comprised pretty much the entire Trentonian Stage and both were tentatively placed in the lower Caradoc of British terminology. I mention these two units because tracing their changes in assignment gives us a local basis for understanding the final global correlations. The taxa present in the rocks of these units are similar but not the same due to the Deicke extinction that occurred at the Platteville-Galena interface of deposition and is marked by the Deicke K-bentonite. The upper (youngest) Series was termed the Cincinnatian and the rocks contained in this series are exposed in possibly the most prolific collecting area in the United States--the tri-state region of Indian, Kentucky, and Ohio. Literally millions of fossils have been collected there and virtually every new excavation exposes these highly fossiliferous shales and limestones.

Then in the mid-1980s, I became aware, by way of the academic literature and several fieldtrip guidebooks, of a subtle reassignment of several units of the Galena Group (see Fig. 2). The upper Galena, including the very fossiliferous Wise Lake Formation and the Dubuque Formation, was now correlated with the Edenian-Maysvillian units of the type Cincinnatian area. The lower Galena was still placed in the Champlainian Series, now renamed the Mohawkian Series. That meant that the Champlainian-Cincinnatian contact occurred in the middle of the Galena Group. I had collected the fossiliferous Wise Lake Formation many times searching for the nautiloids that represented the subsequent recovery fauna after the deposition of Platteville rocks and, as I became aware of later, the Deicke extinction. Curiously, the trilobites I had collected in Wise Lake rocks seemed very similar to those I had found in the type Cincinnatian and one of them was of a common genus--*Flexicalymene*. After much subsequent collecting, I found that several of the Wise Lake nautiloids also compared well with those in the Cincinnatian. Based on this meager evidence that I had collected, the change in assignment of these two Galena formations appeared to be warranted.

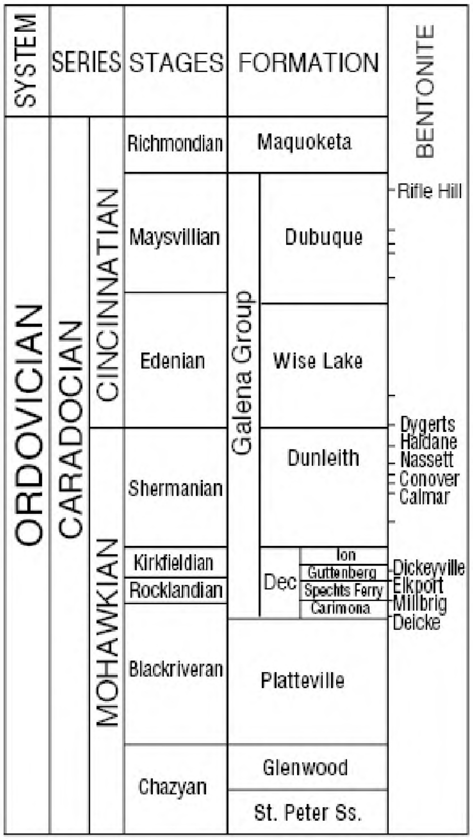


Fig. 2. Chart of the changes to part of the "Champlainian" Series, which has been renamed the Mohawkian Series. The upper two formations of the Galena Group are now assigned to the Cincinnatian Series. (From Simo, J.A., et al., 2001, Featured Faculty Research, The Outcrop, Univ. of Wisc.-Madison.)

By the mid-1990s the British Ordovician had been revised from six Series designations to five and the North American Ordovician was modified, along with many name changes, into four Series--Ibexian (oldest), Whiterockian, Mohawkian (Platteville, etc.), and Cincinnatian (this name will probably never change). The Mohawkian was in turn subdivided into five or so Stages and Sub-stages, which finally confused even an Ordovician Geek like me. Fortunately, cooler heads prevailed and, with the use of K-bentonite beds described below, the Mohawkian Series was re-evaluated and subdivided into only two Stages. The lower (older) Turinian Stage contains all of the Platteville rocks as well as the lower Decorah Shale while the upper Chatfieldian Stage contains the lower Galena (the upper Galena is still assigned to the Cincinnatian Series). The Mohawkian was correlated with the lower part of the British Caradoc Series and was still considered "Middle" Ordovician.

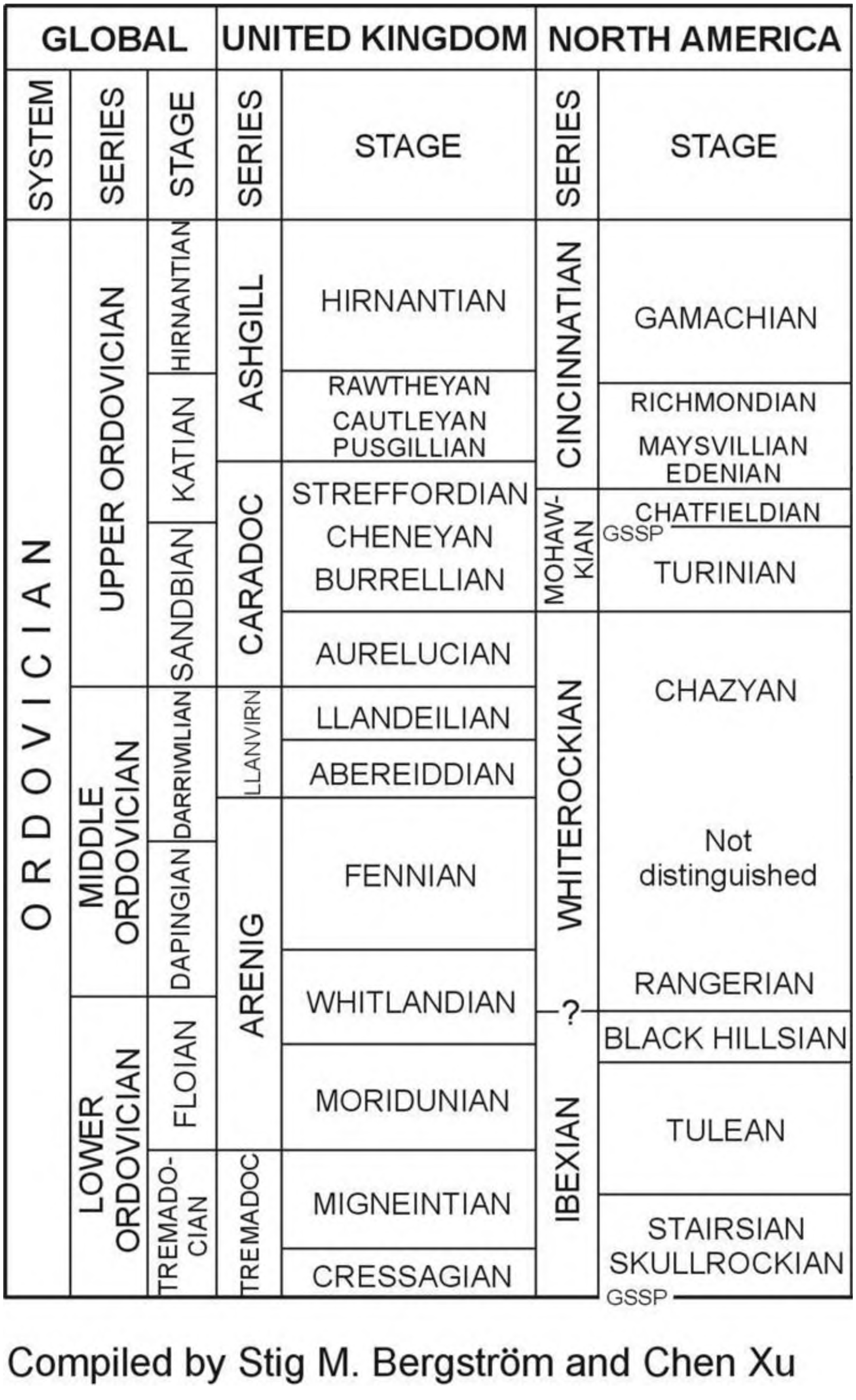
The late 1990s and early 2000s saw the push for Global Stages to correlate the various local and regional Ordovician rock units world-wide. As one might expect, the process of determining these new stratigraphic designations and names was long and argumentative. Essentially two factors needed to be agreed upon by the International Subcommission on Ordovician Stratigraphy (ISOS) for each Global Stage--a type locality and stage boundaries. Type localities must show boundaries clearly and be accessible to future researchers. The lower boundary of each Stage is usually determined by the first appearance (termed First Appearance Datum or FAD) of a particular graptolite or conodont since these fossils are abundant and have world-wide distribution. The boundary is referred to as a Global Stratotype Section and Point (GSSP), more popularly known as a "golden spike". In addition, dependable absolute ages are helpful in determining boundaries at all stratigraphic levels. Unfortunately, rocks that contain the appropriate isotopes needed to determine absolute ages are not always present in boundary rocks, hence the use of fossils. Also, absolute ages are often fraught with uncertainty although with new and refined techniques our resolution of these time boundaries has, and is, improving greatly.

One of the most helpful techniques in resolving the problems of determining absolute ages and correlations, at least for the Ordovician rocks of eastern North America, was the use of K-bentonites. K-bentonites are volcanic ashes that have been altered into potassium-rich clay beds and represent a specific time horizon in the strata (isochronous in geology-speak). There are 60+ bentonite beds in the North American Ordovician. They can be correlated regionally using chemical fingerprinting in which the percent elemental composition of target bentonites is compared (there has even been attempts to correlate several globally). In this way, a bentonite in, say, Minnesota (Deicke) can be correlated with one in Tennessee (T-3). Additionally, these volcanic ash beds can be radiometrically dated fairly precisely using the ^{40}Ar/ ^{39}Ar method. These isochronous markers can also be used to define higher order stratigraphic boundaries particularly when, as with the Deicke, the bentonites are associated with a significant, albeit regional, extinction. Given their versatility it is no wonder why K-bentonite beds are often used as boundaries between stratigraphic units. For example, the Millbrig K-bentonite deposited after (above) the Deicke is the boundary between the Turinian and Chatfieldian Stages.

As type sections and boundaries were chosen and accepted, Series and Stages were reassigned until the Global Stages were gradually approved by the ISOS. The final result was an Ordovician Correlation Chart that consisted of seven Global Stages (see Fig. 3). The Mohawkian is now part of an expanded Upper Ordovician and is correlated with the middle (more-or-less) of the British Caradoc Series. The Turinian (Platteville) is placed in the upper Sandbian Global Stage (fifth Stage from the bottom) while the Chatfieldian (lower Galena) and the type-Cincinnatian are part of the Katian Global Stage (sixth Stage). Each of these Global Stages are subdivided into between two and four Stage Slices (total of 20) that are informal designations but with defined bases, again determined by a graptolite or conodont fossil. The one reassuring aspect of all of this is that the formation and member names of the rocks in which we collect our fossils rarely change giving us a measure of reassurance and stability.

Paleogeography and Climate

The paleogeography of the Ordovician world reflected the highest sea levels in the Paleozoic if not in all of geologic history. Continents were mostly centered on the equator with much of Laurentia (North America) located south of the equator (see Fig. 4). During the Ordovician, the first of several Paleozoic orogenies began the building of the Appalachian Mountains (see Figs. 5 & 6). Off the southeast coast of Laurentia an island arc/trench system formed initiating an active subduction zone resulting in large, active volcanoes. This stage of the mountain building process is called the Taconic Orogen.



GLOBAL			UNITED KINGDOM		NORTH AMERICA	
SYSTEM	SERIES	STAGE	SERIES	STAGE	SERIES	STAGE
O R D O V I C I A N	UPPER ORDOVICIAN	HIRNANTIAN	ASHGILL	HIRNANTIAN	CINCINNATIAN	GAMACHIAN
		KATIAN		RAWTHEYAN CAUTLEYAN PUSGILLIAN		RICHMONDIAN MAYSVILLIAN EDENIAN
			CARADOC	STREFFORDIAN CHENEYAN BURRELLIAN	MOHAWKIAN	CHATFIELDIAN
		SANDBIAN				GSSP TURINIAN
				AURELUCIAN	WHITEROCKIAN	CHAZYAN Not distinguished RANGERIAN
	MIDDLE ORDOVICIAN	DARRIWILIAN	LLANVIRN	LLANDEILIAN		
				ABEREIDDIAN		
			ARENIG	FENNIAN		
		DAPINGIAN				
				WHITLANDIAN		
	LOWER ORDOVICIAN	FLOIAN			? IBEXIAN	BLACK HILLSIAN
				MORIDUNIAN		TULEAN
		TREMADOCIAN	TREMADOC	MIGNEINTIAN		STAIRSIAN SKULLROCKIAN
				CRESSAGIAN		GSSP

Compiled by Stig M. Bergström and Chen Xu

Fig. 3. Global Ordovician Chronostratigraphic Chart showing correlation of British and North American stratigraphic units. (Modified from the Ordovician website www.ordovician.cn.)

Fig. 4. Late Ordovician Palaeogeography

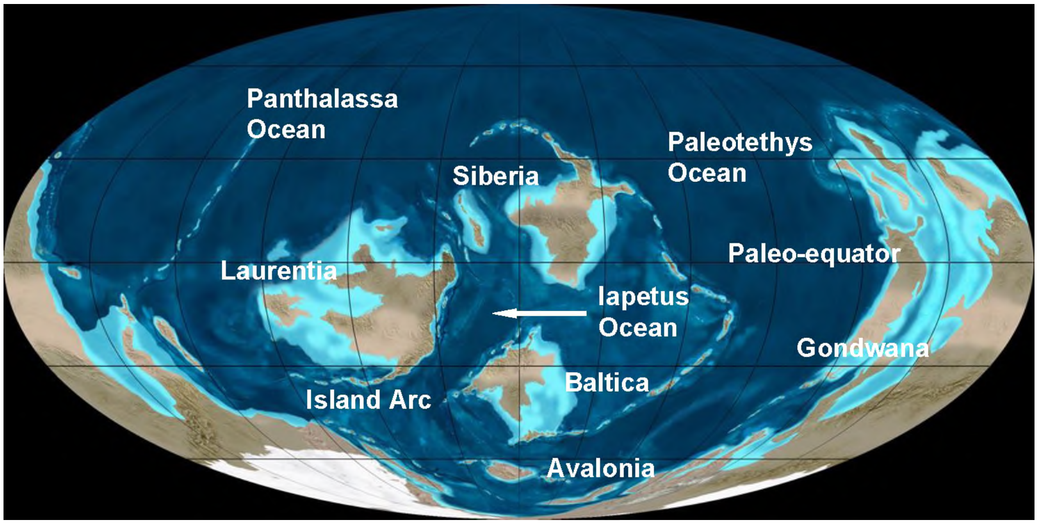


Fig. 5. Laurentia During the Taconic Orogeny

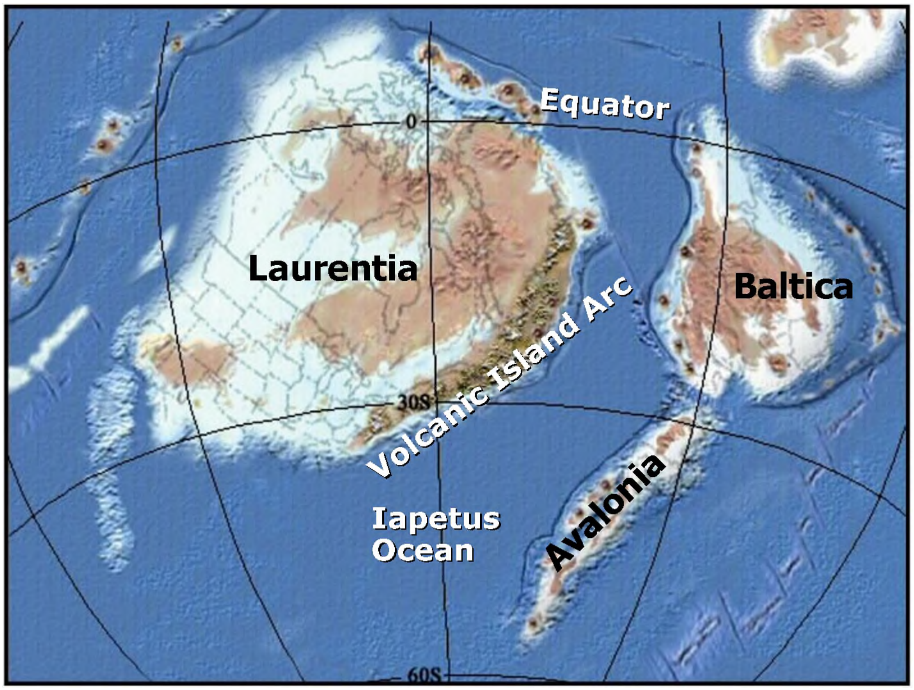
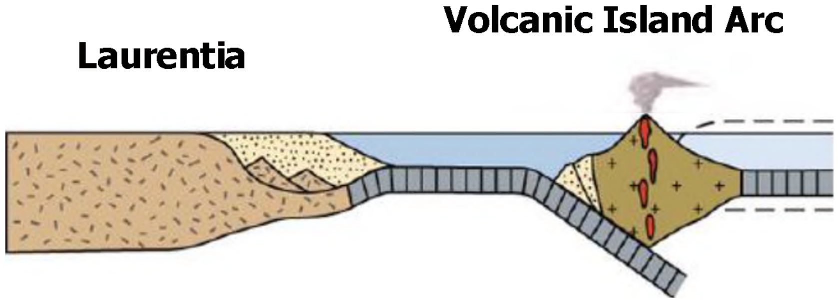


Fig. 6. Geologic Setting of the Taconic Orogeny



The climate of Laurentia during the Ordovician was warm and wet reflecting its position just south of the Equator. Its location between 0^0 and 30^0 south latitude placed Laurentia in the SE Trade Wind Belt. This situation allowed for the effects of the volcanic island arc to be felt in the eastern half of what is now the United States. Many volcanic ash layers were deposited by the erupting volcanoes spewing materials into the atmosphere where the SE Trades transported and deposited them in the shallow cratonic seas (see Fig. 7). They eventually weathered and compacted to form the bentonite beds described above.

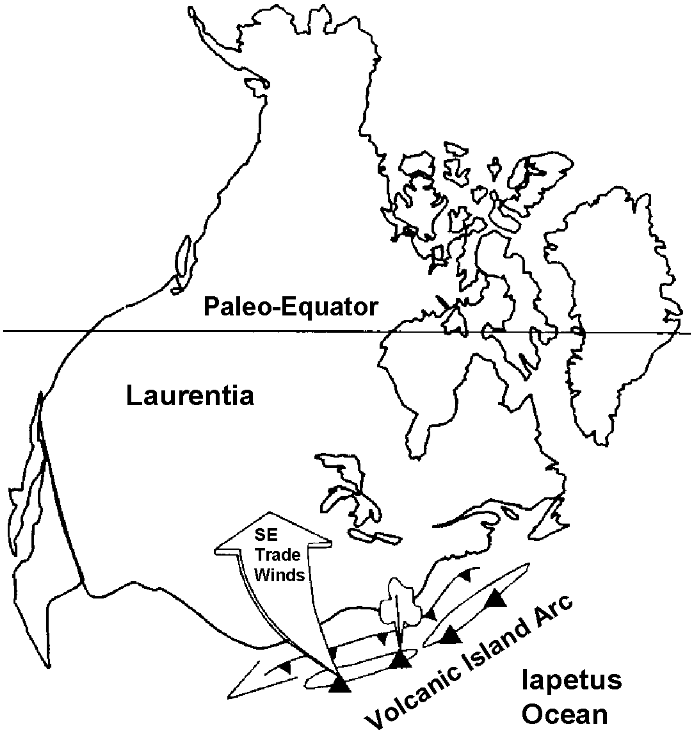


Fig. 7. Position of Laurentia (North America) and the volcanic island arc that was the source of the mid-west K-bentonites deposited by the SE Trade Winds. (Modified from Kolata *et al.*, 1996, GSA Special Paper 313, Fig. 3.)

The Great Ordovician Biodiversification Event

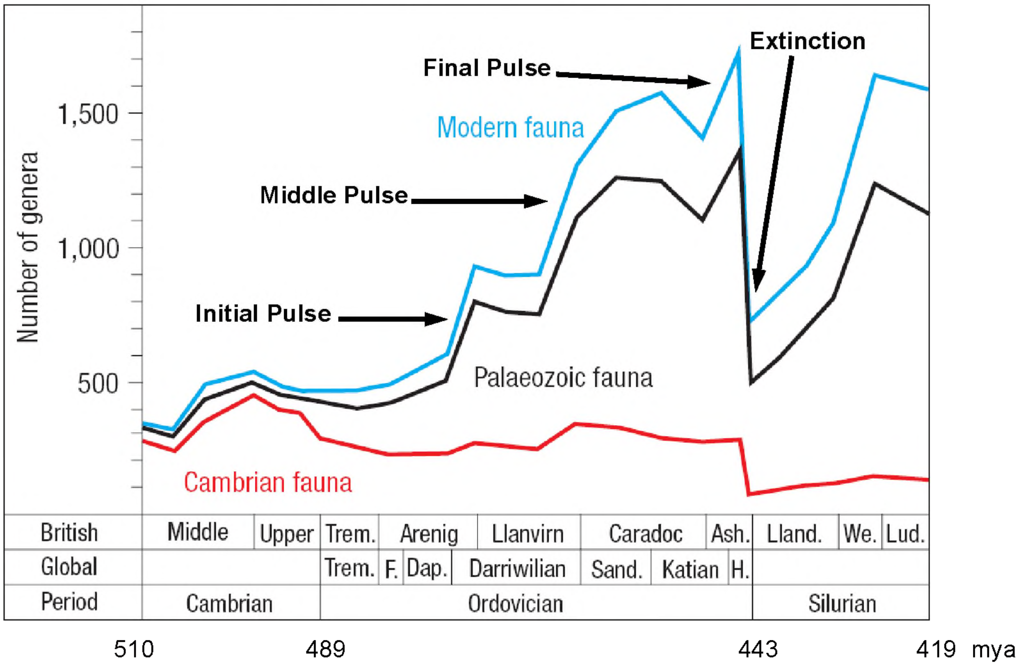
Life experienced its greatest jump in taxonomic diversity during the Ordovician. This series of events is called the Great Ordovician Biodiversification Event (GOBE). The Ordovician radiation is different from either the Ediacaran or Cambrian "Explosions" for several reasons. First, the earlier two both experienced a radiation of body plans, disparity, at the expense of taxonomic diversity whereas during the GOBE only one new phylum, Bryozoa, originated but taxonomic diversity increased dramatically. Second, the Ediacaran and Cambrian radiation events were restricted in time, geologically speaking, with all groups diversifying at about the same time for each event whereas the GOBE radiations, although occurring in definite pulses, were spread pretty much throughout the entire Ordovician. Therefore, the origination of most of the phyla and classes of animals, as well as a varied set of body plans, in the Cambrian set the stage for the Ordovician radiations to fill niche spaces with a diversity of species. The GOBE, it is generally acknowledged, was characterized by the greatest increase in biodiversity in the history of life--there was a two-fold increase in taxonomic orders, a three-fold increase in families, and a nearly four-fold increase in genera. Nautiloids, for example, were represented at the beginning of the Ordovician by only one order but, by the time the Late Ordovician rolled around, had radiated into at least ten orders. Additionally, nautiloids diversified into a wide range of shell shapes and species and reached their all-time peak diversity at this time.

As stated above, the GOBE occurred in definite pulses of radiations (see Fig. 8). Although the most intense diversification took place during the Mid to Late Ordovician (a duration of around 28 million years), taxonomic radiations lasted virtually the entire period (nearly 46 million years). Also, the GOBE was taxonomically selective--some groups diversified robustly whereas others experienced only moderate diversification. The first pulse commenced slowly late in the Early Ordovician then picked up dramatically early in the Mid Ordovician until a plateau in diversity was experienced for the rest of this stage. The second pulse followed this plateau with an even greater rate of diversification during the beginning of the Late Ordovician with peak diversity in the middle of the Late Ordovician. A minor decline in diversity was experienced after this peak. The final pulse occurred near the end of the Late Ordovician when radiations again increased dramatically reaching the highest diversity peak in the entire Ordovician just before the end-Ordovician mass extinction--an event second only to the end-Permian mass extinction in severity. A post-Ordovician recovery initiated a period of relatively stable diversity (the so-called "Paleozoic Plateau"), broken significantly only by the end-Devonian mass extinction, which lasted until the massive end-Permian extinction event.

As with the other radiation events, a plethora of possible causal factors have been proposed to explain the GOBE. These factors include, but are not limited to, intrinsic biological factors, increased volcanism that resulted in an influx of continental nutrients into the oceans, an areal increase in hard substrates, greatest continental dispersal in the Paleozoic, greatest amount of tropical shelf occurrence in Phanerozoic, highest sea levels of Paleozoic, and escalation in the partitioning of marine habitats.

Fig. 8. Details of Ordovician Diversification Event

(modified from Schmitz *et al.*, 2008, Figure 1.)



Now, in a recent paper, Schmitz and colleagues (2008) suggest an intriguing explanation for the onset of the GOBE. The authors claim "that the onset of the major phase of biodiversification ~470 Myr ago coincides with the disruption in the asteroid belt of the L-chondrite parent body--the largest documented asteroid breakup event during the past few billion years" (p. 49). The 470 Ma that they emphasize corresponds approximately to the middle of the first GOBE pulse--specifically, the Mid Ordovician increase in the rate of diversification described above. The asteroid breakup, they say, caused an elevated rate of meteorite bombardment which lasted for 10-30 million years after the initial breakup. Evidence, compiled from sections in Sweden and China, for this event includes rocks enriched with an isotope of osmium commonly found in meteorites, the recovery of unaltered chromite grains with an elemental composition distinct from terrestrial chromite, and the discovery of abundant fragments of the meteorites that were incorporated into the rocks deposited at that time. Additionally, from an analysis of impact craters on Earth, it appears that "impacts may have been more common by a factor of 5-10 during the Middle Ordovician compared with other periods of the Phanerozoic" (p. 52). The authors also compiled data on fossil brachiopods contained in rocks of the same age from Baltoscandia and conclude that, for this region at least, the onset of the two events, meteorite bombardment and brachiopod diversification, "seems to coincide precisely" (p. 52). It has been claimed by others, however, that the initial diversification of the GOBE started before the sustained bombardment.

So, how can impacts cause faunal diversifications instead of the extinctions that are popularly presumed to have resulted from them? It turns out that hard evidence for impact-caused extinctions for all but the end-Cretaceous event is tenuous at best. Apparently, there is a size threshold below which impacts disrupt ecosystems but do not initiate mass extinctions. The authors state that "more minor and persistent impacts could generate diversity by creating a range of new niches across a mosaic of more heterogeneous environments" (p. 52). In other words, the niche partitioning initiated by the numerous impacts resulted in more diverse environments that, in turn, fostered speciation events to fill these new niches. Admitting that these conclusions are speculative, the authors maintain that the most reasonable explanation is that numerous and persistent impacts caused modifications in Earth's biota. This cause and effect scenario is an exciting possibility but has by no means been proven.

An Analysis of Ordovician Life

Any assessment of prehistoric life during a given period of geologic time is biased in favor of hard-shelled, marine animals. This is just the realities of normal fossilization. During the Ordovician, life on land was virtually nonexistent so the marine fossils we find are a good representation of what was alive at that time. Generally speaking, ecological tiering, infaunal organisms, and bioturbation all increased during the Ordovician. Additionally, the first reef communities appeared consisting of rugosids, tabulates, and stromatoporoids. Because of the expanse of shallow cratonic seas and the influx of nutrients from an essentially bare land surface, the abundant faunas were often quickly incorporated into the sediments and fossilized. Fossils can occur as bedding-surface concentrations in limestone, within-bed accumulations of molluscs in dolostones, and ubiquitous fossils in the abundant shales of the Ohio Valley. When describing the Ordovician faunas specifically, it is convenient to return to the older three-series designation (Canadian, Champlainian, Cincinnatian) since the three faunas are somewhat distinct.

The fossils found in Canadian rocks of the Lower Ordovician are more similar to Cambrian fossils than they are to those of the rest of the Ordovician. The Canadian fauna represents the survivors of the Cambrian extinctions and taxa derived from these survivors. The extinctions occurred near, but not right at, the end of the Cambrian. Trilobites suffered three separate extinctions and of the extensive nautiloid fauna of the Late Cambrian (4 orders and 34 genera) only one order and two genera survived into the Ordovician. The dominant constituents of this early recovery fauna were inarticulate brachiopods, molluscs, and some trilobites.

During the Champlainian (now placed in the lower Upper Ordovician), the GOBE was in full attack mode. At this time, sea levels rose and carbonates were the most common rocks deposited. Radiations filled every niche and articulate brachiopods and molluscs dominated the fauna. Also during this time, nautiloids experienced their greatest diversity not only taxonomically with at least 10 orders represented but also morphologically with a variety of shell shapes. The only glitch was the Deicke extinction that occurred at the Platteville-Galena interface (marked by the Deicke K-bentonite bed) and was most pronounced in the Upper Mississippi Valley Area. The fauna was repopulated by survivors and their descendants as well as immigrants. A very diverse and abundant fauna contained in rocks of the Mifflin Formation (Platteville Group), discovered and aggressively collected from a quarry in north-central Illinois, has provided us with an unusually complete glimpse of an Ordovician shallow-water community. Of the nine phyla represented, molluscs dominate with 68% of the total species (43.7% gastropod, 34.5% cephalopod, 14.9% bivalves, 6.9% miscellaneous molluscs). The next most abundant group is brachiopods with a bit over 13% of the total species although, as usual, they were very abundant in terms of specimens available.

The Cincinnatian (upper Upper Ordovician) is divided into three stages: Edenian (oldest), Maysvillian, and Richmondian (youngest). During the Cincinnatian, there was a cooling of the climate and a fluctuation of sea levels that was accompanied by the deposition of shales and interbedded limestones. It is estimated that some shales were deposited in as little as 25 meters of water. The dominant constituents of the fauna were articulated brachiopods, echinoderms, trilobites, and molluscs.

During the Cincinnatian, an interesting faunal modification occurred that has been termed the Richmondian Invasion. It is now known that there were two separate invasions, the first during the Edenian and the second during the Richmondian. Both coincided with global warming and transgressions of the sea in the Cincinnatian Arch area. Between the two invasions, cooling waters and influx of clastic sediments forced the fauna to retreat to the original source area where they were held there by thermal and/or topographic barriers. The source of the invaders (immigrants) was the coeval Arctic Fauna (A.K.A. Red River Fauna) from the western US and Canada. These areas also served as a place of refugia between the two invasions. This invading fauna was more diverse because of a location closer to the paleo-equator (fossils found in warm-water carbonate rocks). Although it was a study of nautiloids that led to the identification of an invasion, many taxonomic groups were involved such as other mollusks, echinoderms, trilobites, brachiopods, bryozoans, and corals. Apparently, the pre-existing Cincinnatian fauna did not fill all niches so the invading taxa, mostly ecological generalists, were able to establish themselves relatively easily. Evidence indicates that there were no significant extinctions during the invasion and the immigrants simply added to the diversity. It also appears that the event was somewhat prolonged and not a quick invasion at the beginning of the Richmondian as once thought. All of the taxa were subject to the end-Ordovician extinction event. (Representative Ordovician taxa are presented at the end of this paper.)

End-Ordovician Glaciation and Extinction

The end of the Ordovician was marked by both a glacial event and a mass extinction. The glaciation is referred to as the Hirnantian (after the last global stage, see Fig. 3) Ice Age and lasted approximately .5-1.0 million years. The large volumes of carbonates deposited at this time locked up atmospheric CO_2 thus effectively ending the period-long greenhouse and lowering global atmospheric temperatures. The result was an ice cap that formed over north Africa and an accompanying lowering of sea levels some 100 meters. Evidence for this is an increase in the C^{13}/C^{12} ratio (termed an excursion) indicating that C^{12} was buried thus depleting atmospheric CO_2. The cause of this ice age is similar to the cause of the Pleistocene Ice Ages--Milankovich Cycles. Referred to as orbital forcing, Milankovich Cycles depend on changes in three aspects of Earth's rotation and revolution--axial tilt (22.1^0-24.5^0), axial precession (gyroscopic motion of axis), and eccentricity (shape of Earth's orbit). It is changes in the eccentricity of Earth's orbit that was dominant during the Hirnantian Ice Age.

Near the end of the Ordovician, life on Earth experienced the second most severe mass extinction in geologic history. The extinction affected the standing diversity greatly--85% of species, 61% of genera, and 26% of families succumbed. The glaciation lowered sea levels which in turn exposed cratonic sea floors. Oceans were cooled an estimated 10^0C. As usual, the tropical species were affected the most--when Earth cools the temperate and polar animals can move south but there is no place for tropical animals to seek refuge. The extinction actually occurred in two pulses. The initial pulse took place as sea levels dropped quickly decimating the epicontinental communities. The final pulse occurred as sea levels rose quickly flooding the shelf areas with anoxic waters and decimating the response fauna that appeared after the initial pulse. In both cases the animals could not adapt quickly enough. The Silurian recovery took some 5-7 million years and the resulting fauna had similar ecological patterns to those of the Ordovician. This recovery resulted in the so-called "Paleozoic Plateau" mentioned above.

Further Reading

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Representative Ordovician Fossils


Lingula elderi


Rostricellula minnesotensis


Platystrophia ponderosa


Holopea ampla

Lophospira serrulata


Maclurites bigsbyi


Cleionychia lamellosa


Oneotoceras percurvatum


Plectoceras robertsoni


Gonioceras occidentale


Cupulocrinus gracilis

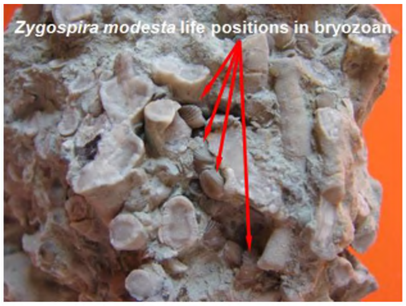

Pleurocystites squamosus


Isorophus cincinnatiensis


Gabriceraurus mifflinensis


Encrinuroides rarus

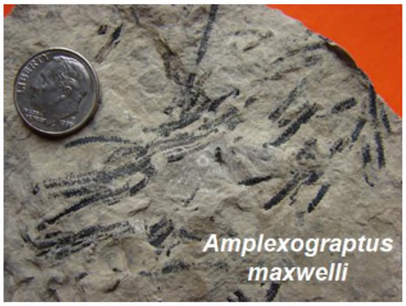

Flexicalymene meeki


Zygospira modesta life positions in bryozoan


Ectenocrinus simplex in stem "log jam"


Illaenus americanus


Eoleperditia fabulites


Amplexograptus maxwelli


DNAG
IN
CM
mm
Receptaculites oweni


Platystrophia sp.
Hebertella sp.
Strophomena sp.
Lepidocyclus sp.
Hiscobeccus sp.


Bryozoan with attached holdfasts


Prasopora sp.


Streptelasma corniculum


Leptotrypa sp.


Rauffella filosa


Basiliella sp. on unpublished nautiloid

Size Does Matter--
The Giant Nautiloids of the Arctic Ordovician Fauna

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Introduction

The Ordovician Period was the Age of the Nautiloid Cephalopods. After a less than auspicious beginning as small (5-6 cm in length) compressed cyrtocones in Late Cambrian tropical stromatolitic limestone facies in China (35 genera, 8 families, and 4 orders), nautiloids underwent explosive evolution world-wide in the Ordovician, reaching their evolutionary peak in terms of geographic distribution, abundance, diversity of form, maximum size, and taxonomic diversity (over 375 genera, in 54+ families, and 10 orders) before the end of the period. Nautiloids were the dominant predators in the Ordovician "Sea Without Fish". The rapid evolution and proliferation of nautiloids in the Ordovician was the result of the achievement of neutral buoyancy coupled with the attainment of stability and mobility up off of the sea floor in the water column (Crick, 1988). This mobile predatory life style was facilitated by the evolution of 1) a variety of gas and ballast-filled chambered shells; 2) a well-developed central nervous system; 3) grasping tentacles coupled with a buccal mass equipped with cutting jaws; 4) an enhanced, more efficient respiratory system with enlarged gills; and 5) a novel method of locomotion – jet propulsion via the forceful expulsion of water from the mantle cavity through the ventral hyponome. As mobile marine predators and scavengers, there is little evidence that nautiloids had any significant competition from other groups for this niche until the rise of jawed fish in the Early Devonian, 35 million years in the future.

The most spectacular nautiloid fauna of all time in terms of diversity of form, numbers of taxa, abundance of individuals, and in particular, the giant size of individual species (many in excess of 200 cm in length), is the so-called "Arctic Ordovician Fauna" of Nelson (1959) and others. This fauna is characteristic of widespread tropical carbonate platform facies of Late Ordovician age across much of cratonic Laurentia, from what is now northern Greenland to southern New Mexico (Foerste, 1929; Miller, 1932; Nelson, 1959; Flower, 1970, 1976).

The Arctic Ordovician Carbonate Facies

These giant nautiloids are associated with very widespread (minimum area of 6.5×10^6 km^2; Villas et al., 2002), shallow marine carbonate platform facies distributed across what is now the western U.S. and Canada, the Arctic Archipelago, and adjacent portions of northern Greenland (i.e. Laurentia) (see Figure 1). Ross (1976) described these strata as representing "the greatest inundation (of the continent) in North American history." These strata consist of an average of 100 m (Villas et al., 2002) of primarily massive-bedded, burrow-mottled fossiliferous limestone, often altered to dolomite, of Late Ordovician Edenian through Richmondian age (453-443 mya). The Arctic

Ordovician facies was deposited under tropical conditions in the "carbonate zone" in the Late Ordovician (Witz, 1980) with North America rotated clockwise from its present position and roughly bisected by the Ordovician equator. Similar facies and faunas also occur in the Late Ordovician of Scandinavia (Strand, 1933; Frye, 1982, 1986) as the Baltic plate was closing in on Laurentia from the east at the this time (Scotese and McKerrow, 1990).

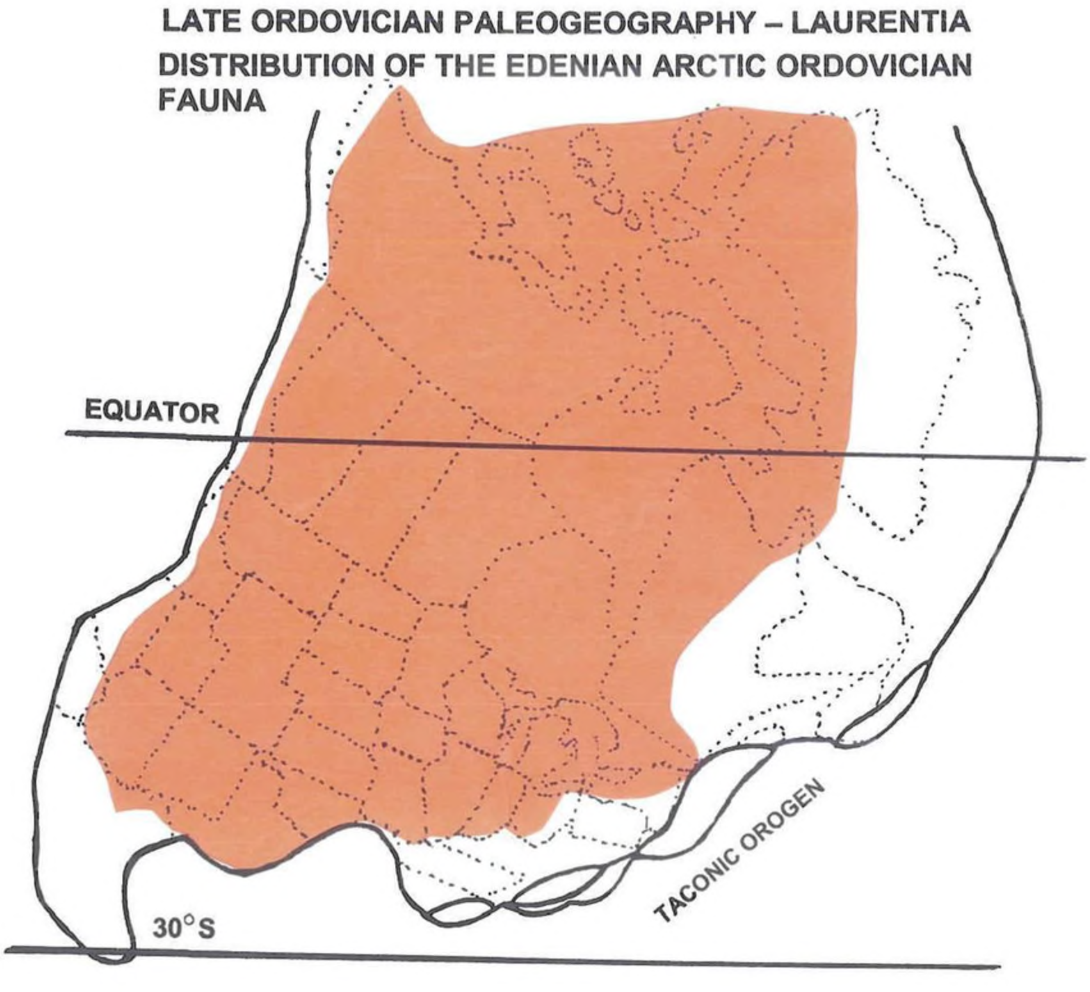

Figure 1. Map showing the geographic distribution of the Arctic Ordovician Fauna and its associated limestone facies in Laurentia in the Late Ordovician. (Modified from Nelson, 1959, Figure 1.)

These carbonate strata and their associated faunas are thought to represent deposition under tropical, shallow-marine, subtidal open-shelf conditions in clear warm waters with depths probably just at or above storm-wave base. The lack of clastic sediments and the presence of abundant representatives of the problematic green alga *Fisherites reticulatus* (Owen) and large diameter colonial coral coralla attest to the clarity of the water and the presence of some current activity affecting the bottoms of these cratonic seas. Although large coralla of the tabulate corals *Catenipora,* *Manipora,* and *Palaeofavosites* are locally common, they consist of isolated colonies and well-developed, wave-resistant coralline "reefs" are typically not developed.

Regional names for local pieces of this extensive sheet of Late Ordovician carbonate rock include the Montoya Group in New Mexico (Flower, 1957A,1970); the Fremont Formation in Colorado (Sweet, 1954); the Lander Sandstone and Bighorn Dolomite in Wyoming (Richards and Nieschmit, 1961; Goodwin, 1964); the Red River and Stony Mountain Formations in southern Manitoba (Foerste, 1929, Nelson, 1959, Jinn and Zhan, 2001); the Bad Cache Rapids and Churchill River Groups in northern Manitoba (Nelson, 1963); the lower portion of the Beaverfoot Formation in British Columbia (Norford, 1969; Buttler, Elias, and Norford, 1988); the Cape Phillips Formation and Cornwallis Group on Cornwallis Island, Nunavut (Sweet and Miller, 1957); the Amadjuak and Akpatok Formations on Baffin Island, Nunavut (Miller, Youngquist, and Collinson, 1954; Sanford and Grant, 2000); and the Cape Calhoun and Borglum River Formations in northern Greenland (Troedsson, 1926; Christie and Peel, 1977).

These strata locally contain a very diverse marine biota (100+ species in the Selkirk Member of the Red River Formation in S. Manitoba, Jin & Zhan, 2001), including receptaculitid alga (Finney et al., 1994); solitary horn corals (Elias, 1991) and compound corals (Leith, 1952); stromatoporoids and sponges (Bolton, 1988);a diverse set of orthid, strophomenid, and rhynchonellid brachiopods (Jin & Zhan, 2001); gastropods (Nelson, 1959,1963; Bolton, 2000); trilobites (Westrop and Ludvigsen, 1983; Rudkin et al., 2003); and a diverse nautiloid fauna (Troedsson, 1926; Foerste, 1929; Miller, 1932; Miller, Youngquist, and Collinson, 1954; Nelson, 1963; Bolton, 2000).

Besides the diversity and abundance of individual species in these facies, the other interesting aspect of this Arctic Ordovician Fauna is the large size of individuals collected from these strata. Compound coral coralla can be nearly a meter in diameter in these strata. The disc-shaped thalli of the problematic alga *Fisherites reticulatus,* the largest known receptaculitid, are dish-plate in size. Telephone-pole like aulacerid sponges up to 4 m in length and 300 mm in diameter are common in the Beaverfoot Formation in British Columbia. The largest strophomenid brachiopods of all time (*Tetraphalerella churchillensis* and *Oepikina lata*) occur in the Selkirk Member of the Red River Formation and its correlatives in Manitoba. Giant gastropods include dish-plate like specimens of *Maclurina manitobensis,* the largest known Paleozoic gastropod (up 250 mm in diameter, Rohr et al., 1992), as well as the high-spired forms *Fusispira* and *Hormotoma* up to 160+ mm in height (Nelson, 1963). The locally conspicuous trilobite fauna includes *Isotelus rex* from northern Manitoba, which, at 720 mm in length, is the world's largest known trilobite (Rudkin et al., 2003).

Arctic Ordovician Nautiloid Faunas

The diverse nautiloid fauna, along with other elements of the total biota, consist of a distinctive mixture of early Late Ordovician (Turinian) relics plus a large number of newly-evolved Edenian taxa. This fauna is dominated by often gigantic (meter+ in length) longiconic endocerids, actinocerids, and dissidocerids; massive vase-shaped breviconic oncocerids and discosorids (up to 200 mm in diameter); and robust, evolutely-coiled and gyroconic members of the Aspidoceratidae (up to 500+ mm in diameter).

Across much of the outcrop area, the "Arctic Ordovician Fauna" actually consists of two somewhat distinct faunas (Nelson, 1959; Elias, 1991; Jin & Zhan, 2001). The giant forms are primarily associated with the massive-bedded, *Thalassinoides* - burrowed wackestones typical of the older Edenian to Maysvillian "Red River" portion of the facies. In the Williston Basin and the east-central US, nautiloids and other invertebrates in younger Richmondian "Stony Mountain" facies typically are smaller in size than their Edenian counterparts and differ from these older faunas in terms of the individual taxa present and their relative abundance (Okulitch, 1943; Flower, 1946; Jin and Zhan, 2001). These Richmondian strata are usually more clastic-rich and locally consist of interbedded thin fossiliferous packstone and shale representing deposition in open shelf marine environments impacted by clastic source areas. However, this does not appear to be the case with Richmondian facies in British Columbia (Beaverfoot Formation, Frey & Norford, 1995), the Hudson Bay region of northern Manitoba (Churchill River Group, Nelson, 1963), or in the Arctic Archipelago (Akpatok Formation, Bolton, 2000) where these younger facies are also massive-bedded carbonates supporting large individuals.

In the western US and the Williston Basin, these packets of fossil-bearing strata are typically separated by an erosional surface or a sequence of laminated dolomudstone and bedded anhydrite representing a local retreat or a restriction of open marine cratonic seas in the area in the latest Maysvillian-earliest Richmondian, leading to restricted abiotic hypersaline conditions (Elias, 1991).

Cyrtogomphoceras Fauna

The really big nautiloids typically are part of the *Cyrtogomphoceras* Fauna characteristic of the Edenian-Maysvillian portion of the section (Frey & Norford, 1995). This nautiloid fauna is quite diverse as well, consisting of 31 genera, belonging to 15 families, and nine orders (see Figure 2). These taxa have been described from the Second Value Formation in New Mexico (Flower, 1957A and unpublished); from the Lander Sandstone and the Steamboat Point Member of the Bighorn Dolomite in Wyoming (Miller, 1932; Foerste, 1935); the Dog Head and Selkirk Members of the Red River Formation in southern Manitoba (Foerste, 1929); the Bad Cache Rapids Group in northern Manitoba (Nelson, 1963); in the Amadjuak Formation on Baffin Island and across the Arctic Archipelago (Foerste, 1928; Miller, Youngquist, and Collinson,1954; Bolton, 1977, 2000), and from the Cape Calhoun Formation in northern Greenland (Troedsson, 1926).

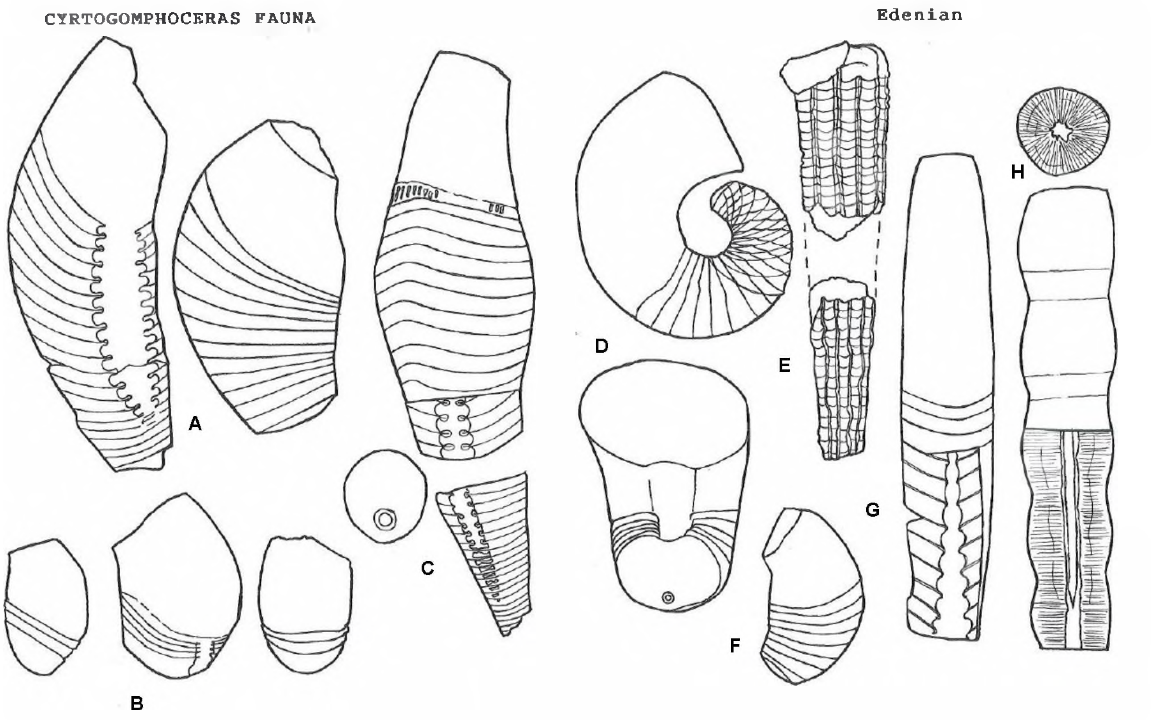

Figure 2. Line drawings of some of the characteristic nautiloid genera that make up the Edenian *Cyrtogomphoceras* Fauna.

A. Discosorid *Cyrtogomphoceras* (d-v section; lateral view of steinkern)
B. Ascocerid *Probillingsites* (lateral and ventral views of steinkern; d-v section)
C. Discosorid *Westonoceras* (d-v section; adapical cross-section)
D. Aspidoceratid *Charactocerina* (lateral exterior; whorl profile)
E. Orthocerid "*Kionoceras*" (shell exterior showing ornament)
F. Oncocerid *Neumatoceras* (lateral exterior)
G. Actinocerid *Paractinoceras* (d-v section)
H. Dissidocerid *Narthecoceras* (cross-section and d-v section of siphuncle)

Longiconic Orthocones:

Longiconic orthocones typically dominate nautiloid faunas in these strata and include specimens of the slender annulated endocerid *Endoceras* 3-4 m in length with maximum shell diameters over 150 mm; specimens of the problematic dissidocerid *Narthecoceras* known from isolated siphuncles a meter+ in length with diameters of 80 mm; and specimens of the actinocerids *Actinoceras* and *Armenoceras* over a meter in length with maximum shell diameters of 100mm. The soft-part anatomy of these longiconic forms is largely unknown. Well-preserved longiconic orthocerids from the Silurian and Devonian indicate a coleoid-like radular mass and 10 coleoid-like arms (compared to living *Nautilus* with about 90 tentacles). The dorso-myarian retractor musculature characteristic of all longiconic nautiloids appears to be much reduced in size (Mutvei, 1957; 2002) compared to the ventro-lateral retractor muscle scars present in living *Nautilus* and its presumed ancestral stock – the cyrtoconic and breviconic Oncocerida, plus all Ordovician coiled forms. It may be the method of propulsion in these longiconic forms was somewhat different than that of *Nautilus* (Mutvei, 2002). In addition, these longiconic taxa have phragmocones weighted down apically with dense calcareous endosiphuncular deposits. This mass, along with the great lengths of many of these forms, would seem to make these giants unwieldy, rather awkward swimmers that would not have been very maneuverable in pursuit of prey (Ward, 1987). This has led many authors to speculate that at least mature individuals were benthic crawlers rather than active nektonic swimmers (Troedsson, 1926; Teichert, 1933; Flower, 1957B; Barskov et al. 2008). Somewhat smaller longiconic taxa, including species of the genera *Ormoceras, Paractinoceras, Gorbyoceras,* and *Ephippiorthoceras*, were 300-500 mm in length and were likely somewhat more maneuverable nekto-benthic swimmers, living much of their lives up off of the bottom (Frey, 1989; Barskov et al. 2008). A number of these taxa studied by the author have thin holoperipheral growths of hitchhiking bryozoa that completely encircled conchs of these forms, providing additional evidence supporting a primarily nektonic life habit for these taxa (Baird et al.,1989).

Orthoconic "Flatfish":

Unique to the Arctic Ordovician nautiloid fauna are the unusual dorsal-ventrally depressed actinocerids *Kochoceras, Selkirkoceras,* and *Lambeoceras*. These taxa consist of large, variably-depressed orthoconic shells just over a meter in length and up to 300 mm in width, with short camerae, and a strongly-flattened venter. *Kochoceras* is a rapidly-expanding longiconic form with a strongly-flattened venter and convex dorsum. *Lambeoceras* and *Selkirkoceras* have shorter, broader shells that are flattened dorsally and ventrally leading to a depressed, lenticular cross-section. All three taxa also have large-diameter siphuncles filled adapically with massive annulosiphonate deposits, weighting down the shell. Troedsson (1926) inferred that *Kochoceras*, based on its strongly flattened venter and massive annulosiphonate deposits, was likely a largely benthic form, living on the bottom. Flower (1957B), citing the work of Teichert (1933) with regard to estimates of shell buoyancy compared to the mass of annulosiphonate deposits, concluded that actinoceroids like *Kochoceras, Selkirkoceras,* and *Lambeoceras*, were obviously the "flatfish" among nautiloids, living as benthos, likely crawling on the bottom. A lack of encrusting epibiota on the dorsal surfaces of preserved shells of species belonging to these genera fuels some speculation that these forms may have been ambush predators, living partially buried right under the substrate surface like living flounders.

Breviconic and Longiconic Cyrtocones:

The Arctic Ordovician nautiloid fauna also has a diverse set of large breviconic and longiconic cyrtocones belonging to the orders Oncocerida and Discosorida. These include a variety of large vase-like brevicones (up to 200 mm in diameter) including the endogastrically-curved discosorid *Cyrtogomphoceras* and the more or less straight slender discosorid *Landeroceras* and the globose oncocerid *Diestoceras.* These forms are somewhat problematic in terms of their life habit due to the combination of a large body chamber and a comparatively short, closely-septate phragmocone (= buoyancy-limiting body plan) coupled with the presence of well-developed, buttressed, ventromyarian retractor musculature and a well-developed ventral hyponomic sinus, both features characteristic of swimming forms. It is thought the cephalopodium of members of the Order Oncocerida was somewhat similar to that of their distal descendent *Nautilus,* consisting of many short tentacles. Evidence at hand supports reconstructing these breviconic forms as nekto-benthic saltaters, spending much of their time on the bottom as mobile crawlers but having the ability to swim up off of the bottom for short periods of time (Frey, 1989; Barskov et al., 2008).

Associated with the robust, vase-shaped forms are a variety of slender, more gracile longiconic cyrtocones including the discosorid *Westonoceras* and the oncocerid *Winnipegoceras*. Both taxa have slender, variably-curved shells consisting of longiconic, closely-septate phragmocones and adorally-tapering body chambers with ventromyarian muscle scars, and well-developed ventral hyponomic sinuses. *Westonoceras* has a stick-like phragmocone with a sub-central siphuncle consisting of expanded segments with complex endosiphuncular deposits. Some species of *Winnipegoceras* have very slender, strongly exogastrically-curved phragmocones with empty, narrow-diameter ventral siphuncle segments and lengthy, tubular body chambers that taper to a narrow opening. The curved, often compressed longiconic phragmocones and well-developed ventral hyponomic sinuses typical of these forms suggests that these forms spent more time up off of the bottom compared to their more robust breviconic brethren (Barskov et al., 2008).

Also unique to the Arctic Ordovician nautiloid fauna is an evolutionary series of compressed to very compressed longiconic oncocerids consisting of *Richardsonoceras*, a compressed Turinian relic; *Exomegoceras*, a compressed intermediary form with a rounded dorsum and an acute venter; and *Digenuoceras*, a very compressed form with an acute dorsum and venter. Flower (pers. comm., 1981) described a complete specimen of *Digenuoceras* from the Selkirk Formation at the Garson quarries in southern Manitoba as being more of a gyroconic shell almost a meter in diameter. The life habit of these highly-compressed longiconic cyrtocones or loosely-coiled, disjunct gyrocones remains uncertain pending more complete knowledge of their shell morphology but the highly-compressed, discoidal cross-sections suggest a swimming life habit.

Coiled Shells:

The Arctic Ordovician nautiloid fauna includes a variety of coiled taxa belonging to the family Aspidoceratidae. These include both loosely-coiled, evolute forms with disjunct body chambers like *Aspidoceras* and *Wilsonoceras*, and robust, more tightly-coiled and more rapidly-expanding shells like *Charactoceras* and *Charactocerina* (Foerste,1929; Miller, 1932; Nelson, 1963). Described species of *Wilsonoceras* have shells up to 500 mm or more in diameter. The nature of the retractor muscle scars is currently unknown for this family but their ancestral stock (Tarphyceratidae) and members of the related Uranoceratidae have well-developed ventromyarian peripracts (Mutvei, 1957; 2002). Species of *Charactoceras* studied by the author indicate the presence of a well-developed, broadly-curved hyponomic sinus in this genus.

Ward (1987) and Barskov et al. (2008) state that openly-coiled serpenticones like *Aspidoceras* and *Wilsonoceras* were poor swimmers due to the potential for shells to “pin-wheel” following even modest pulses of hyponomic power. Barskov et al. (2008) suggest that taxa with these types of shells, with their high buoyancy and limited stability, were passive planktonic floaters over a wide range of depths. However, Crick (1988) indicated that the development of disjunct body chambers with maturity limited this “pinwheeling” problem in these forms, giving them some swimming ability. In contrast, the more tightly-coiled, almost involute shells and comparatively short body chambers of *Charactoceras* are indicative of a life habit more like that of living *Nautilus* (high stability and lower buoyancy); swimming forms living near the bottom and using the hyponome to maneuver over the bottom for short distances (Ward, 1987; Barskov et al. 2008).

Ascocerids:

The most unusual shell morphology present in the nautiloids of the Arctic Ordovician Fauna is that of the ascocerids *Probillingsites, Shamattawaceras, Billingsites,* and *Schuchertoceras*. Large specimens of *Probillingsites* and *Billingsites* with lengths of up to 255 mm and 110 mm, respectively, occur in these massive-bedded burrow-mottled wackestone facies in the Fremont, Portage Chute, and Cornwallis Formations (Sweet, 1955; Nelson, 1963; Sweet and Miller, 1957). Members of the Ascocerida are characterized by the ontogenetic truncation of cyrtoconic deciduous juvenile portions of shells from a highly-modified, inflated breviconic "mature" conch (although for a dissenting opinion regarding the truncation of the shell see Frye, 1982 and Dzik, 1984).

Discussions of the complex ontogenetic shell changes in this group are presented in Kesling (1962) and Furnish and Glenister (1964). These taxa attained hydrostatic equilibrium in the adult form via the development of dorsally-located ascoceroid camerae, bringing the center of buoyancy into close alignment with the center of gravity (i.e., the underlying body chamber). By shedding the longiconic juvenile portions of the phragmocone and developing a streamlined, inflated mature conch with ventro-myarian retractor muscles, the adult ascocerid would seem to have been perfectly adapted to an active nektonic mode of life as has been suggested by numerous authors (Flower, 1957; Kesling, 1962; Furnish and Glenister, 1964). Barskov et al. (2008) suggested that the more elongate forms like *Probillingsites* were likely swimmers and the more bulbous forms like *Billingsites* and *Schuchertoceras* were more likely planktonic floaters. The life-habit of the longiconic cyrtoconic juvenile stages is more speculative as these stages are poorly-known. They may have been more nekto-benthic forms, similar in habit to the longiconic cyrtocones described above.

Billingsites Fauna

The *Billingsites* Fauna is characteristic of the younger Richmondian portions of the Arctic Ordovician carbonate facies, including the Beaverfoot Formation in British Columbia (Frey and Norford, 1995); the Stony Mountain Formation in southern Manitoba (Okulitch, 1943); the Churchill River Group in northern Manitoba (Nelson, 1963); the Maquoketa Group in Iowa (Foerste,1936); the Richmond Group in Indiana and Ohio (Flower, 1946); and the Vaureal and Ellis Bay formations on Anticosti Island, Quebec (Foerste,1928B). In contrast with the older "Red River" facies and faunas, facies are more clastic rich and individual nautiloids are typically smaller in size than their Edenian-Maysvillian counterparts (Foerste, 1928B; Okulitch, 1943; Flower, 1946). Longiconic taxa are less than two meters in total length; breviconic oncocerids have shell diameters less than 70 mm; and coiled forms rarely exceed 200 mm in diameter.

Nautiloids are less conspicuous elements of these younger Richmondian faunas due to the smaller size of individuals, the fewer numbers of individuals, and the somewhat less diverse nature of the nautiloid fauna. A number of characteristic "Red River" taxa, including the robust discosorids *Cyrtogomphoceras* and *Landeroceras,* the small actinocerid *Paractinoceras,* the curved longiconic oncocerid *Winnipegoceras*; the plicate coiled form *Charactocerina*, the large evolutely-coiled genus *Wilsonoceras*, and the primitive ascocerid *Probillingsites*, are either absent or much less common in these younger Richmondian strata. Common taxa include the longiconic endocerid *Endoceras*; the longiconic actinocerids *Actinoceras* and *Armenoceras;* the smaller longiconic pseudorthocerids *Ephippiorthoceras* and *Gorbyoceras*; the ascocerids *Billingsites* and *Schuchertoceras*; the breviconic oncocerids *Beloitoceras* and *Diestoceras*; and the coiled genera *Aspidoceras* and *Charactoceras* (Figure 3).

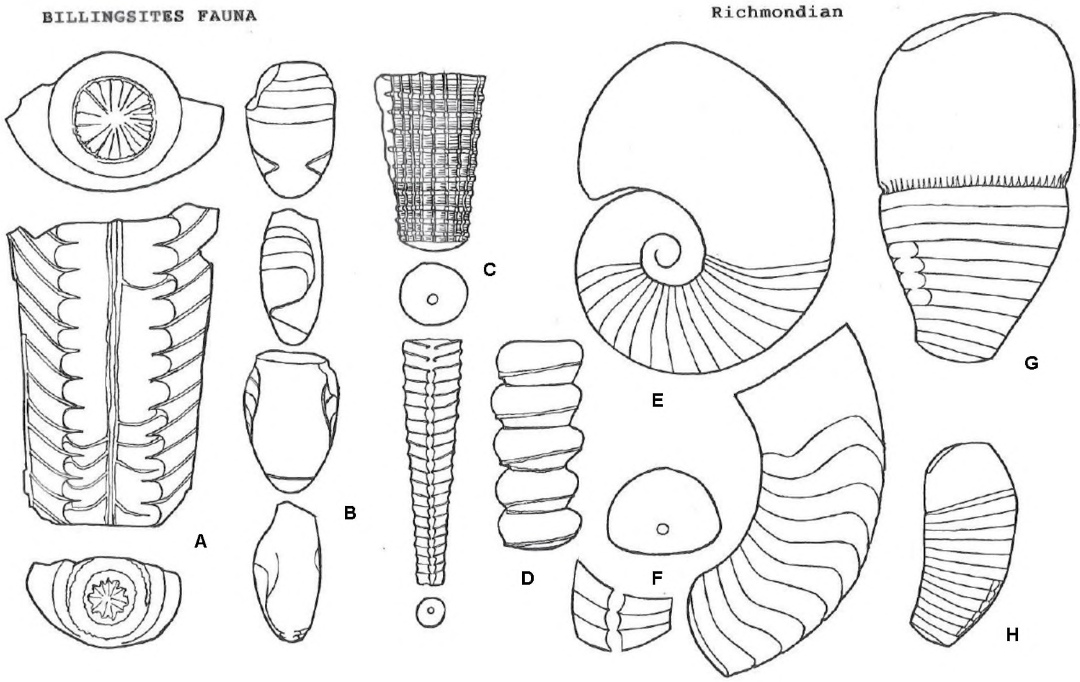

Figure 3. Line drawings of some of the characteristic nautiloid genera that make up the Richmondian *Billingsites* Fauna.

A. Actinocerid *Armenoceras* (adoral and adapical cross-sections; section through siphuncle)
B. Ascocerid *Billingsites* (dorsal, lateral, ventral, and d-v section through mature conch)
C. Pseudorthocerid *Gorbyoceras* (adoral exterior showing ornament; adoral and apical cross-sections; and d-v section)
D. Actinocerid *Huronia* (exterior view of siphuncle)
E. Aspidoceratid *Charactoceras* (lateral exterior)
F. Aspidoceratid *Aspidoceras* (cross-section; d-v section; lateral exterior)
G. Oncocerid *Diestoceras* (lateral view of a large steinkern showing siphuncle)
H. Oncocerid *Beloitoceras* (lateral view of steinkern of most of the shell)

Where did the Arctic Ordovician Nautiloid Fauna come from?

The diverse, often gigantic nautiloids characteristic of the tropical Arctic Ordovician Fauna in the Late Ordovician (Edenian-Richmondian) have their origins in the older early Late Ordovician "*Gonioceras Fauna*" associated with similar tropical open shelf carbonate platform facies of Turinian to early Chatfieldian age (457-454 mya) across much of eastern and northern North America. This fauna occurs in carbonate facies extending from the southern Appalachians (Stones River Group in Tennessee) to the upper Midwest of the US (Platteville Group in Illinois, Wisconsin, and Minnesota), eastward to New York and Ontario (Black River Group), and northward into what is now the Canadian Arctic (Frobisher Bay Formation on Baffin Island) and northern Greenland (*Gonioceras* Bay Formation). This fauna became locally extinct in the southern and Midwestern US at the end of the Turinian but continued into the early Chatfieldian in New York state, Arctic Canada, and Greenland. Not only are the ancestral stock of the Arctic Ordovician nautiloids to be found in these strata, but the ancestral stock of most all of the other taxa characteristic of Arctic Ordovician Fauna, are to be found in these strata as well (receptaculitid alga, tabulate and rugose corals, orthid and strophomenid brachiopods, gastropods, and many of the trilobites).

The Arctic Ordovician nautiloid fauna includes a number of surviving Turinian relics like *Endoceras, Actinoceras, Ormoceras, Gorbyoceras, Beloitoceras, Oncoceras, Diestoceras, and Richardsonoceras.* These relics, in turn gave rise to a larger number of new taxa derived from these Blackriveran pre-cursors. *Actinoceras* gave rise to *Kochoceras* and *Paractinoceras* (Flower, 1976). *Redpathoceras* evolved through *Probillingsites* into *Billingsites* and *Schuchertoceras* (Flower, 1963). *Beloitoceras* likely gave rise to *Oncoceras* and then *Neumatoceras* (Flower, 1946). The Blackriveran genus *Sinclairoceras* seems to be the direct ancestor of the compressed oncocerid *Winnipegoceras.* As indicated above, the Arctic Ordovician includes the entire evolutionary sequence from the compressed Turinian relic *Richardsonoceras* through the increasing more compressed, discoidal forms *Exomegoceras* and *Digenuoceras. Ulrichoceras* in Platteville gave rise to the endogastric discosorids *Cyrtogomphoceras* and *Landeroceras* and to the exogastric discosorid *Westonoceras* via *Teichertoceras* (Flower & Teichert, 1957). The coiled Aspidoceratidae in the Edenian-Richmondian Arctic Ordovician facies appear to have arisen from Turinian-early Chatfieldian Plectoceratidae with thin-walled ventral siphuncles like *Avilionella* and *Plectoceras.*

Interestingly enough, some of the earliest "giant" nautiloids are found in the Turinian *Gonioceras* Fauna, including species of *Endoceras* possibly as much as 9-10 m in length (Teichert and Kummel, 1960); specimens of the actinocerid *Actinoceras* at least 600 mm in length (collections of the author); specimens of the Turinian "flatfish" actinocerid *Gonioceras* at least 450 mm in length (Troedsson, 1926); and specimens of the evolutely-coiled *Plectoceras* up to 230 mm in diameter (Foerste, 1928C).

Where did the Arctic Ordovician Nautiloid Fauna go?

Across much of North America, the Ordovician-Silurian boundary is marked by a widespread erosional unconformity, representing the retreat of these shallow, tropical epeiric seas off of the craton and subsequent subaerial exposure and erosion of the latest Ordovician strata prior to the return of the these shallow cratonic seas across Laurentia in the Early Silurian. The retreat of the Arctic Ordovician seas from cratonic portions of what is now North America is associated with Late Ordovician glaciation centered in what is now North Africa. Formation of an ice cap in Gondwana tied up enough water to cause sea level to drop world-wide, resulting in a significant loss of shallow marine real estate, which, in association with fluctuating water temperatures, caused the extinction of many tropical marine Ordovician species and genera (Berry and Boucot, 1973; Sheehan, 1988; Brenchley, 2004) including much of the Arctic Ordovician Fauna. Victims included most of the characteristic nautiloid genera, including all of the "flatfish" actinocerids, most of the breviconic and cyrtoconic oncocerids and discosorids, all of the truncated ascocerids, and all of the coiled Aspidoceratidae. In addition to these nautiloids, other victims of this extinction event included the tabulate and rugosan corals, the aulacerid sponges, most all of the large gastropods, most all of the brachiopod and bryozoan genera, and most all of the trilobites, including the giant *Isotelus rex*.

The Silurian return of elements of the Arctic Ordovician Fauna

Some of the elements of the Arctic Ordovician nautiloid fauna, however, found refugia along the margins of the Laurentian continent (north-central North America around Hudson Bay, Anticosti Island in Quebec, and the Canadian Arctic) and survived into the Early Silurian. These include the longiconic actinocerids *Actinoceras, Armenoceras, Huronia,* and *Ormoceras* and the dissidocerid *Narthecoceras* (Foerste, 1924; Flower, 1968). These forms are joined in Early Silurian carbonate facies in Laurentia by some newly-evolved actinocerids including *Huroniella* and *Megadiscosorus;* the dissidocerid *Donacoceras;* plus a diverse new set of breviconic discosorids including *Discoceras, Endodiscosorus, Lowenoceras, Stokesoceras,* and *Tuyloceras* (Foerste, 1924; Flower & Teichert, 1957; Flower, 1968).

These nautiloid taxa form the *Discosorus-Huronia* Fauna characteristic of Early to Middle Silurian (Aeronian-Wenlockian) reefous carbonate platform facies across much of cratonic Laurentia north of what is now the United States (Frey and Holland, 1997). This fauna has been documented in these strata in northern Manitoba west of Hudson Bay (Foerste and Savage, 1927); along James Bay in Quebec (Flower, 1968); in Northern Michigan (Foerste, 1924); at Lake Timiskaming in western Ontario (Flower, 1968); and on Anticosti Island in Quebec (Foerste, 1928B). This *Discosorus-Huronia* Fauna was replaced in younger late Middle Silurian (Wenlockian –Ludlow) carbonate reef and platform facies by the *Phragmoceras* Fauna, a completely new, more cosmopolitan nautiloid fauna, the elements of which have been documented from equivalent strata in Bohemia, Sweden, and Great Britain.

Why So Big?

As indicated above, one of the interesting characteristics of the Arctic Ordovician Nautiloid Fauna is the large to gigantic size of many individuals. As is also indicated above, the exceptionally large size of individuals is not restricted to the nautiloids alone, but is a feature characteristic of the entire spectrum of marine organisms associated with this fauna. Finnegan and Droser (2008) documented the increasing size of both trilobites and brachiopods in shallow marine, subtidal carbonate/clastic facies through the Ordovician, reflecting a general increase in biomass in Ordovician benthic communities through time. They associated this increase in size through time with as being, in part, a consequence of Cope's Rule – the tendency for taxonomic lineages to increase in size through time. Jin and Zhan (2001), commenting on the combined high diversities, increased abundance, and gigantism of the marine biotas in the Selkirk Member of the Red River Formation, related these features to the optimal environmental conditions for these biotas as represented by the Selkirk facies – shallow, open marine, paleoequatorial, epicontinental sea carbonate platform environments.

In a similar vein, Rudkin et al. (2003), in their discussions of the giant trilobite *Isotelus rex* in these strata, indicated that the large size was likely the result of "conditions of ample food supply, elevated atmospheric CO_2, and a warm, equatorial setting conducive to faster growth rates and large maximum size potential in organisms with pervasively calcified skeletons, since it is far less difficult to metabolically precipitate and maintain $CaCO_3$ skeletons at higher temperatures". As they go on to say, among living marine invertebrates with calcium carbonate skeletons, many of the largest and most heavily mineralized forms are tropical in their distribution (="hypercalicified" tropical taxa of Stanley and Hardie, 1999). While this concept refers primarily to reef-building taxa and sediment-producing organisms, a similar trend is evident with regard to the occurrence and distribution of the largest living marine neogastropods – all large (> 250 mm in length), mobile, bottom-dwelling predators in tropical shallow marine environments. Indo-Pacific examples include the triton *Charonia tritonis* (up to 500 mm), the helmet *Cassis cornuta* (up to 300 mm), the false trumpet *Syrinx aruanus* (up to 910 mm in length and the largest known gastropod), and the volute *Melo amphora* (up to 500 mm in length) in shallow tropical marine environments in northern Australia and adjacent portions of Indonesia. Western Atlantic examples include the occurrence of the triton *Charonia variegata* (up to 400 mm), the helmet shell *Cassis madagascariensis* (up to 300 mm), the fasciolarid *Triplofusus gigantea* (up to 600 mm), the melongenid *Sinistrofulgur sinistrum* (up to 450 mm), and the turbinellid *Turbinella angulata* (up to 360 mm), all from shallow sub-tropical to tropical marine environments in Florida and the Caribbean. It is likely that Rudkin et al. (2002) are correct in linking these same phenomena with the gigantism characteristic of the Arctic Ordovician Nautiloid Fauna.

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LATE ORDOVICIAN TRILOBITES FROM THE UPPER MISSISSIPPI VALLEY

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Plate 1 is a summary of trilobite classification and evolution from the Treatise. Absolute duration of trilobite genera in North America was calculated for the Late Cambrian Pterocephalid and Ptychaspid biomeres and for the Ordovician. North America is limited to the North American Craton of the Ordovician and includes, Greenland, Spitzbergen, northwestern Scotland (especially the Girvan district), western Newfoundland, and northwestern Ireland, but excludes much of Alaska and Florida. Generic duration for the two biomeres and each part of the Ordovician is distributed in a Poisson distribution. An absolute chronology for the Ordovician was calculated from Sweet's (1984) Composite Standard Section (CSS) based on conodonts and three high precision dates. Since there were many trilobite collections made from the same sections as the conodonts, it was a relatively trivial matter to transpose the trilobites into the CSS. First and last appearances were calibrated and then graphed (See Plate 2a-d.).

The old numerical dates are now obsolete (See “A Geologic Time Scale 2004”, Gradstein et al, Cambridge.) but are sufficiently close for many purposes.

The pattern of Cambrian trilobite history is notably different from that of the Ordovician. There are five cycles of radiation followed by extinction, the classic biomeres, during the Cambrian. These are 1) the Atdabanian-Lenian Olenellid biomere, terminated by an extinction of 72 per cent; 2) the early Middle Cambrian Plagiura-Poliella Zone to Glossopleura Zone biomere terminated by a 36 per cent extinction; 3) the late Middle and early Late Cambrian Marjumiid biomere, terminated by an 80 per cent extinction; and 4, 5) the Late Cambrian Pterocephaliid and Ptychaspid biomeres, each terminated by extinctions of 95 per cent. The durations of Cambrian trilobite genera are short because of this pattern of multiple radiation, and because they have been reset by extinction.

In contrast, the diversity of Ordovician genera as a function of time is much simpler. The mean duration of trilobite genera increases from 7.7 m.y. for the Ibexian, to 16.4 m.y. for the Whiterockian, 20.8 m.y. for the Mohawkian, and 22.1 m.y. for the Cincinnatian. A plot of numbers of trilobite genera in North America during the Ordovician, at intervals of 2.5 to 5 m.y. shows a linear rise from 13 at the base of the Ibexian, to 73 at the base of the Whiterockian, and a gradual sag to a nadir of 47 during the middle third of the Whiterockian (a gradual extinction of 36 per cent), clearly due to the well known eustatic drop in sea level. It is followed by a linear rise to an absolute peak of 107 genera at the top of the Whiterockian. This is the greatest diversity of trilobites of all time. A linear decrease to 61 Richmond genera is interrupted only by the relatively minor catastrophic extinction in a tenth of the continent as a result of the Deicke eruption at the end of the Turinian (= old Blackriveran).

Minor increases in diversity are the result of recruitment from across the Iapetus, and evolution in situ. In the last 2 or 3 m.y. of the Ordovician, terminal extinction resulted in a reduction to 14 genera of trilobites, an extinction of 73 per cent.

There are only three significant extinctions in the record of trilobites in North America during the Ordovician. The first is the mid-Whiterockian extinction, which extends from CSS 450 to CSS 70O, or from 483 to 469 m.y. This extinction involved a drop of 36 per cent from the peak number of trilobite genera in the earliest Whiterockian. It is most easily explained by the MacArthur and Wilson (1967) theory of island biogeography. There is a reduction of over 50 per cent in the total area of the continental shelf open to shallow water trilobites between the late Ibexian and the mid-Whiterockian. This reduction in area is due to the well known eustatic drop in sea level that produced the "Knox unconformity" and the end of the Sauk Sequence.

The second is the catastrophic extinction over the eastern half of the U.S.A. produced by the Deicke K-bentonite eruption (CSS 979) at the end of the Turinian (= old Blackriveran). This eruption spread ash from the subduction zone in southern Appalachia to the present north and west as far as the Transcontinental Arch, the old Proterozoic Penokean mountains, and the area north of the Great Lakes. The total volume of the eruption was 1000 cubic kilometers or one cubic township (6 miles^3)! Before compaction to 3 to 5 inches, there was a layer of 15 inches of fluffy ash on the sea floor in Minnesota. The extinction rate was about 17 per cent of the trilobite genera in the continent. The short duration of the Rocklandian and Kirkfieldian stages is a direct result of the rapid community changes made during the repopulation of the devastated area. Initial repopulation came first from deeper water faunas along the present eastern coast, then from shoal waters in Oklahoma, and finally, with about equal facility from the other side of the Transcontinental Arch or from across the Iapetus Ocean. Initial repopulation in the Chatfieldian (old Trentonian) sea first occurred in trilobites with planktonic larvae (*Isotelus gigas* and *Eomonorhachis intermedius*) and later in forms with nonplanktonic protaspis such as *Dolichoharpes ottawaensis, Ceraurus plattinensis, Cerarurus pleurexanthemus* and *Ceraurus icarus*. None of these occur below the Millbrig K-bentonite. It took almost 4 million years for the Chatfieldian fauna to be as diverse as the latest Turinian faunas.

The major feature that determined which animals reached the Upper Mississippi Valley first was apparently the time their larvae spent in the plankton. The first two trilobites to reach southern Minnesota after the Deicke eruption were *Isotelus gigas* and *Eomonorachus intermedius* which are the only Chatfieldian trilobite genera that had planktonic larvae, with a major metamorphosis from the protaspis to meraspid stages, all the others had direct development. The other trilobites took far longer to reach Minnesota. *Ceraurus plattinensis* is the next to occur at 37 inches above the Deicke, or about 74,000 years, a rate of spread of 35 miles per year.

The brachiopods that appeared early had larvae with long planktonic life, at a 30 day planktonic life as in many modern brachiopods it would only take about 40 generations to reach Minnesota from the end of the Transcontinental arch in Oklahoma. Similarly, although not listed here, the Bryozoa with their planktonic larvae arrived early.

The various worms and/or arthropods responsible for the trace fossils *Arenicolites, Bifungites, Chondrites, Planolites,* and *Thallassinoides* all arrived immediately after the Deicke was deposited, and presumably had planktonic larvae.

The third extinction is the well known terminal Ordovician extinction of eustatic and cooling origin. It resulted in a loss of 73 per cent of the Richmondian trilobites and is the biggest trilobite extinction after the Cambrian biomeres.

Durations of genera within the Ordovician and the three well sampled biomeres follow a distinctive pattern. Early in the interval concerned, durations are short, and they increase exponentially with time. The mean duration of genera is highly dependent on the elapsed time since the last major extinction. Neither the small Deicke extinction nor the early Whiterockian extinction at 36 per cent was large enough to reset the evolutionary rates of trilobites. In many ways, the entire Ordovician corresponds to a typical Cambrian biomere.

Each Cambrian biomere and the entire set of Ordovician trilobites represents a normal adaptive radiation; each is exactly comparable to the latest Cretaceous and Paleocene adaptive radiation of ungulates (Sloan 1987a) in progressive duration of taxa, and rates of evolutionary change.

Most of the taxa in the Ibexian originated as immigrants from deeper water or from other cratons. Each immigrant species then underwent a radiation on this craton, with initial short duration of species, and rapid diversification of genera to produce distinctively North American families and subfamilies. Rates of immigration increased in the Mohawkian, and became more rapid and progressive in the Chatfieldian, and the Cincinnatian.

Chatterton and Ludvigsen (1976) documented a series of four trilobite shelf biofacies of increasing depth. In order, they are the *Bathyurus*, *Isotelus*, *Calyptaulax-Ceraurinella*, and *Dimeropyge* biofacies. Sloan (1987b) calibrated the first three as being from water shallower than 50 meters, on the basis of coexistence with Chlorophyta. Fortey (1983) added the olenid biofacies of deep water trilobites, and Fortey and Owens (1987) added two more Ordovician deep water biofacies. These are the cyclopygid biofacies of large-eyed mesopelagic trilobites that occur deeper than 200 m and the atheloptic benthic biofacies of blind or small-eyed trilobites thought to occur at depths greater than 300 m. As previously documented by Whittington (1966), Whittington and Hughes (1972, 1974) and others, the pioneer immigrations across the Iapetus to North America first occurred in deep water, with later migrations onto the shelf. Three examples of Whiterockian or Turinian (= old Blackriveran) migrants that moved onto the shelf from deep water after the Deicke eruption at the end of the Turinian (= old Blackriveran) are *Flexicalymene*, *Brongniartella*, and *Cryptolithus*.

I have found several evolutionary series of species and Ludvigsen (1979) found others. They are shown in two figures below. In Asaphidae. *Isotelus latus* from the Decorah and the lower Trenton of Ottawa is the ancestor of *Isotelus maximus* from the Cincinnatian, *Isotelus gigas* of the Chatfieldian steadily increased its length from 1" above the Deicke to the upper Prosser, where it reaches a maximum size of 30" (extrapolated from isolated hypostomes). Isotelus *walcotti* from the Platteville is the ancestor of *Isotelus iowensis* from the Maquoketa. *Anataphrus borealis* was described from Baffin Island, and is found in the Chatfieldian of Minnesota and Iowa. It is a gregarious species, always found in clusters. *Isotelus simplex* Raymond 1913 is properly named *minnesotensis* because Foerste first named it in 1887. It too is gregarious and has the early stages of the higher vertical thickness typical of *Anataphrus*. This trend is elaborated in *Vodgesia vigilans*. Finally *"Homotelus" bromidensis* is also a fairly typical isotelid that is gregarious. I refer them all to *Anataphrus*. *Isotelus* *homalonotoides* Walcott from the Decorah has eyes elevated on low stalks and so I strongly suspect it is the ancestor of *Ectenaspis beckeri* of the Maquoketa and the Richmondian of Manitoba. The Cerauridae also has several species in evolutionary series. Ludvigsen described several in 1979; I added others from the Upper Mississippi Valley. Contemporary species differ on the two sides of the Transcontinental Arch, a major barrier during the Ordovician.

ACKNOWLEDGMENTS

I gratefully acknowledge the help of Frederick C. Shaw, Harry B. Whittington, Reuben J. Ross Jr., Walter C. Sweet, Allison R. Palmer, Thomas E. Bolton, and especially Ronald P. Tripp, who went out of their way to provide references and useful criticism during the development of these papers. They are of course not responsible for the conclusions I have reached.

FURTHER READING

Cooper, J.D., Droser, M.L., and Finney, S.C. (eds.). 1995. **Ordovician Odyssey**. The Pacific Section Society for Sedimentary Geology, Fullerton, CA, 498 p.

Sloan, Robert E. (ed). 1987. **Middle and Late Ordovician Lithostratigraphy and Biostratigraphy of the Upper Mississippi Valley**. Minnesota Geological Survey, Report of Investigations 35, 232 p.

Sloan, Robert E., 1991, A chronology of North American Ordovician trilobite genera, in **Advances in Ordovician Geology**, C.R. Barnes and S.H. Williams (ed.), Geological Survey of Canada, Paper 90-9, p.165-177

Webby, B.D., Paris, F., Droser, M.L., and Percival, I.G. 2004. **The Great Ordovician Biodiversification Event**. Columbia University Press, New York, 484 p.

Most primary sources are listed in Sloan, Robert E., 2005, **Minnesota Fossils and Fossiliferous Rocks**, 220 pp. Privately printed in edition of 1000; still available at $30 post paid in the U.S. and Canada.

The book is designed to serve several purposes. It is a picture book and locality source for interested amateurs. For professionals, it is a guide to the literature, and summary of Minnesota stratigraphy to date, the first general one since Stauffer and Thiel (1941). This book is also designed to be a quick and easy guide to the collection and identification of the fossils of Minnesota. Although this book cannot possibly be a complete list of all the fossils yet found, it has about 70% of those currently described and about 95% of the common ones.

The book has an introductory chapter of 26 pages. It includes a brief introduction to the geology of Minnesota, and to the major uses of paleontology, stratigraphy, paleoecology and the study of evolution. The mechanics of evolution are summarized, as is the current classification of the Animal

Kingdom and the Cambrian explosion with up to date references.

Chapter 2 is on the Late Cambrian rocks and fossils with 21 pages, 14 of them with pictures of 109 of the fossils arranged by zone. There is a detailed cross section of the Cambrian rocks from Taylors Falls to Reno along the St. Croix and Mississippi rivers showing the rock facies, members, fossil zones and localities. There is also a zonal chart showing the vertical distribution of all the trilobite species within the zones.

Chapter 3 is on the Early Ordovician Prairie du Chien Group, with 16 pages, including all of the 83 fossils described from Minnesota. It includes some 17 fossil localities.

Chapter 4 covers the Late Ordovician (formerly the Middle and Late Ordovician); it is 100 pages long with pictures of 338 fossils. There are 12 detailed measured sections of important fossil localities. There is also a very detailed discussion of the massive extinction at the Deicke K-bentonite in the upper Platteville Formation.

Chapter 5 covers the Devonian, is 8 pages long with pictures of a few of the typical fossils. The Devonian of northernmost Iowa has been described far more fully than the Minnesota Devonian, and is summarized, with copious references.

Chapter 6 is on the Cretaceous, is 34 pages long and contains pictures of 52 typical fossils and some 42 types of pollen. The Early Cretaceous (usually called Pre-Cretaceous) deep weathering interval is summarized, and the highly variable mid-Cretaceous sediments of the state are described in some detail with detailed locality descriptions.

The Pleistocene chapter is 12 pages long and has illustrations of the large extinct mammals found in Minnesota. A map showing the distribution of all the extinct megafauna in Minnesota is included. The Late Wisconsin and Holocene mammals of Iowa are listed, with references. H. E. Wright Jr.'s works on the late Wisconsin and Holocene changes in vegetation are summarized.

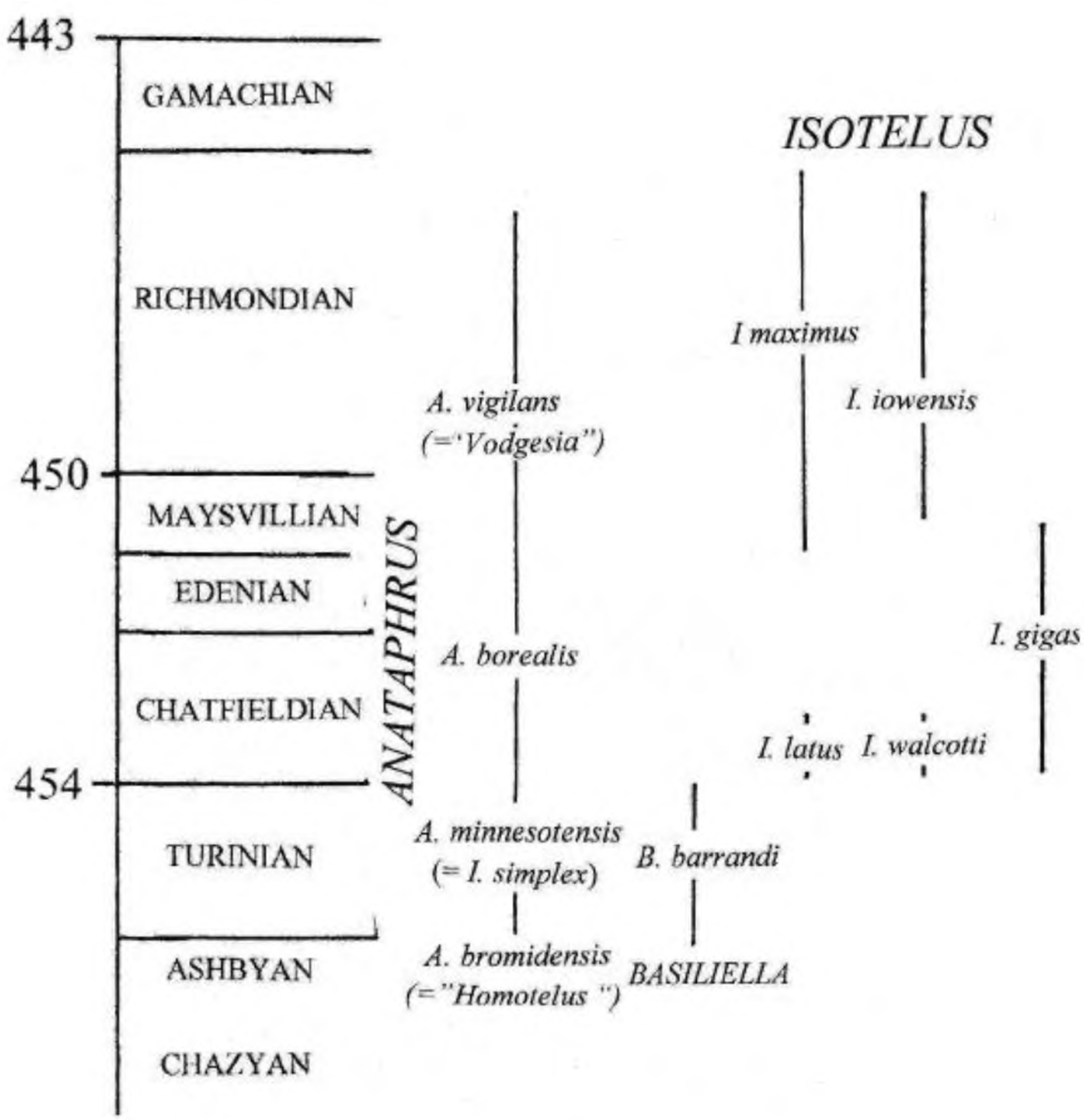


Fig. 1. Phylogeny of the Family Asaphidae during the Late Ordovician of the Upper Mississippi Valley.

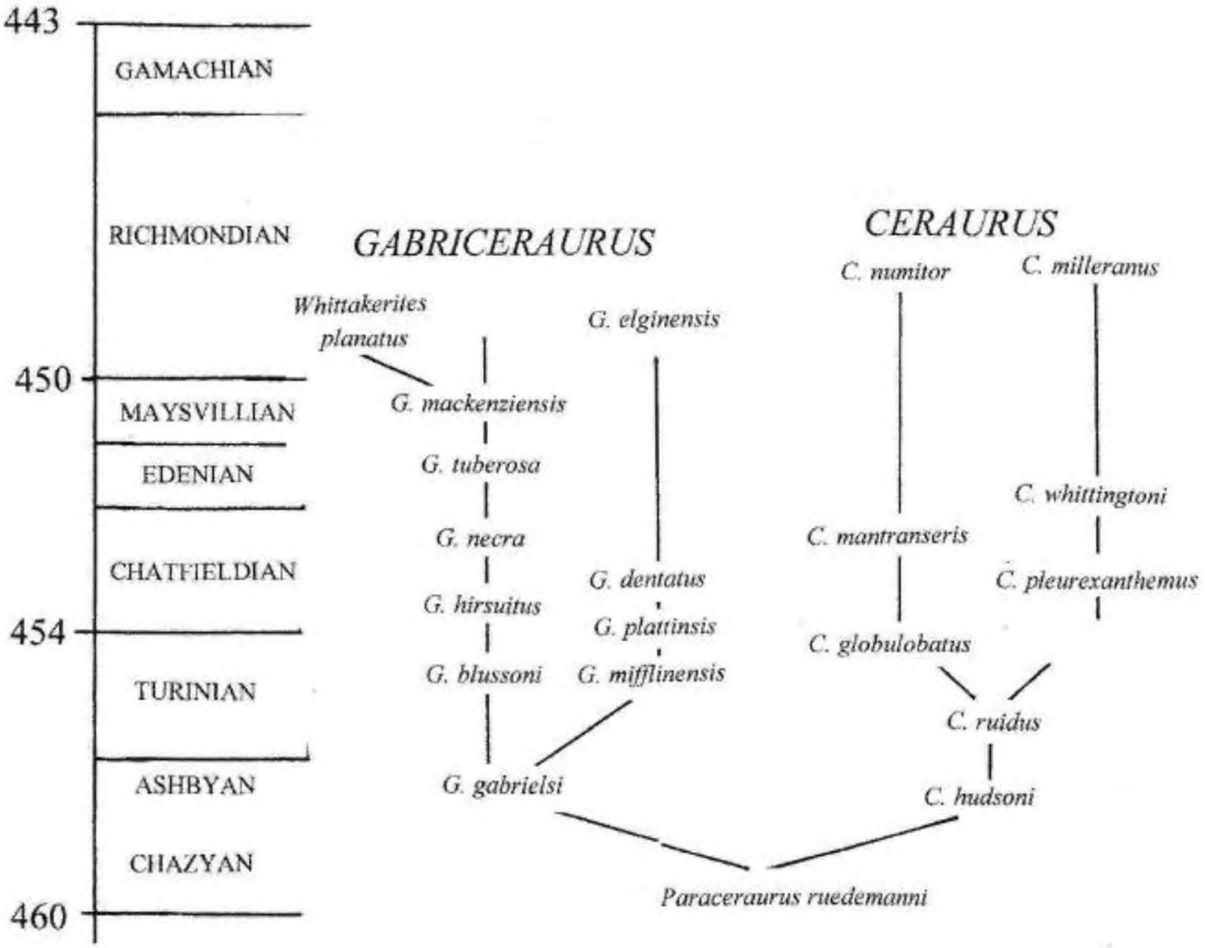


Fig. 2. Revised Phylogeny of the Family Ceraurídae during the Late Ordovician of the Upper Mississippi Valley, mostly derived from Ludvigsen (1979) and a bit from my studies. Left hand columns of both *Gabriceraurus* and *Ceraurus* are species from North of the Transcontinental Arch, right hand columns are from South of the Arch.

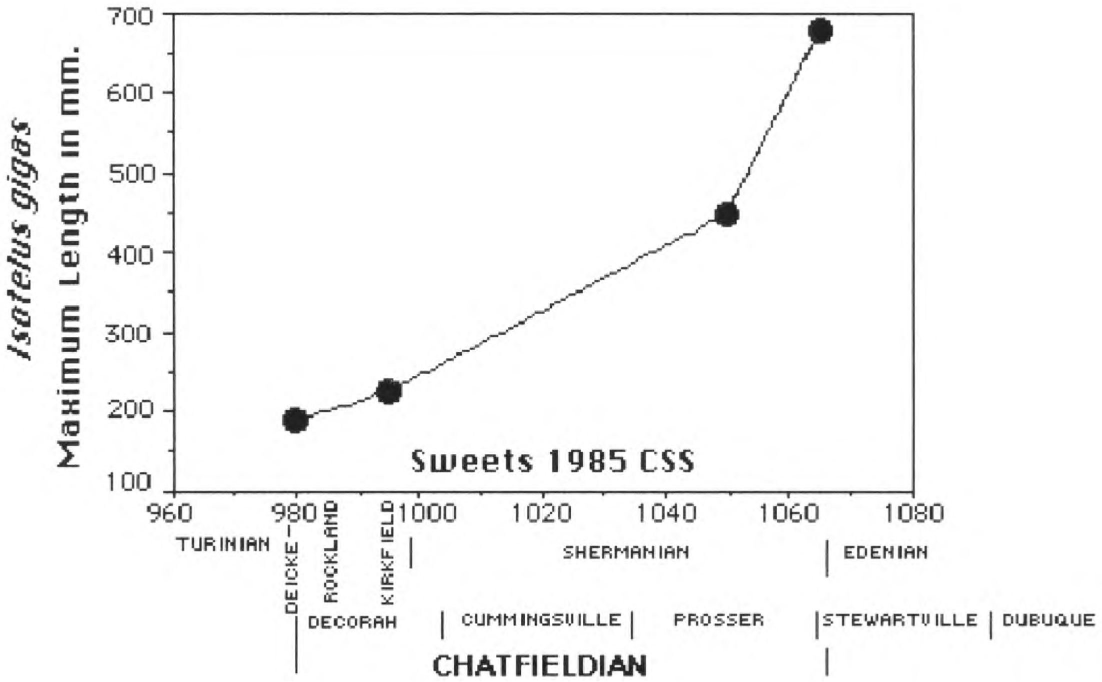


Fig. 3. Change in maximum size of *Isotelus gigas* during the Chatfieldian.

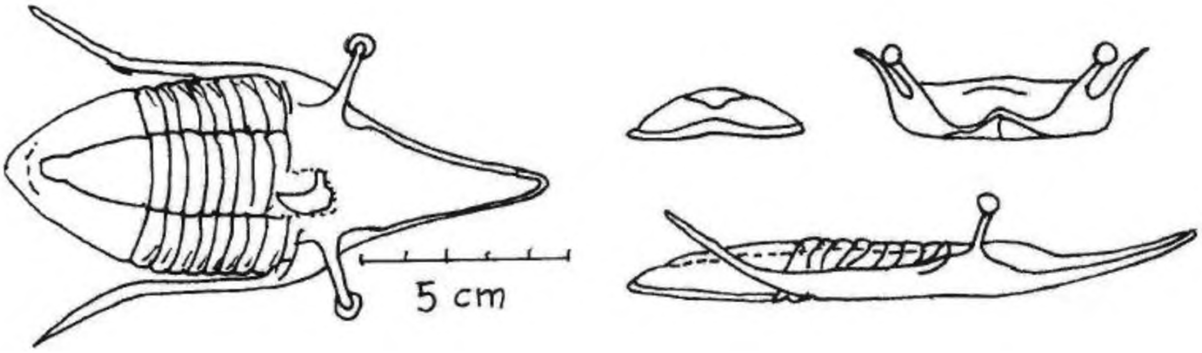


Fig. 4. *Ectenaspis beckeri*, Maquoketa Group.

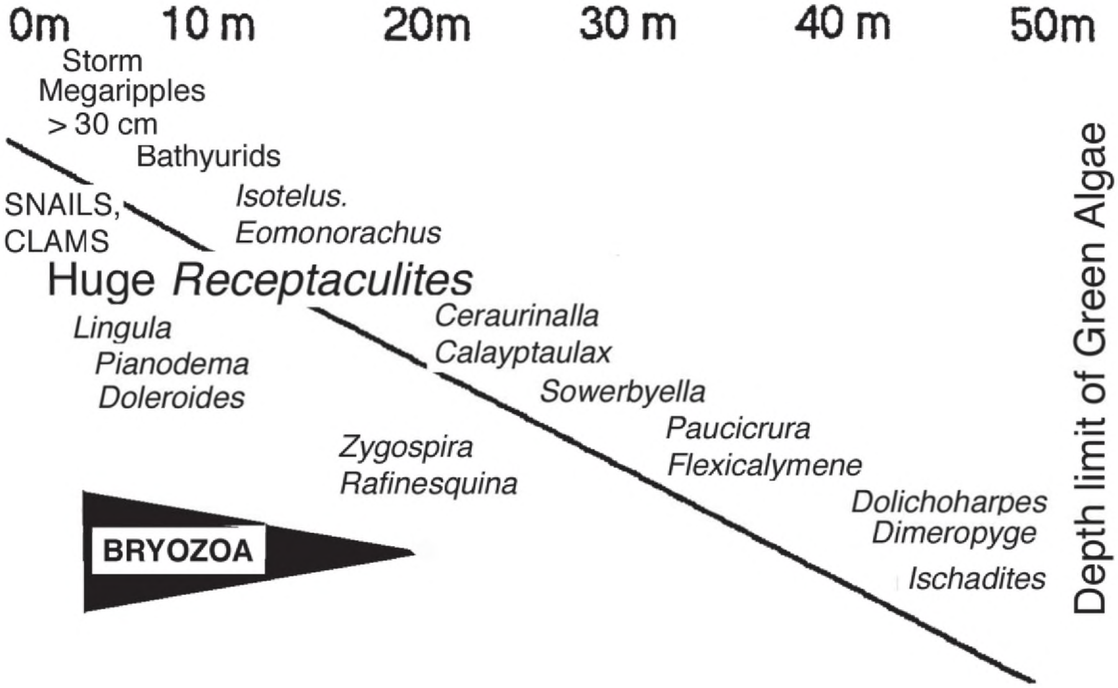


Fig. 5. An estimate of Chatfieldian paleoecology, with genera plotted in what appears to be their optimum depth. Based on data collected by Sloan, Schneider, Rice and Des Autels. Deeper shelf facies and trilobites are to be found in the Kimmswick Formation of Southern Illinois and adjacent Missouri.

EXPLANATION OF PLATES

Plate 1. A diagram of the evolution of trilobites from the Treatise of Invertebrate Paleontology Volume O part 1, revised.

Plate 2 a-d. Stratigraphic ranges of North American trilobites from Sloan, R. E., 1991, A chronology of North American Ordovician trilobite genera; in Advances in Ordovician Geology, C.R. Barnes and S.H. Williams (ed.), Geological Survey of Canada, Paper 90-9, p.165-177, 1991.

Plate 3. Trilobite Biostratigraphy of the Upper Mississippi Valley. The region covered is from Rockford, IL to St Paul, MN. The collection examined now consists of about 1550 items, 450 from DeMott, 1987, 400 from the U of MN collection, 276 from Art Gerk (U of IA) 225 from Dennis Kolata, 41 from Cal Levorson (U of IA), 34 from Glenn Crossman, 28 from Brian Grossman, and 10 from John Catalani. Casts of most specimens remaining in these amateur collections are in the U of MN collection. Species are listed by order and family. Main references are Clarke, 1894, MN Geol & Nat. Hist. Surv. Final Rpt, Vol. III part 2; DeMott, 1987, MN Geol. Surv. RI 35, Slocum, 1916, IA Geol. Surv. Bull 27, and Walter, 1927, IA Geol. Surv. Ann Rpts, v 31.

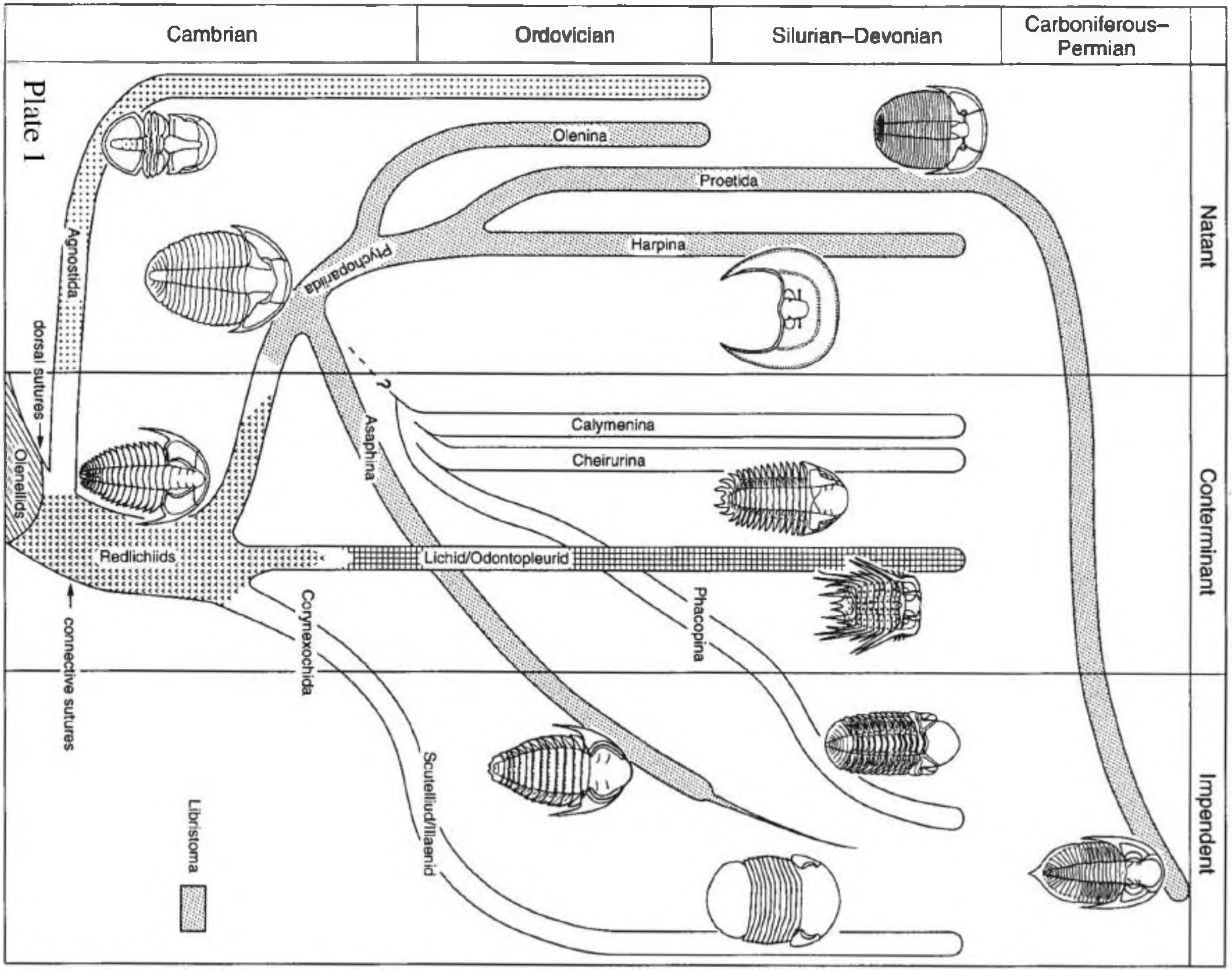
Plate 4. Trilobites from Clarke, 1894, all life size. 1a,b *Calyptaulax callicephala* Prosser–Dubuque. 2 *Achatella achates* Prosser. 3a,b *Anataphrus vigilans* Maquoketa. 4 *Isotelus iowensis* Maquoketa. 5a,b *Nahannia susae* Maquoketa. 6a,b *Bumastus trentonensis* Cummingsville-Prosser. 7a,b *Amphilichas cucullus* cephalon only Cummingsville-Prosser. 8 *Eobronteus lunatus* Prosser. 9a,b *Amphilichas robbinsi* cephalon only, Maquoketa. 10 *Odontopleura parvula* Decorah. 11a-d *Illaenus americanus*, Cummingsville-Prosser.

Plate 5. Platteville and Decorah Trilobites from DeMott, 1987, all life size. Platteville means below the Deicke bentonite, Decorah means above the Deicke. 1a,b *Hypodicranotus* sp. Platteville. 2a-e *Anataphrus minnesotensis* (= *Isotelus simplex*) Platteville. 3a-f *Basiliella barrandi* Platteville. 4a,b *Bumastoides milleri* Platteville. 5a-c *Thaleops ovata* Platteville. 6a-c *Dolichoharpes reticulata* cephalon only, Platteville. 7a-d *Ceraurinella scofieldi*, Platteville. 8a,b *Ceraurinella templetoni*, Platteville. 9a-c *Raymondites longispinus* Platteville. 10 *Cybeloides cimelia*, Platteville. 11a,b *Sceptaspis lincolnensis* Platteville and Decorah. 12a,b *Amphilichas* cf. *cucullus* cephalon and pygidium, Platteville. 13a-d *Encrinuroides rarus* Platteville. 14a-e *Gabriceraurus mifflinensis* Platteville.

Plate 6. Trilobites mostly from the Levorson and Gerk collection at the University of Iowa. All life size except 1 and 15. 1 *Basiliella barrandi* (half size) Platteville. 2 *Hypodicranotus* n. sp., ventral view, Platteville. 3 *Dolichoharpes ottawaensis* Cummingsville-Prosser. 4 *Anataphrus minnesotensis* (= *Isotelus simplex)* Platteville. 5 *Calyptaulax callicephala* Prosser–Dubuque. 6 *Gabriceraurus mifflinensis* Platteville. 7 *Ceraurinus icarus* Prosser 8 *Cybeloides winchelli* Prosser. 9 *Isotelus gigas* Decorah- Sinsinewa. 10 *Sphaerocoryphe maquoketensis* Maquoketa. 11 *Failleana indeterminatus* Prosser. 12 *Bathyurus extans*, Platteville. 13 *Raymondites longispinus* Platteville. 14 *Illaenus americanus* Cummingsville-Sinsinewa. 15 *Hemiarges paulianus* X4 Decorah-Prosser. 16a-e *Eomonorachus intermedius* Decorah- Prosser.

Plate 7. Mostly Maquoketa Trilobites, mostly from the Levorson and Gerk collection at the University of Iowa. All life size. 1a,b *Amphilichas bicornis* Maquoketa. 2 *Isotelus gigas* upper Prosser, largest known hypostome, compare with the hypostome of 3 to estimate the maximum size of this species. 3 *Isotelus iowensis* in ventral view to show hypostome. 4 *Ectenaspis beckeri*. Maquoketa, only known entire specimen, immature. 5 *Gabriceraurus dentatus* Decorah. 6a-c *Bumastoides beckeri* Maquoketa. 6a in life position, buried in the sea floor with only the head out. 6b dorsal view, 6c frontal view in life position with head in feeding position above the sea floor.

Plate 1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Olenellids
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connective sutures
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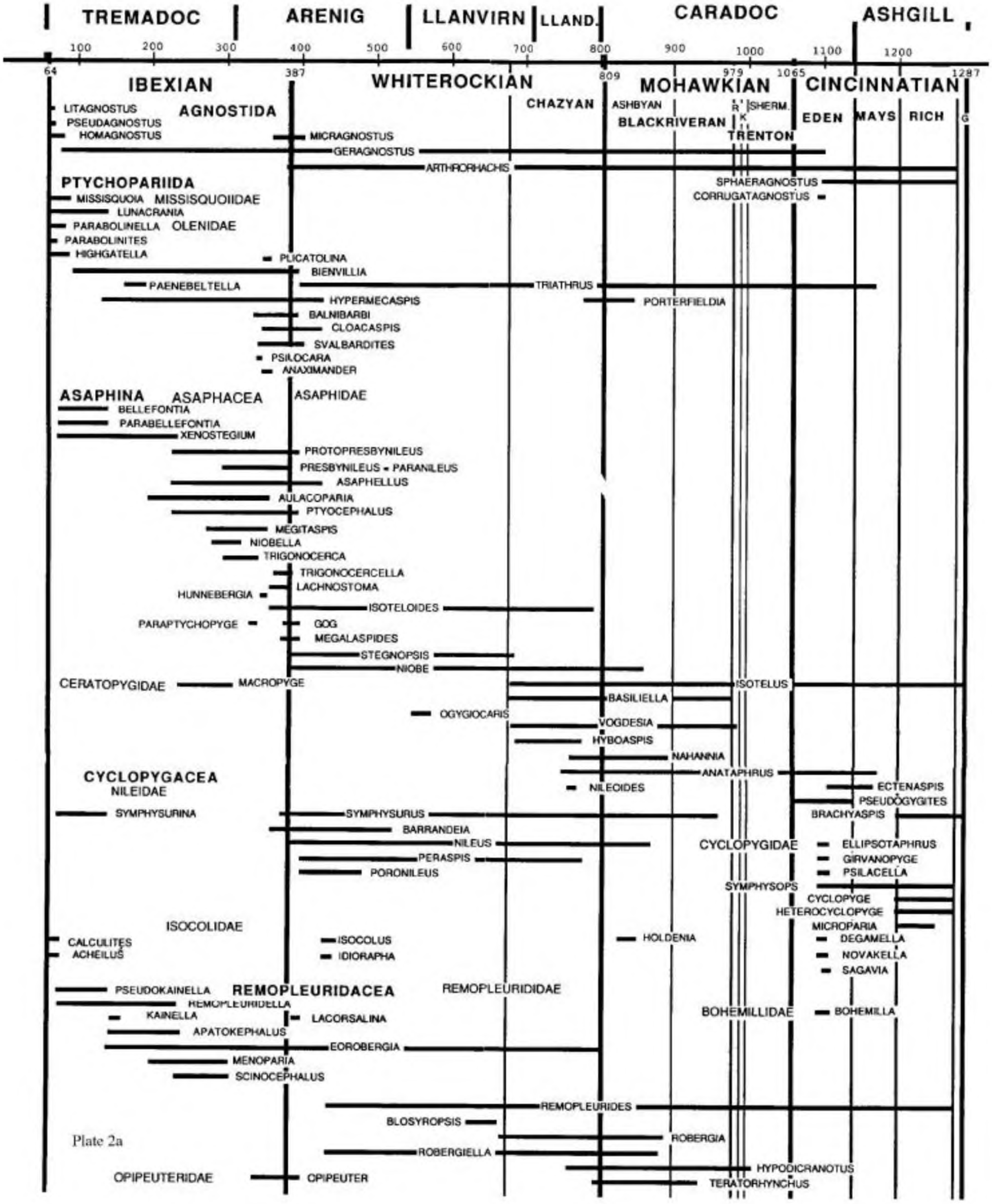
Lichid/Odontopleurid
Phacopina
Corynexochida
Scutelluid/Illaenid
Libristoma ▨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PARABOLINITES
HIGHGATELLA
PLICATOLINA
BIENVILLIA
PAENEBELTELLA
TRIATHRUS
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REMOPLEURIDELLA
BOHEMILLIDAE
BOHEMILLA
KAINELLA
LACORSALINA
APATOKEPHALUS
EOROBERGIA
MENOPARIA
SCINOCEPHALUS
REMOPLEURIDES
BLOSYROPSIS
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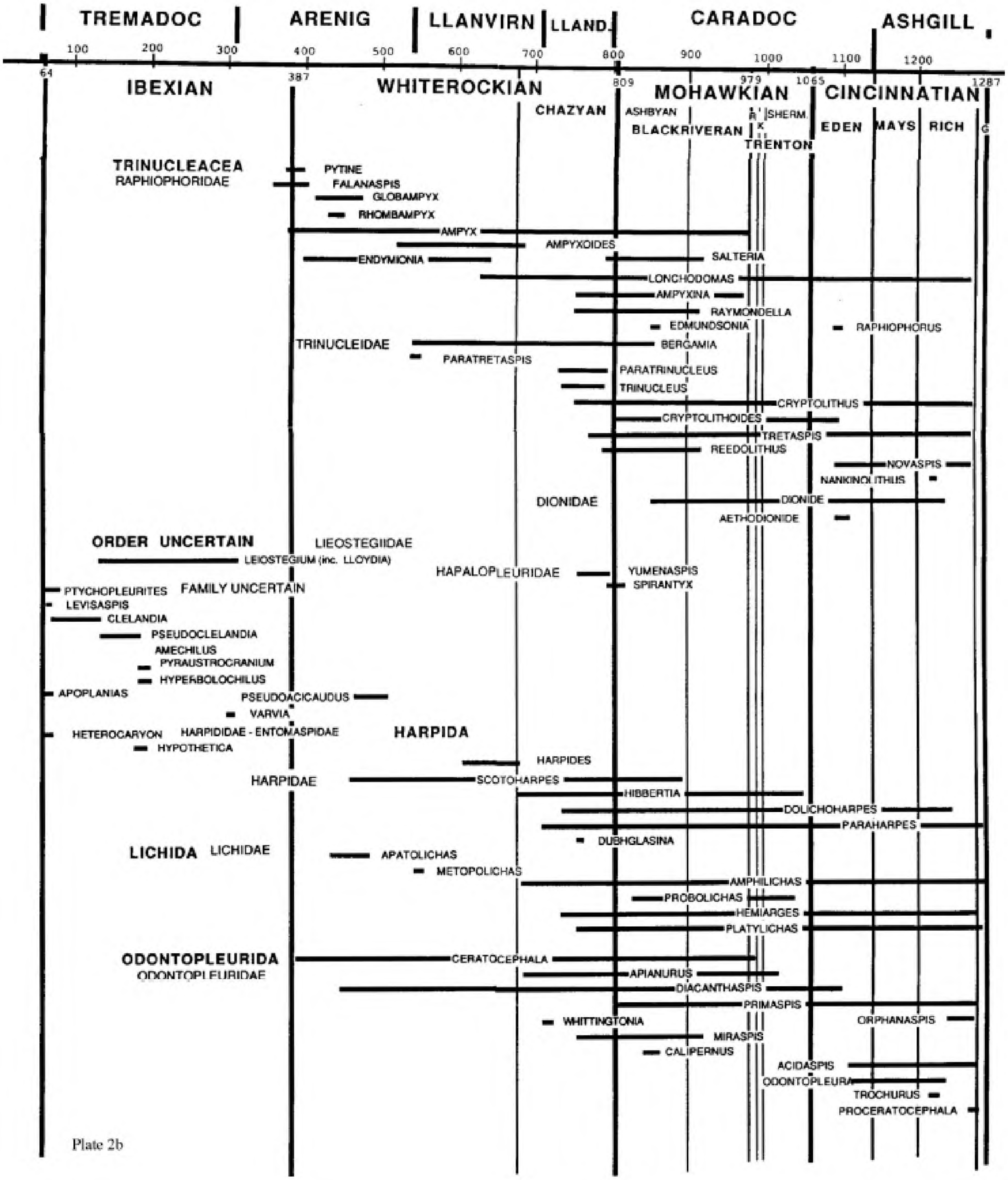
OPIPEUTERIDAE
OPIPEUTER
HYPODICRANOTUS
TERATORHYNCHUS

Plate 2a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METOPOLICHAS
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PROBOLICHAS
HEMIARGES
PLATYLICHAS
ODONTOPLEURIDA
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CERATOCEPHALA
APIANURUS
DIACANTHASPIS
PRIMASPIS
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ACIDASPIS
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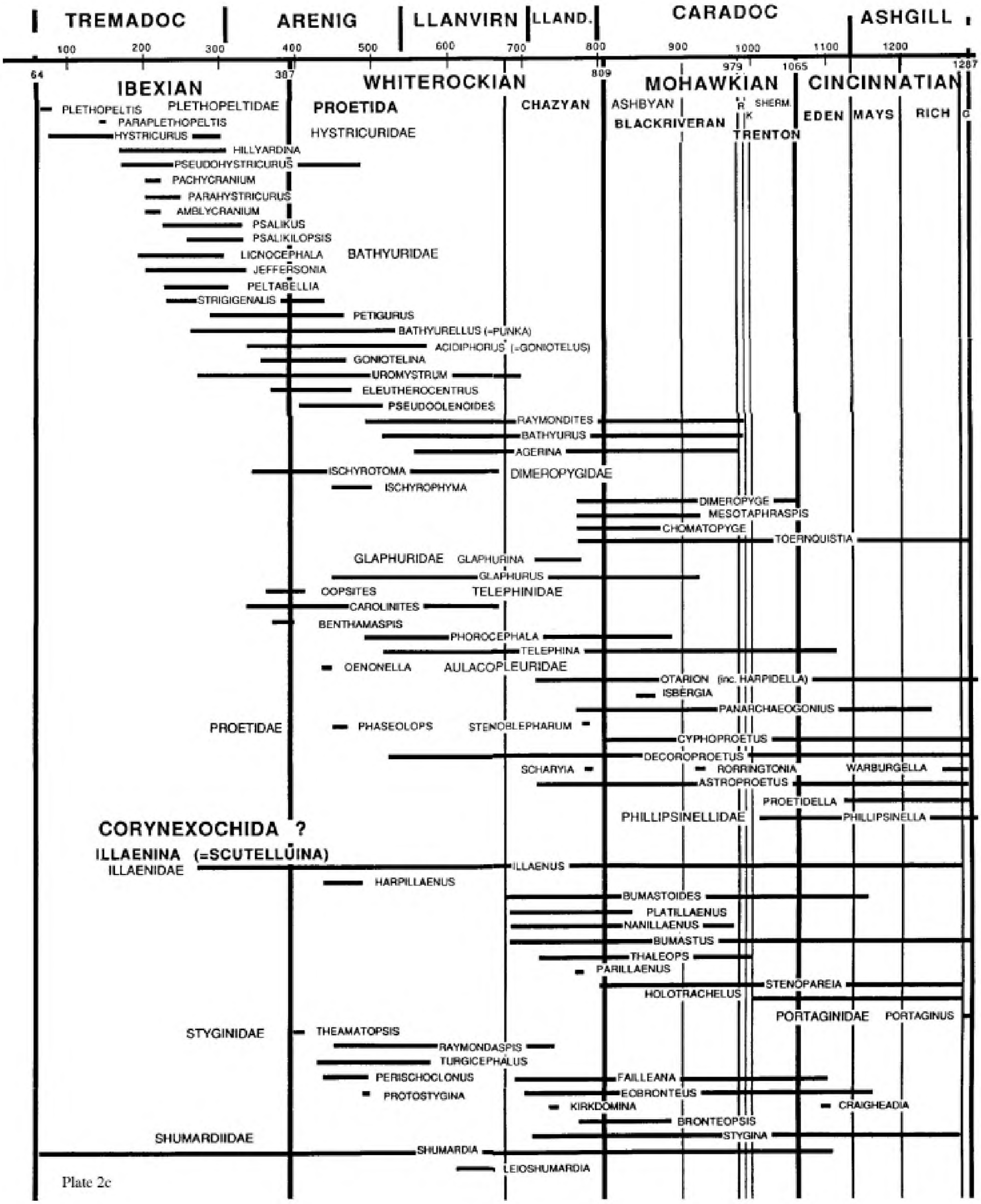
TROCHURUS
PROCERATOCEPHALA

Plate 2b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JEFFERSONIA
PELTABELLIA
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PETIGURUS
BATHYURELLUS (=PUNKA)
ACIDIPHORUS (=GONIOTELUS)
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ELEUTHEROCENTRUS
PSEUDOOLENOIDES
RAYMONDITES
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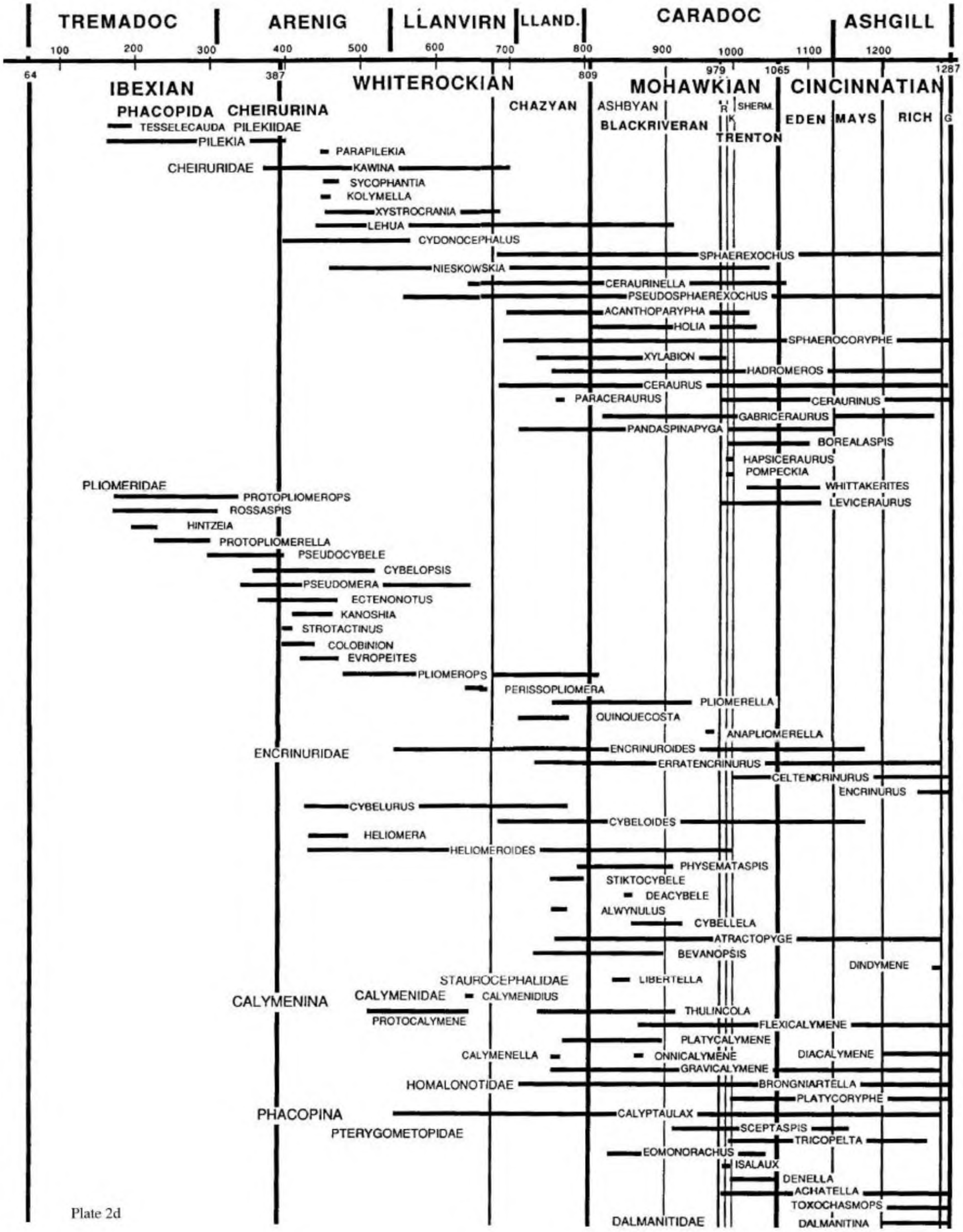
Plate 2c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BOREALASPIS
HAPSICERAURUS
POMPECKIA
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STROTACTINUS
COLOBINION
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QUINQUECOSTA
ANAPLIOMERELLA
ENCRINURIDAE
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CELTENCRINURUS
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CYBELLELA
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BEVANOPSIS
DINDYMENE
STAUROCEPHALIDAE
LIBERTELLA
CALYMENINA
CALYMENIDAE
CALYMENIDIUS
THULINCOLA
PROTOCALYMENE
FLEXICALYMENE
PLATYCALYMENE
CALYMENELLA
ONNICALYMENE
DIACALYMENE
GRAVICALYMENE
HOMALONOTIDAE
BRONGNIARTELLA
PLATYCORYPHE
PHACOPINA
CALYPTAULAX
PTERYGOMETOPIDAE
SCEPTASPIS
TRICOPELTA
EOMONORACHUS
ISALAUX
DENELLA
ACHATELLA
TOXOCHASMOPS
DALMANITIDAE
DALMANITINA

Plate 2d

Plate 3

ASAPHIDA
Basiliella barrandi (Hall 1851)
Anataphrus minnesotensis (Foerste 1887)
Anataphrus borraeus Whittington 1954
Anataphrus vigilans (Meek & Worthen 1875)
Isotelus gigas DeKay, 1824
Isotelus latus Raymond, 1913
Isotelus cf. *I walcotti*
Isotelus iowensis Owen, 1852
Ectenaspis homalonotoides (Walcott, 1877)
Ectenaspis beckeri (Slocum, 1913)
Nahannia susae (Whitfield, 1882)
Hypodicranotus n. sp.

HARPIDA
Dolichoharpes reticulatus Whittington 1949
Dolichoharpes ottawaensis (Billings, 1865)

PROETIDA
Bathyurus extans (Hall, 1847)
Raymondites longispinus
Raymondites spiniger (Hall, 1847)
Ditomopyge galenensis (Clarke, 1894)
"Proetus" parviusculus Hall 1866
Cyphaspis slocumi Raymond 1925

CALYMENINA
Flexicalymene senaria (Conrad, 1841)
Flexicalymene fayettensis (Slocum, 1913)
Flexicalymene gracilis (Slocum, 1913)
Diacalymene mammalilata (Hall 1861)

CHEIRURINA
Anapliomera shirlandensis DeMott 1987
Ceraurinella scofieldi (Clarke, 1894)
Ceraurinella templetoni DeMott 1987
Gabriceraurus mifflinensis DeMott 1987
Gabriceraurus dentatus (Raymond & Barton, 1913)
Gabriceraurus elginensis (Slocum, 1913)
Ceraurus plattinensis
Ceraurus pleurexanthemus Green 1832
Ceraurus milleranus Miller & Gurley, 1894
Ceraurinus icarus (Billings, 1860)
Sphaerocoryphe maquoketensis Slocum, 1913
Sphaeroexochus new Species
Encrinuroides rarus (Walcott).
Encrinuroides vigilans (Hall)
Encrinuroides pernodosus (Slocum, 1913)
Cybeloides cimelia Ludvigsen 1976
Cybeloides iowensis Slocum, 1913
Cybelurus winchelli (Clarke, 1894)

PHACOPINA
Sceptaspis lincolnensis
Calyptaulax plattevillensis
Calyptaulax callicephalus (Hall, 1847)
Calyptaulax larrabei (Slocum, 1913)
Achatella fredericki (Slocum, 1913)
Eomonorachus intermedius (Walcott, 1877)

ILLAENINA
Thaleops ovatus Conrad 1843
Thaleops divericatus DeMott 1987
Illaenus conradi Billings 1859 = ceph b, pyg 2
Illaenus angusticollis Billings 1859
Illaenus americanus Billings 1859
Bumastoides milleri (Billings 1859)
Bumastoides porrectus (Raymond, 1925)
Bumastoides billingsi (Raymond & Narraway 1908)
Bumastoides beckeri (Slocum, 1913)

SCUTELLUINA
Eobronteus lunatus (Billings, 1857)
Failleana indeterminatus (Walcott, 1879)

LICHIDA
Amphilichas cucullus (Meek & Worthen, 1865)
Amphilichas bicornis (Ulrich, 1892)
Probolichas robbinsi (Ulrich, 1892)
Hemiarges paulianus (Clarke, 1894)

ODONTOPLEURIDA
"Odontopleura" parvula Clarke 94

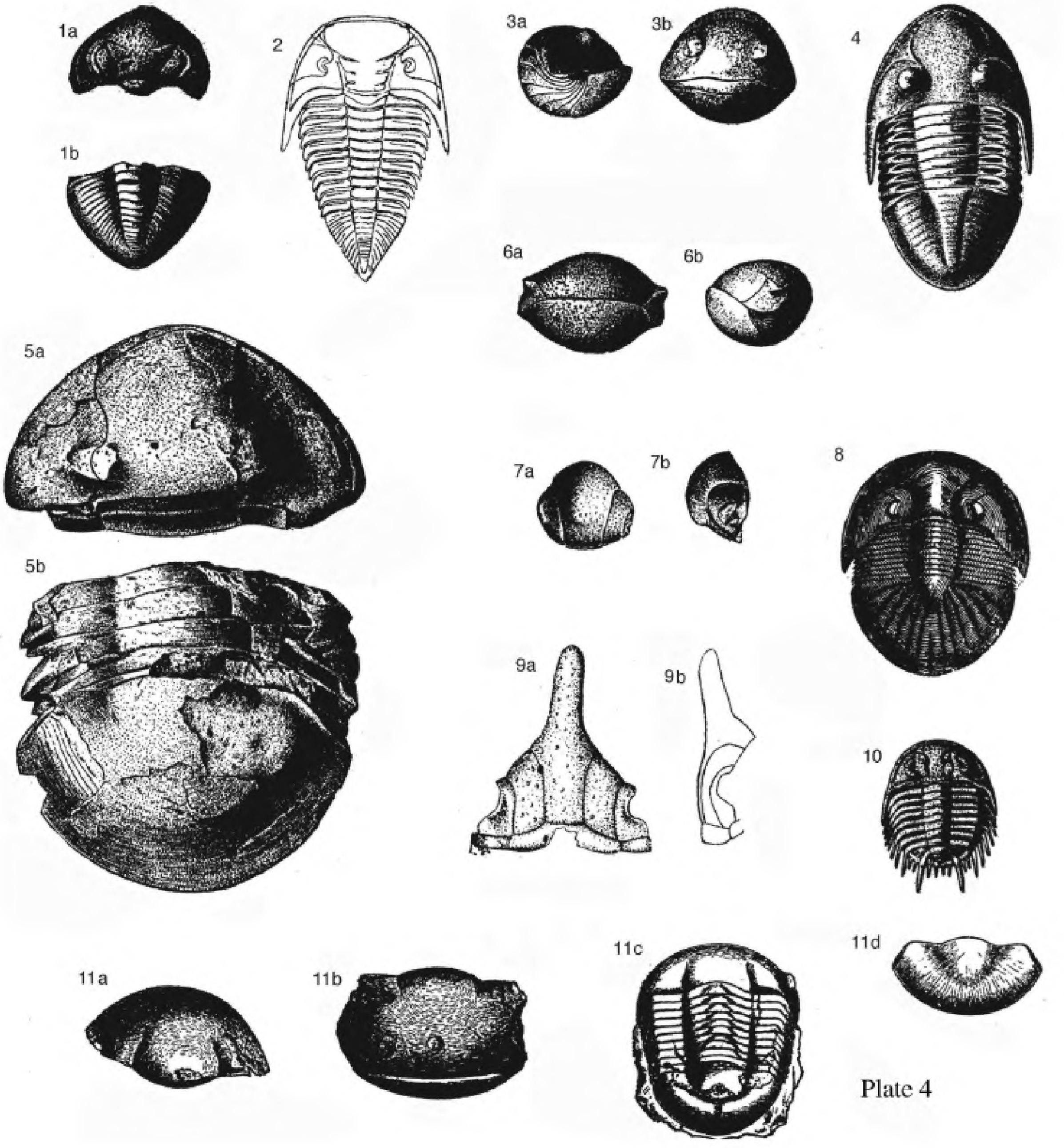

Plate 4

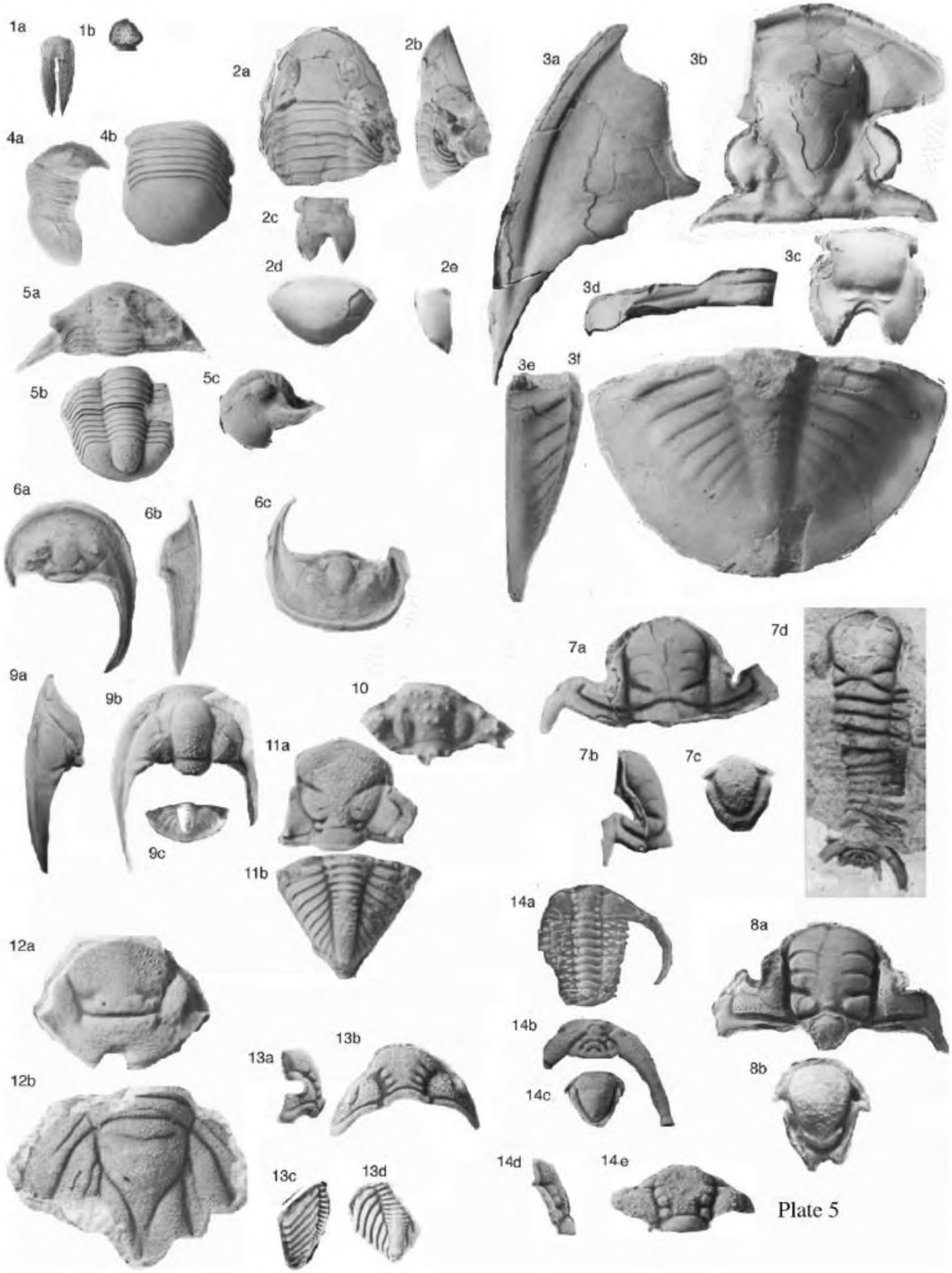
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Plate 5

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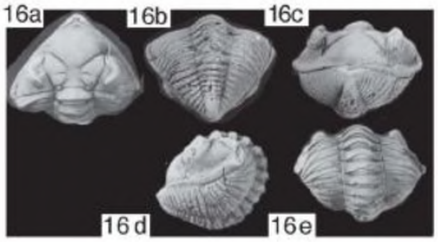

Plate 6

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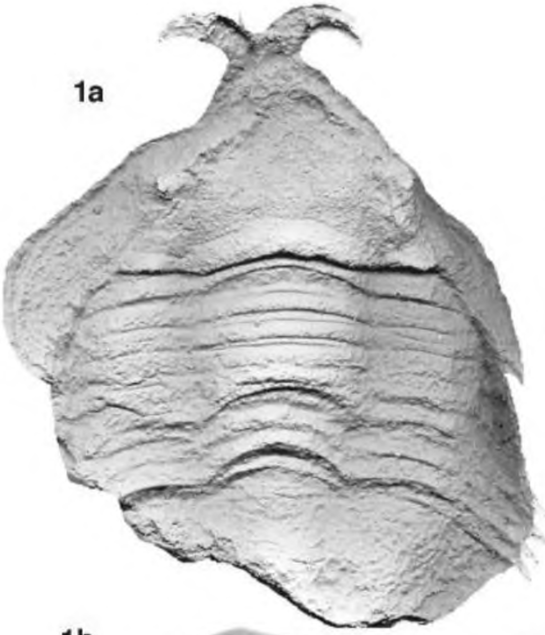

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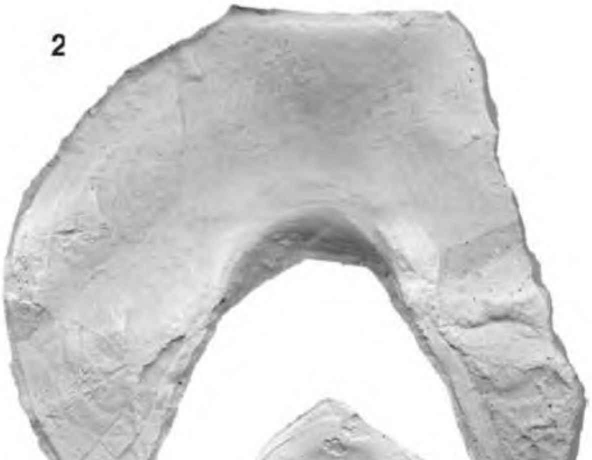

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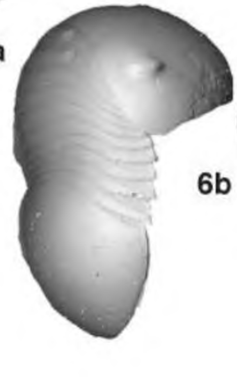

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Plate 7

Research in the Cincinnatian Series (Upper Ordovician) Through Space and Time

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Introduction

For anyone interested in Ordovician geology or paleontology, one of the most extensively studied and well-loved areas for collecting rocks and fossils is the Cincinnati Arch region of Kentucky, Indiana, and Ohio. The rocks exposed here are the North American standard section for the Cincinnatian Series, meaning that this rock interval is the best example on the continent for rocks of this age (Upper Ordovician, approximately 452.5 -443 million years old, Webby et al. 2004). The limestones, siltstones, and shales in this region constitute over 250 meters of stratigraphic exposure (Meyer and Davis, 2009) and are extremely fossiliferous, making for an excellent stomping ground for professional and amateur paleontologists alike. In this article, I will discuss what makes these rocks so special, highlight some of major avenues of research conducted in this region, and provide an overview of my past, present, and future research in the Cincinnatian.

A Long Legacy of Research

Despite the fact that numerous books, official field guides, and hundreds of journal articles have been written about the Cincinnatian, this area continues to be a rich proving ground for many different kinds of studies. Because the rocks are so well exposed (Figure 1) and contain abundant, exceptionally preserved fossils, this region is perfect for testing paleontological hypotheses. Formal study of these rocks began as early as the mid-19th century (for a detailed account of the history of paleontology in this region, see Meyer and Davis, 2009) and many of the most influential geologists and paleontologists in the late 1800's and early 1900's were known to have spent time studying the rocks in the Cincinnati area. More than a few prominent paleontologists (notably Charles Schuchert, and E.O. Ulrich) began their careers as a part of the Cincinnati School, laying the foundation for paleontological study by students, amateurs, and professionals.

Broadly speaking, the paleontology of the type Cincinnatian consists of communities of tropical marine organisms, including but not limited to brachiopods, crinoids, trilobites, bryozoans, snails, nautiloids, and clams. During the Ordovician, North America was oriented such that the Cincinnati Arch region was in the southern hemisphere and at a latitude of approximately 20° south. The fossils preserved here hail from a range of surroundings, from shallow high-energy ocean environments, to deeper water, muddy settings. This difference in environments is attributed in large part to a change in water depth. The sea floor in this region gently sloped from the shallow water in the southeast part (Figure 2) of the region to the deepest part of the region to the northwest. Many researchers have focused their attention on changes in the presence, absence and variation in the abundance of fossil communities, studying how the fauna changes according to variation in water depth, both across the region but also stratigraphically through the Cincinnatian Series (Bulinski, 2007; Holland et al. 2001, 2000; Miller et al., 2001; Webber, 2002).

Figure 1: Example of an exposure of Cincinnatian rock along the AA Highway in Kentucky. Outcrops of Cincinnatian rock are extensive throughout the region, providing excellent opportunities for research and collecting.

The ability to distinguish different fossil communities paleoecologically through space and time is one of the reasons why these rocks have been frequently used as a test case for studying fine-scale paleobiological patterns. The Cincinnatian fossil record is of high enough quality to pick up signatures of faunal patchiness, or variation in fossil composition at the scale of a single bedding plane (Holland, 2005; Webber, 2005). The fine stratigraphic scale has also been used to investigate patterns in morphological change and disparity of crinoids (Deline, 2009; Meyer et al., 2002), trilobites (Webber and Hunda, 2009; Hunda, 2009) and bryozoans (Pachut and Fisherkeller, 2002) among other fossil groups.

Beyond the analysis of the paleoecological character of the Cincinnatian itself, these rocks have been used to test broader ideas. For example, a study by Patzkowsky and Holland (1997) used brachiopod faunas from the Middle and Upper Ordovician of the Cincinnati Arch region to test the idea of coordinated stasis (Brett and Baird 1995). Coordinated stasis is a concept describing periods of relative quiescence in the fossil record with little ecological change, separated by short phases of biotic turnover. Patzkowsky and Holland (2007, 1996) also used the Cincinnatian to investigate patterns of migration and biotic invasion which was a phenomenon known to occur throughout the fossil record but it is difficult to study the dynamics of such an occurrence without a very high quality fossil record. The extensive exposures and exceptional preservation of the Cincinnatian makes for excellent proving ground for studying this phenomenon.

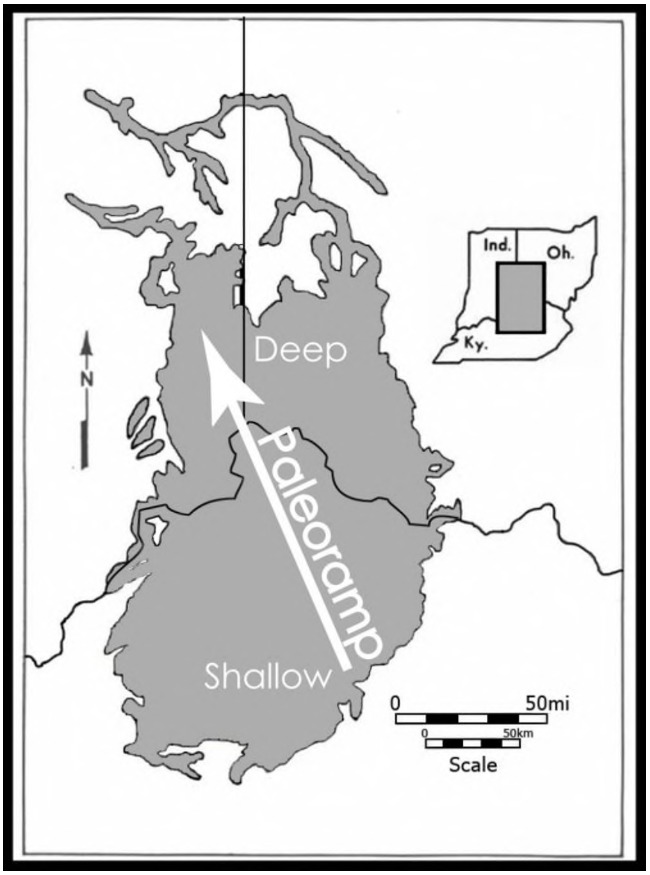

Figure 2: A map of the area where the Cincinnatian series are exposed at the surface in the tri-state region of Ohio, Indiana and Kentucky. The arrow indicates the change in water depth during the late Ordovician.

The geology of the Cincinnatian has also been extensively studied, especially noting how the lithology of the rocks change through time and throughout the region a function of changing water depth, the influence of hurricane-like storm activity, and changes in sediment production (Tobin, 1982; Jennette, 1986; Holland, 1993; Jennette and Pryor, 1993; Holland and Patzkowsky, 1996; Brett and Algeo, 2001; Holland et al., 2001). The type of geology that relates to the study of rock layers with respect to such variables is known as sequence stratigraphy. Several researchers have greatly advanced our understanding of both how the rocks were deposited, and how sequence stratigraphy relates to the paleoecological patterns that are observed throughout the region (e.g., McLaughlin et al., 2008, 2004; Brett et al., 2008; Brett and Algeo, 2001; Holland, 1993). For anyone interested in learning more about the stratigraphy of the Cincinnatian, I recommend a new book published in 2008 by the Cincinnati Museum Center entitled *Stratigraphic Renaissance in the Cincinnati Arch: Implications for Upper Ordovician Paleontology and Paleoecology*.

My Past, Current and Future Research in the Cincinnatian

I can attribute my career in paleontology, in large part, to these rocks. As an undergraduate student, my first introduction to field paleontology was a result of a field trip in 2001 led by Dr. Mark Patzkowsky from Penn State University as a part of our geobiology class. We packed into a 15-passenger van and drove the nearly seven hours to have the opportunity to study the famously fossiliferous strata and do some collecting. At that point in my studies I was unsure which kind of geology to pursue as a career, but after seeing these massive exposures of gray rocks packed with fossils (and filling a duffle bag full to take home with me), I was sold. I was going to be a paleontologist.

My love for the type Cincinnatian did not end with this field trip. I applied and was accepted to graduate school at the University of Cincinnati in 2002. I spent the next six years of my life working on my doctorate and developed a dissertation topic working with the Cincinnatian. I am now on the other side of graduate school, as a professor in Louisville, Kentucky, close enough to the Cincinnatian to take my own students there on day-long field trips. I consider myself very lucky to have started my career in a very paleontologically rich part of the country.

Past Research

One theme of my dissertation research was assessment of the relationship among biodiversity patterns at multiple geographic and environmental scales (Bulinski, 2007). For this research I collected a high-resolution dataset assembled from bulk samples from the lowest part of the Cincinnatian (Figure 3), a portion referred to as the Fulton submember of the Kope Formation from southern Ohio and northern Kentucky. Initially, I analyzed the paleoecological signature of fossil assemblages at the smallest scale, that of individual bulk samples, through which I was able to target directly the two primary components of fossil diversity, *richness*, the number of different kinds of organisms sampled, and *evenness*, which describes the relative numbers of each kind of organism. Using multivariate analytical techniques such as Detrended Correspondence Analysis, a method that arranges samples according to the similarity and differences among the relative abundance of fossil taxa, I was able to recognize ecological variation that correlated with the changes in water depth through the region as well as variation in lithological character. I also used these data to test the behavior of an evenness metric, another example of how the fossil communities of the Cincinnatian are useful for testing paleontological hypotheses and methodologies.

Another portion of my dissertation focused on ecological variation in the Cincinnatian as a function of geographic area. In this part of my study I was particularly interested in how rare fossils are distributed within the entire region (Bulinski, 2008). Much of the species richness within communities comes from uncommon or rare taxa, though within many paleontological analyses, rare taxa are often omitted or ignored because they are not perceived to control overarching paleoecological patterns but, rather, are thought to introduce background noise to analyses. Nevertheless, despite the sampling issues that affect the recovery and distribution of rare taxa within communities, they may reveal important ecological signals because numerically uncommon or geographically restricted genera are often considered to be more limited in their tolerance for different environmental variables. For this reason, rare taxa may be the most sensitive to climatic change, habitat disturbance, and changes in the distribution of diversity through time.

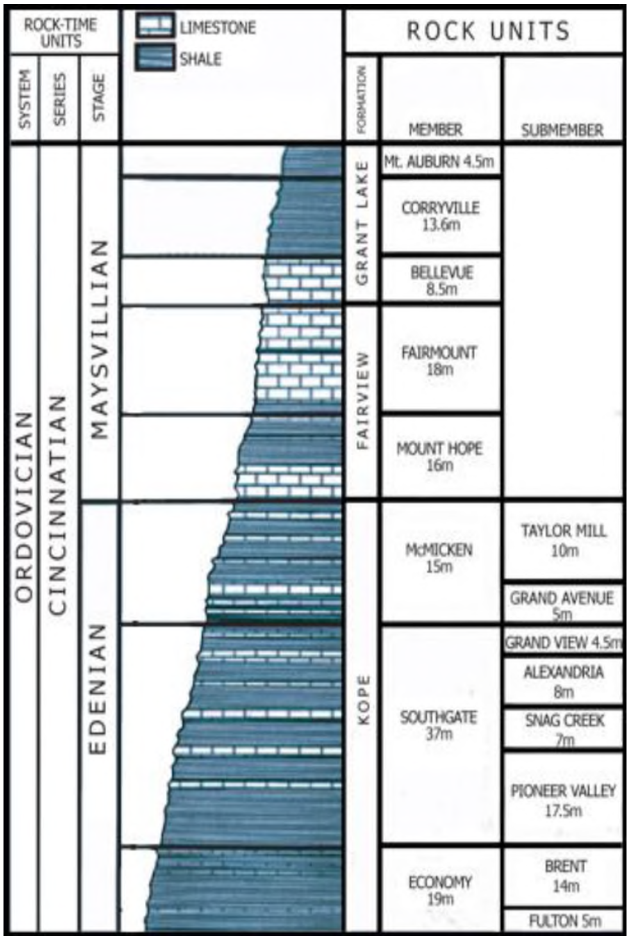

Figure 3: A stratigraphic section indicating the different formations, members and submembers of the Kope Formation.

Because of the extensive amount of data available from the many studies of the Cincinnatian, I was able to compile a large database of fossil occurrences from every accessible journal article, masters' thesis, doctoral dissertation, and professional geological publication that focused on the geology and paleoecology of the Kope Formation and equivalent strata in the tri-state region of Ohio, Kentucky and Indiana. I combined these data with data from my own bulk samples from the Fulton submember of the Kope Formation. These data were assembled into a database of genus-level fossil occurrences and locality information including latitude and longitude coordinates. In total, the dataset consisted of 141 unique genera represented by 9,826 occurrences among 2,337 collections sourced from 52 localities.

To study the behavior of rare taxa through the region, I divided up the area where Cincinnatian rocks were exposed at the surface into an array of geographic gridding schemes (Figure 4). The maximum and minimum coordinates of fossil collections included in the study (39.83° N, 37.59° N, 83.75° W, and 85.02° W) were used as boundaries for framing the study area into a rectangular grid that was subsequently divided into smaller geographic areas of equal size. In total, five binning schemes were employed here: vertical halves (divided by the longitudinal midpoint of the study area), horizontal halves (divided by the latitudinal midpoint of the study area), quarters, ninths, and sixteenths. These geographic areas served as different sampling "bins". If a fossil collection was found within the latitude and longitude coordinates for that bin it was included in the analysis. In this way, I was able to compare how different components of biodiversity, like rarity and richness, varied across the region from bin to bin, and also as a function of geographic scale (i.e., comparing bins that comprise a quarter of the field area to those that comprise a 16th).

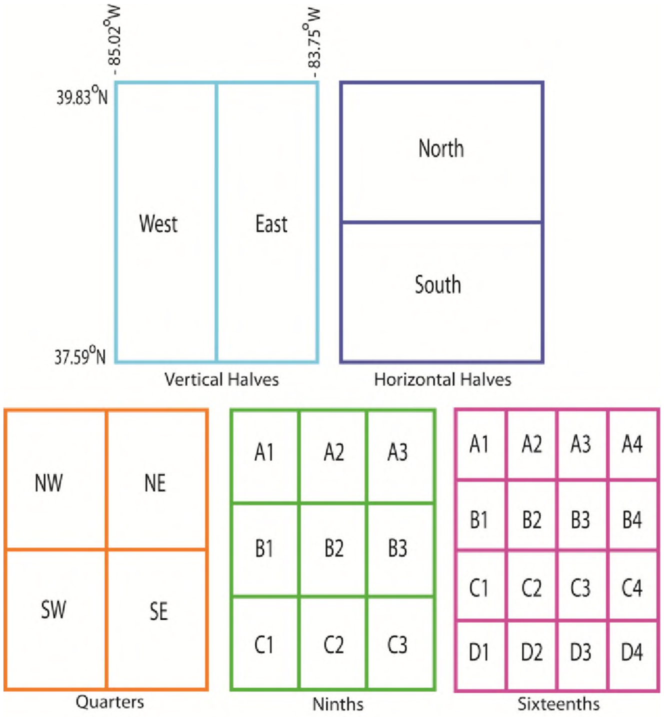

Figure 4: Binning scheme used to divide fossil data from the Cincinnatian into a variety of different geographic areas for analysis. Boundaries between bins were determined by latitude and longitude.

I was able to demonstrate that richness varied directly as a function of geographic area, depicting a clear positive relationship between richness and geographic sampling size, which was not unexpected, as a greater amount of diversity is expected when investigating larger habitat area. This relationship is known as the species-area effect. A more significant result from this study is that the proportion of rare fossils did not increase with increasing geographic bin size. It appears as though the amount of rare taxa found within a region varies independently of geographic area.

Current Research

Since the Cincinnatian is luckily still very accessible to myself and my students, I have continued to pursue research in this region. My current research focuses again on properties of biodiversity but this time focusing on lithological properties and stratigraphic scale. For this new research, we collected a total of 108 bulk limestone, siltstone and shale samples from four localities in the Pioneer Valley member of the Kope Formation in northern Kentucky. I chose this time to focus on the effects of lithology on biodiversity because in my dissertation research I observed variation in paleoecological structure as a function of lithology. Secondarily, aside from studies that focus on exceptionally preserved fossils within shale deposits, most studies of diversity in the Cincinnatian involve the more easily sampled limestone and siltstone beds. The shale horizons, often regarded as largely barren, are frequently left unsampled despite their delicately-preserved and rare faunal elements. The shale horizons are somewhat more difficult to study. For this research we filled gallon sized bags with the shale which is a soft rock and easily falls apart when removed from the outcrop (Figure 5). My student and I carefully picked through each bag of shale, splitting apart layers and identifying the fossil fragments to generate our data. The effort involved in sampling shale is one of the main reasons why it is relatively undersampled in studies of the Cincinnatian. Interestingly, in our ongoing research, we found that the shale was no less diverse than the limestone and siltstone samples, though one must process a much larger volume of rock to yield comparable amounts of richness among the different rock types (Bulinski,et al., 2009).

Figure 5: Example of a shale bulk sample from the Kope Formation. Shale is a soft mudstone and splits apart easily making it difficult to sample and conduct fossil counts when compared to limestone.

Another avenue of our current research will be to parse the sampled fossil communities into an array of temporal intervals analogous to the geographic gridding schemes used in my previous work. Since some studies seek to characterize biodiversity of a region by amalgamating data from a locality or several localities to get an overall assessment of richness, we would investigate the way in which richness, evenness and proportional rarity varies according to stratigraphic scale (Bulinski and Johnston, 2010). By combining strata into a number of binning schemes (e.g., bed-level, multiple beds, entire outcrop) it may be possible to determine how much of the variation in diversity is lost through this process of amalgamation. This study could be used to calibrate or make comparisons among future paleoecological studies that seek to model how biodiversity has changed over long intervals of geological time.

Conclusion

The type Cincinnatian has played a essential role in the development of many important paleontological studies over the last century and a half. Without these rocks we certainly would not know as much about shallow marine communities from the Ordovician, or as much about how paleocommunities are organized in general. I have no doubt that the Cincinnatian will continue to bear fruitful research for many years to come. These rocks are a treasured natural laboratory for researchers, amateurs, and students of paleontology. I owe my career to the Cincinnatian and I continue to bring my own students to experience paleontological field work and to learn about the paleoecology of the Ordovician.

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The Platteville Molluscan Fauna

John A. Catalani

Introduction

The Platteville Group of the Upper Ordovician is estimated to have lasted for only 1-2 million years. In this time, an incredibly diverse molluscan fauna evolved that was associated with the normal Ordovician taxa such as brachiopods, trilobites, and echinoderms. Analysis of this fauna indicates that the nautiloids exploded in diversity to fill virtually every food-gathering niche available. In terms of nautiloid evolution it appears that the Platteville fauna represents the acme of nautiloid diversity. The Platteville Group, along with the Galena Group, traditionally was placed in the Middle Ordovician Champlainian Series. An intense study of Ordovician rocks and fossils in the last 20 years or so has reassigned many of the units to better correlate with British as well as Global stratigraphy. The result is the placement of both Groups into the Upper Ordovician with the upper two Formations of the Galena Group correlated with the lower Cincinnatian strata and the renaming of several stage names (see Fig. 1).

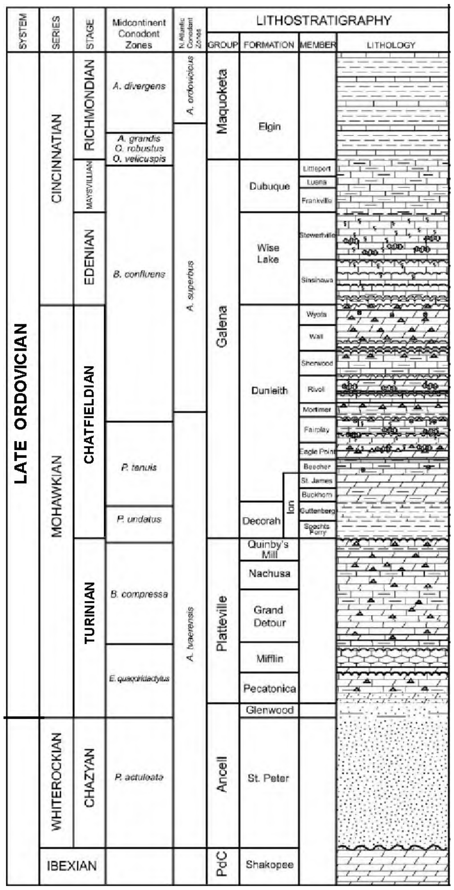

Fig. 1. Chart of the Late (Upper) Ordovician of the Upper Mississippi Valley Region. The "Champlainian" Series is now called the Mohawkian Series. The upper two formations of the Galena Group have been re-assigned to the Cincinnatian Series. (Modified from Chetel *et al.*, 2005, *Sedimentary Geology*.)

The Nautiloid Fauna

The formations of the Platteville Group in the area in which I collect (northern Illinois and southern Wisconsin east of the Wisconsin Arch) consist almost exclusively of dolostones. In the dolostone facies, the fauna is dominated by a large molluscan assemblage contained within the beds. The limestone facies, mostly found west of the Wisconsin Arch, consists of a brachiopod-dominated faunal assemblage preserved mostly on bedding planes. The stratigraphy of the Platteville Group as defined in Illinois consists of five formations. The most fossiliferous of these formations are the Mifflin and the Grand Detour (formations two and three as one travels up section). The Mifflin is not subdivided into members but the Grand Detour has three members two of which are very fossiliferous: the Cowen, the basal member, and the Forreston, the uppermost member.

The molluscan fauna of these rock units is abundant, diverse, and well preserved. In the dolostone facies, most of the body fossils are preserved as dolomitic steinkerns (internal molds) with the outer shell missing. Many of those not familiar with these well-preserved steinkerns dismiss them as simply “mud filled tubes”--nothing could be further from the truth. The internal molds typically preserve morphologic structures in excellent detail facilitating specimen identification to the species level. And occasionally, internal features of the nautiloids, specifically septal necks and connecting rings, are visible when specimens are sectioned. Additionally, the weathered siphuncles of actinocerids often show the endosiphuncular canals.

The diversity of the nautiloids in Platteville rocks is truly amazing. Not counting the new taxa I have found (approximately 5 new genera and 12 new species), I have collected 49 species in 27 genera representing 9 of the 10 nautiloid orders present during the Ordovician (although recent work has placed the number of orders in a state of flux). When the nautiloid taxa contained in the three rock units are tallied separately, one finds that diversity increases through time. In the Mifflin Formation, 30 species in 22 genera are found. In Grand Detour rocks, the Cowen Member contains 38 species in 26 genera and the Forreston Member contains 43 species in 26 genera. Possible reasons for this increase include immigrants from other areas, expanded ecological niches, speciation events, or, as seems most likely, a combination of these factors.

One of the most persistent assumptions about the Ordovician nautiloid fauna is that the majority of shells are straight with a circular cross-section. This is a false assumption. The order that contains the most diverse nautiloid taxa is the Oncocerida. In this order, most of the members display a small, curved, breviconic conch with the siphuncle exposed (in steinkerns) along the outer edge. The Oncocerida comprises approximately 28% of the Platteville genera and 43% of the species. For example, one Oncocerid genus, *Beloitoceras*, contains 9 species and one that is unpublished (see Fig. 2). Members of the Oncocerida are also the most commonly found specimens particularly in the Grand Detour.

Fig. 2. The nine published species of *Beloitoceras*. From left: *B. pandion*, *B. janesvillense*, *B. plebeium*, *B. lycum*, *B. isodorus*, *B. houghtoni*, *B. carveri*, *B. norwoodi*, *B. huronense*.

Another assumption made concerning Nautiloids is that they were all active predators. Again, not true. It is fairly obvious that such a high diversity of shell forms and buoyancy solutions indicates that these guys must have occupied many niches and utilized many lifestyles. Although predation is the dominant lifestyle for today's coleoid cephalopods (*Nautilus* is mainly a scavenger), the number of body forms is limited. Squids, octopods, and cuttlefish each settled on a basic body plan with little variation. Platteville nautiloids, however, are classified into nine orders and displayed a variety of conch shapes (see Fig. 3) ranging from straight to various degrees of curvature to open coiling to closed coiling to forms that truncated juvenile shells to reduce weight. Additionally, scattered among these types were various, or lack of, solutions to neutral buoyancy ranging from small and large forms with small chamber volumes that were confined to the substrate to true neutrally buoyant forms that used water or mineral ballast and were able to navigate the water column to those with large chamber volumes and no counterweight deposits floating in the plankton. Therefore, although we are clearly speculating, it seems almost certain that these creatures assumed many ecological roles: active predators, ambush predators, scavengers, grazers, and filter feeders. Besides, with this much diversity, competition would have been fierce had they all been active predators. Such competition would have very quickly decreased the diversity leaving only a few extremely adapted forms. The evidence, however, points to the opposite.

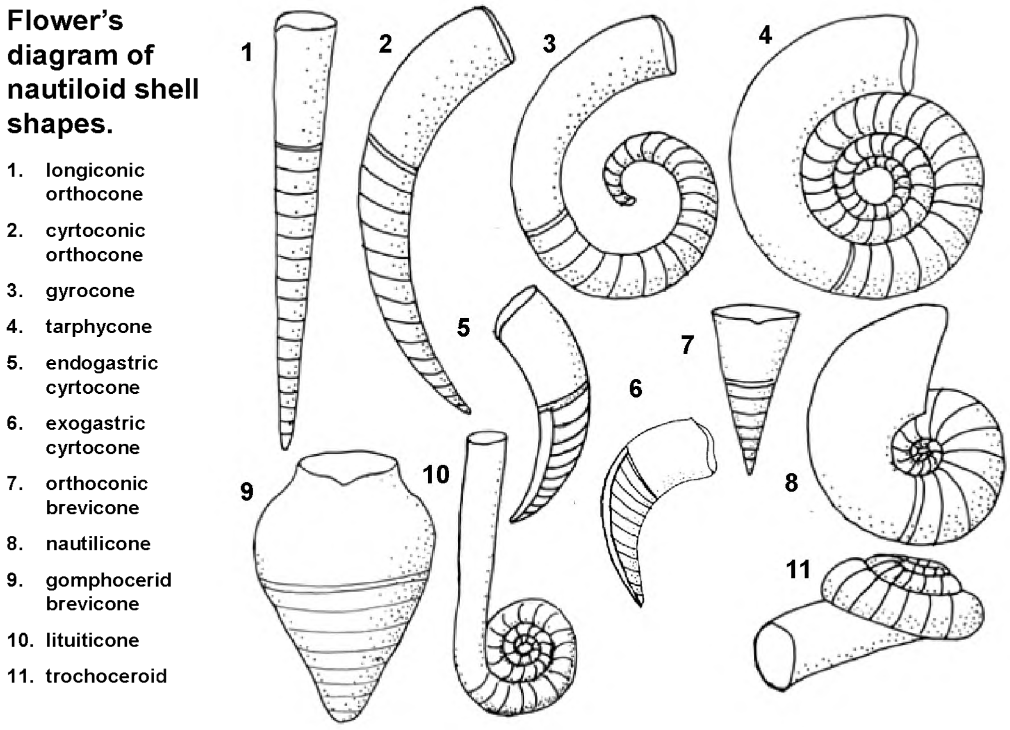

Fig. 3. Nautiloid shell shapes. (Modified from Flower, 1964, Figure 2.)

The Other Molluscs

Nautiloid specimens are not the only fossils that display morphologic features. The steinkerns of the other molluscs display such features as well. Pelecypods, for example, often preserve features such as adductor muscle scars, taxodont teeth, and the pallial line showing the position and extent of the radial pallial muscles. Such features would not be accessible on body fossils with the outer shell intact (Fig. 4). Internal molds of gastropods, on the other hand, show little detail. Two gastropods, *Lophospira serrulata* and *L. (Eunema) helicteres*, are virtually indistinguishable when only their steinkerns are compared. However, for body fossils with the outer shell preserved (see limestone discussion below), surface ornamentation makes identification of the two species very easy. In fact, it was the use of latex impressions of the external molds that revealed this ornamentation and facilitated the recognition of the original five Platteville species of *Lophospira* (Tofel and Bretsky, 1987).

Fig. 4. Comparison of steinkern (left) and shelled-fossil (right) of *Cleionychia lamellosa* both from the Mifflin Formation of Lee County, Illinois. The steinkern clearly shows a circular adductor muscle scar

From my evaluation of Platteville non-nautiloid mollusc diversity, I have identified 32 species in 22 genera of gastropods and 17 species in 11 genera of pelecypods. There are several interesting aspects of these other Platteville molluscs. First, from a list of the taxa present, it is apparent that the diversity of gastropods and pelecypods is much less than that of the nautiloids. Since I have made an effort to collect the entire fauna, collecting bias was, hopefully, minimized. It seems reasonable to assume that the morphological sophistication of the nautiloids, particularly neutral buoyancy, allowed them to take advantage of environments and lifestyles unavailable to the other molluscs. Second, there does not appear to be any change in diversity through time. In fact, the diversity of gastropods and pelecypods is almost identical in the two formations. The Mifflin diversity is actually greater than that of the Grand Detour by one genus and three species of gastropod and two species of pelecypod. Not big numbers but definitely not the pattern shown by nautiloid diversity.

Another aspect centers on a controversial group of gastropods collectively referred to as bellerophonts. These gastropods consist of planispiral (symmetrically coiled) univalved (lacking an operculum) shells. The controversy involves the class assignment of these forms to either the gastropods or the monoplacophorans (monos, for short) or both. Features used by workers in defense of these assignments include the number, position, arrangement, and symmetry of retractor muscles indicated by muscle scars preserved on internal molds. Unfortunately, retractor muscle arrangement is unknown for most bellerophonts. On the overall use of muscle scars in determining the taxonomic position of the bellerophonts, Wahlman (1992, p. 53) concludes that, since there is overlap in muscle patterns between gastropods and monos, these features "cannot be used exclusively as a reliable criterion in determining the class-level assignment of bilaterally symmetrical molluscan univalves". Wahlman (p. 58) further concludes that most bellerophonts were indeed gastropods and that "so far, only sinuate bellerophontiform taxa have been proven to be monoplacophorans". In terms of the Platteville taxa, the genus *Sinuites* is the only bellerophont that would be considered a mono. This controversy is far from settled and "a great deal more detailed morphological analysis is needed to clarify the phylogenetic role of bellerophontaceans" (Wahlman, p. 58).

True monos (in the traditional sense) display a very low diversity in the Platteville but are fairly abundant mainly in Mifflin rocks. However, they show an interesting trend: a dramatic increase in size through time. Monos collected in Mifflin rocks are usually thumbnail-size or smaller while those in Grand Detour rocks are comparative giants, up to 6 cm in height (see Fig. 5). Although the systematics of Platteville monos is provisional at best, I have been able to distinguish four forms in Mifflin strata and three, possibly four, forms in Grand Detour rocks, not counting *Sinuites*. It appears that only two forms crossed the Mifflin/Grand Detour boundary.

Fig. 5. Size comparison of typical Mifflin Formation monoplacophoran (left) and Grand Detour Formation monoplacophoran (right).

Pelecypod preservation in Mifflin rocks is also quite interesting. As with the other molluscs, pelecypods are usually randomly dispersed in the large "pockets" in which the fossils occur. Occasionally, however, pelecypods are found packed in a relatively small volume with few, if any, other taxa present. They occur in rocks of both facies and they are so closely packed that I refer to such deposits as "clam coquinas". The vast majority of the individual specimens are relatively small examples of the single genus *Vanuxemia* and the volume of these coquinas rarely exceeds several cubic feet. Often, when preserved in dolostone, most of the body fossils in these coquinas are dissolved leaving empty cavities with only sporadic steinkerns present. Rarely, thin-bedded, diverse coquinas consisting of all classes of Platteville molluscs have also been recovered.

Other, more obscure molluscs are present in Platteville rocks including two species of rostroconchs, three recently described species of polyplacophorans (Pojeta et al., 2003; Hoare and Pojeta, 2006), and one type of hyolithid (considered by some a separate phylum).

A Limestone Anomaly

Although, as stated above, dolostone dominates Platteville exposures in the northern Illinois/southern Wisconsin "outcrop" area, we are fortunate that there is an anomalous occurrence of the limestone facies of the Mifflin Formation exposed in a quarry located geographically in the middle (more or less) of the dolostone exposures. This fortuitous occurrence permits us to compare the faunas of the two facies. Additionally, besides the normal bedding planes crowded with fossils, this site provides us with beautifully preserved body fossils complete with outer shells displaying surface ornamentation that weather out individually--a veritable Lagerstätte (see Fig. 6). Unfortunately, despite the presence of the outer shell and the often spectacular ornamentation displayed by these fossils (such as the *Lophospira* species mentioned above), internal structures used to classify and identify specimens are usually lacking since many of the fossils, particularly the nautiloids, are filled with calcite spar. Because of this, I have not been able to identify many of the nautiloid specimens to the species level. The limestone fossils have given me a renewed appreciation of the nautiloid steinkerns that I had been collecting years before the discovery of the limestone exposure. Although the limestone specimens are "eye candy" for collectors, the real science of systematics and determination of the new nautiloid taxa was accomplished using the internal molds.

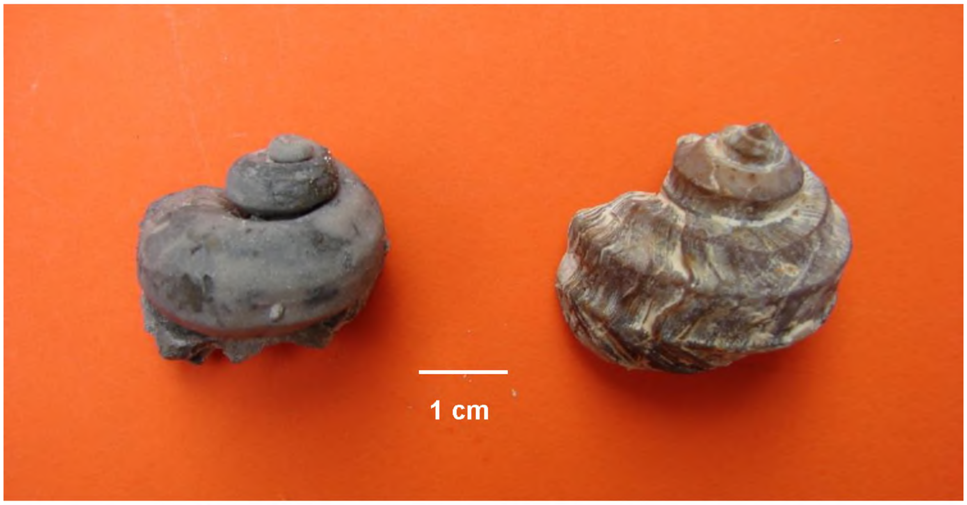

Fig. 6. Two specimens of *Trochonema beloitense* from Lee County, Illinois. The left is from the dolostone facies and the right is from the limestone facies. Note the ornamentation on the limestone specimen.

An analysis of the taxa contained in the limestone facies and a comparison with the fauna of the dolostone facies has resulted in some surprising conclusions. First, the diversity of the Mifflin fauna at this single locality is truly amazing: 128 species in 102 genera in 9 (more or less) phyla. Second, a diversity pattern very different from that of the dolostone fauna emerges: gastropods are more diverse than nautiloids. There are 38 species in 25 genera of gastropods and 30 species in 23 genera of nautiloids. Additionally, there are 13 species in 10 genera of pelecypods. Dolostone exposures of the Mifflin have yielded 27 species in 19 genera of gastropods and 13 species in 9 genera of pelecypods. Therefore, the limestone diversity appears to be much higher for gastropods, about the same for pelecypods, and lower for nautiloids (from numbers given earlier). However, it must be understood that the dolostone numbers are compiled using all exposures while the limestone fauna is represented by only the one site. One attempt to address the faunal differences between the two facies was a paper by Byers and Gavlin (1979). This study, however, was based on exposures west of the area I have been investigating and on the west flank of the Wisconsin Arch. Unfortunately, from the distribution and abundance of taxa presented in their Tables 1 and 2, it appears their “dolomite facies” did not actually represent true dolostone sections. Therefore, most of their conclusions would not apply to the situation I have described above.

Conclusion

I marvel at the diversity of molluscs preserved in Platteville rocks. A molluscan diversity of 20 to 30 species at a single locality is not uncommon and one locality exposing Forreston rocks contains around 65 species. Topping even this, however, is the limestone locality that has yielded almost 90 species of molluscs, 68% of the entire fauna. The differences between the molluscs found in the true dolostone facies and those collected in the limestone facies deserve closer attention, as does the more basic conundrum of the occurrence of a limestone exposure surrounded by dolostone.

Unfortunately, further research is hampered by the present liability mindset that has resulted in a lack of access to many of the quarries exposing significant sections. We may be forced to rely on a reassessment of existing collections, which reinforces the importance of collectors arranging to archive their fossils with recognized repositories. I consider myself fortunate to have been able to amass my collection of Platteville material during a time of relatively easy access to collecting sites--a collection that I doubt could be assembled today.

Further Reading

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Mifflin Molluscan Fauna Dolostone Facies

Nautiloids:
- Actinoceras beloitense
- Actinoceras janesvillense
- Gonioceras occidentale
- Cartersoceras shideleri
- Cyrtocerina crenulata
- Cameroceras multicameratum
- Endoceras annulatum
- Allumettoceras planodorsatum
- Beloitoceras carveri
- Beloitoceras janesvillense
- Beloitoceras lycum
- Beloitoceras norwoodi
- Beloitoceras pandion
- Beloitoceras aff. C. huronense
- Cyrtorizoceras aff. C. minneapolis
- Oncoceras tetreauvillense
- Tripteroceras planoconvexum
- Zittelloceras beloitense
- Zittelloceras clarkeanum
- Anaspyroceras cylindratum
- Anaspyroceras lesueuri
- Whitfieldoceras clarkei
- Whitfieldoceras mumiaforme
- Gorbyoceras sp.
- Monomuchites annularis
- Proteoceras spp.
- Centrocyrtoceras annulatum
- Centrocyrtoceras sp.
- Chidleyenoceras cf. C. chidleyense
- Plectoceras occidentale
- Plectoceras robertsoni
- Trocholites sp.
- Ulrichoceras beloitense

Gastropods:
- Clathrospira subconica
- Ecculiomphalus beloitense
- Ecculiomphalus undulatus
- Eotomaria supracingulata
- Eotomaria vicinus
- Fusispira spicula
- Gyronema duplicatum
- Holopea ampla
- Holopea insignis
- Hormotoma gracilis
- Liospira vitruvia
- Lophospira milleri
- Lophospira perangulata
- Lophospira serrulata
- L. (Eunema) helicteres
- Maclurites bigsbyi
- Phragmolites triangularis
- Pterotheca attenuata
- Raphistoma peracutum
- Salpingostoma buelli
- Strophostylus textilus
- Subulites beloitensis
- Subulites dixonensis
- Tetranota sexcarinata
- Tetranota wisconsinensis
- Trochonema beloitense
- Trochonema umbilicata
- Sinuites rectangularis

Pelecypods:
- Cleionychia lamellosa
- Cleionychia sp.
- Ctenodonta nasuta
- Ctenodonta sp.
- Cyrtodonta janesvillensis
- Cyrtodonta persimilis
- Cyrtodontula sp.
- Deceptrix sp.
- Endodesma compressum
- Vanuxemia dixonensis
- Vanuxemia rotundata
- Whiteavesia modioliformis

Grand Detour Molluscan Fauna Dolostone Facies

Nautiloids:

- Actinoceras beloitense
- Actinoceras bigsbyi
- Actinoceras janesvillense
- Gonioceras kayi
- Gonioceras occidentale
- Cartersoceras shideleri
- Cyrtocerina crenulata
- Cameroceras multicameratum
- Cameroceras aff. C. alternatum
- Endoceras annulatum
- Allumettoceras planodorsatum
- Allumettoceras aff. p. carletonense
- Beloitoceras carveri
- Beloitoceras janesvillense
- Beloitoceras lycum
- Beloitoceras norwoodi
- Beloitoceras pandion
- Beloitoceras plebeium
- Beloitoceras aff. C. houghtoni
- Beloitoceras aff. C. huronense
- Beloitoceras aff. C. isodorus
- Cyrtorizoceras aff. C. minneapolis
- Loganoceras cf. L. regulare
- Manitoulinoceras neleum
- Oncoceras abruptum
- Oncoceras collinsi
- Oncoceras tetreauvillense
- Richardsonoceras beloitense
- Richardsonoceras simplex
- Richardsonoceras aff. R. romingeri
- Richardsonoceras aff. R. scofieldi
- Tripteroceras oweni
- Tripteroceras planoconvexum
- Zittelloceras beloitense
- Zittelloceras clarkeanum
- Anaspyroceras cylindratum
- Anaspyroceras lesueuri
- Metaspyroceras sp.
- Whitfieldoceras mumiaforme
- Gorbyoceras sp.
- Monomuchites annularis
- Proteoceras spp.
- Centrocyrtoceras annulatum
- Centrocyrtoceras sp.
- Chidleyenoceras cf. C. chidleyense
- Plectoceras occidentale
- Plectoceras robertsoni
- Trocholites sp.
- Redpathoceras sp.
- Ulrichoceras beloitense

Gastropods:

- Clathrospira subconica
- Ecculiomphalus undulatus
- Ectomaria prisca
- Eotomaria supracingulata
- Gyronema duplicatum
- Helicotoma umbilicata
- Holopea ampla
- Holopea insignis
- Holopea rotunda
- Hormotoma gracilis
- Liospira vitruvia
- Lophospira milleri
- Lophospira perangulata
- Lophospira serrulata
- L. (Eunema) helicteres
- Maclurites bigsbyi
- Omospira laticincta
- Phragmolites fimbriatus
- Pterotheca attenuata
- Salpingostoma buelli
- Subulites beloitensis
- Subulites dixonensis
- Tetranota sexcarinata
- Trochonema beloitense
- Trochonema niota
- Sinuites rectangularis

Pelecypods:

- Aristerella nitidula
- Cleionychia lamellosa
- Cleionychia sp.
- Ctenodonta nasuta
- Cyrtodonta janesvillensis
- Cyrtodonta sp.
- Cyrtodontula sp.
- Endodesma compressum
- Tancrediopsis gibberula
- Vanuxemia suberecta
- Whiteavesia modioliformis

"Always Serious About Cephalopods"

James E. Preslicka

Ahhh, the Ordovician - a time dear to the hearts of all Nautiloid Cephalopod devotees! The time when the Nautiloids ruled the high seas! What could be better than giant Endocerids prowling the waters eating anything they wanted to, whilst myriad shapes and sizes of smaller cephalopods swam about below them? Eventually along came those doggoned jawed fish who took over many of the ecological niches once filled by cephalopods, and over time those early vertebrates gave rise to...us - ok, maybe that fish takeover thing wasn't such a bad occurrence after all!

Figure 1. An orthoconic (straight shelled) nautiloid (*Cameroceras*), feeding on a helpless gyroconic (loosely coiled) nautiloid, as a school of breviconic (bullet shaped) nautiloids swim by. From Wikimedia Commons.

Seriously now, the Ordovician holds a place near and dear to my own heart, and I was ecstatic when this topic was announced for Expo 32. More years ago than I now care to admit, I was a budding Geology student at the University of Iowa (I just can't bring myself to call the department "Geoscience" as UI does now). While there, I caught the cephalopod bug from one Dr. Brian F Glenister, now a UI Professor Emeritus. The title of this article was a saying of his. Anyhow, this cephalopod bug is of course terminal, there is no cure, and the only treatment is the continual collection of multitudes of cephalopod fossils!

I vividly remember asking him about a good collecting site to visit back in about 1992 I guess - it was to be my first fossil collecting trip with my old college buddy Doug Hanson. Dr. Glenister recommended a small stream cut exposure near Clermont, in northeast Iowa. It exposed rocks from the Upper Ordovician Maquoketa Formation. He knew the site to be rich in trilobite fossils, which we were mainly interested in at the time. However, within the first few minutes at this site, I spotted something that looked for all the world like a small piece of rebar - straight and heavily ribbed. Doug somehow managed to clamber up the steep slope and knock the thing down to me.

Figure 2. The author's *Spyroceras* (now called *Monomuchites*) *clermontense* specimen from the Elgin Beds of the Maquoketa Formation near Clermont, Iowa. Pocketknife is approx. 9.0cm for scale. Photo by the author.

Figure 3. This specimen of *Endoceras* is from the Elgin Beds of the Maquoketa Formation near Graf, Iowa. Pocketknife is approx. 9.0 cm for scale. Photo by the author.

That fossil was later identified as a *Spyroceras* (now known as *Monomuchites*) *clermontense*, a straight shelled nautiloid cephalopod. To this day I still have not found a larger or better preserved *S. clermontense*. Well, not to be outdone, Doug managed to find a large "*Cyclendoceras*" specimen (now referred back to the genus *Endoceras*) near the top of the exposure as we were getting ready to leave. We had to stand on a rickety and rotten old fence section which someone had dumped in the creek bed and stretched up just enough to reach the layer where the fossil was at. I can still recall how dead our arms were - it was quite cold, late fall I think. We had to hammer for extended periods with our arms above our head. They fell asleep and ached terribly, forcing us to take turns attempting to remove the fossil. It was worth every bit of the pain though. Doug found many more *Endoceras* specimens over the years, but none will be quite as special - or can lead to quite a story retelling as that first one still does.

Needless to say, we were hooked on cephalopods from that trip forward. Now, of course I will not turn down a trilobite or crinoid or especially an echinoid if one comes my way, but for me it is always, **always, always** about the **CEPHALOPODS**!! That first collecting trip interested me greatly in the Ordovician in general and the Maquoketa Formation in particular.

Figure 4. Panorama of the outcrop near Clermont, Iowa which exposes the Elgin Member of the Maquoketa Formation. Photos by Doug Hanson.

In Iowa, the Ordovician is comprised of 3 major suites of rocks - the Prairie Du Chien Dolomite, a Lower Ordovician unit, mostly non-fossiliferous. It is covered by the Saint Peter Sandstone, which is in turn overlain by what used to be referred to as the Champlanian Series rocks, which include the wonderfully fossiliferous Platteville & Galena Groups. The Maquoketa Formation lies above the Galena Group.

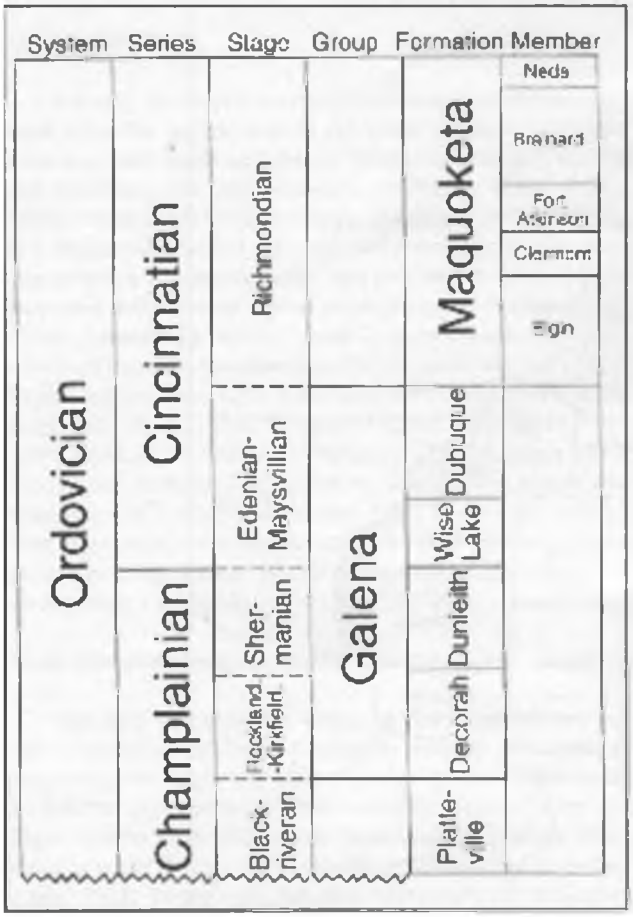

Figure 5. Partial Ordovician stratigraphic column showing the relative ages of the Platteville Formation (or Group in Illinois), Galena Group, and the Maquoketa Formation. From Raatz & Ludvigson 1996, p 146.

Geologists love to look for repeating cycles of sedimentary rock formation - Earth is such a relatively stable place that environmental conditions often change at very slow rates over extremely long periods of time. Things such as orbital cycles, slow movement of continents, and changing of sea currents all contribute to sea levels rising and falling over great periods of time. A sea level rise is called a Transgression, a drop is known as a Regression. One complete rise and fall is referred to as a marine cycle or Cyclothem.

The Maquoketa Formation contains 3 such complete cycles of sea level rise and fall: the Elgin, the Clermont - Fort Atkinson, and the Brainard Cycles; and part of a 4th: the heavily eroded Neda Cycle (Witzke & Heathcote 1997b). Interestingly each was apparently related at least in part to the advance and retreat of glaciers on the southern hemisphere super-continent of Gondwanaland. Sound familiar to today's climate change troubles? Of particular interest is the lowermost cycle in the Maquoketa, which is contained in the rocks of the Elgin Member.

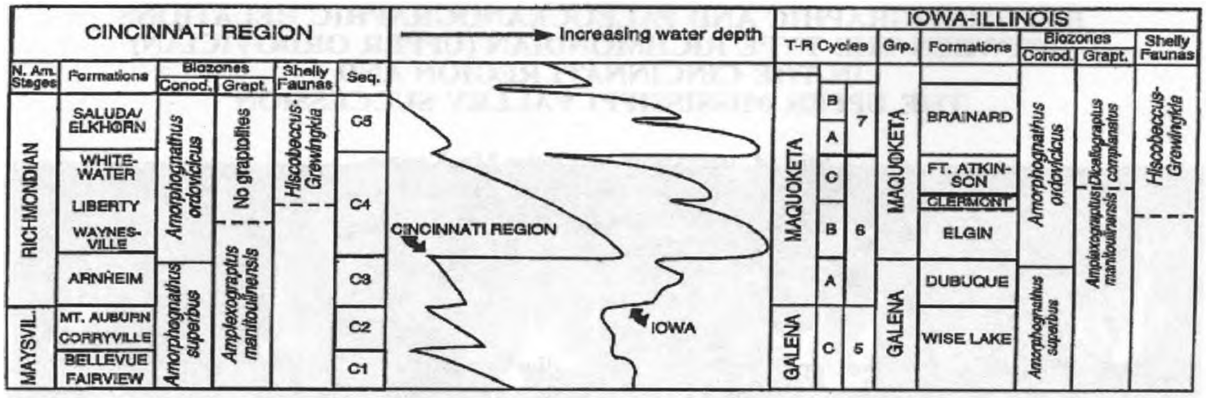

Figure 6. Upper Ordovician sea level curve. Note the sea level maximum coinciding with the base of the Elgin Member of the Maquoketa Formation. From Bergstrom & MacKenzie 2005, page 36.

A major sea level rise is recorded at the base of the Elgin, where very black shales overlie the top of the Dubuque Fm. These shales in places are actually a phosphorite. They tell us that the seaway in the central North American plate suddenly deepened at that formational boundary. The phosphate indicates that an upwelling current of cold anoxic (low oxygen), but nutrient rich water spilled up onto the shelf near what is now the Iowa-Illinois border (Witzke & Heathcote, 1997a).

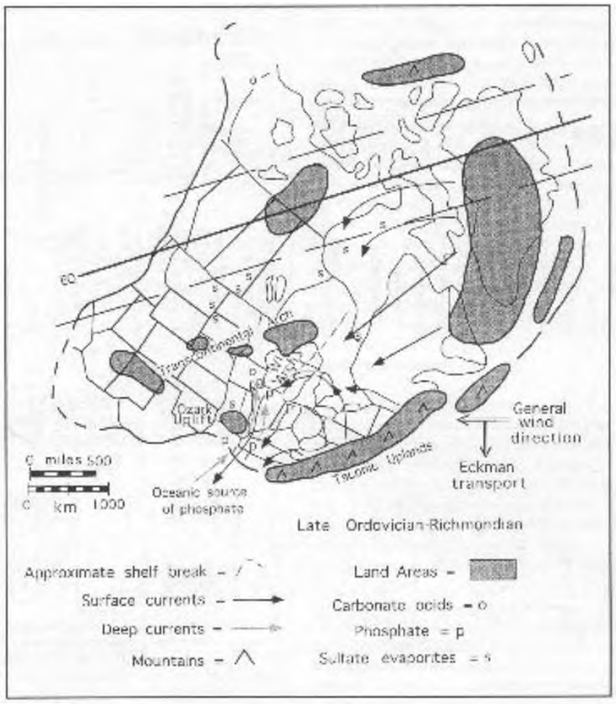

Figure 7. Upper Ordovician Paleogeographic map of the North American continental plate. Note position of the equator (EQ), the Taconic mountainous area, and seaway circulation/current patterns. From Raatz & Ludvigson 1996, page 148.

At the time the North American plate was crashing into the European plate, and this collision formed a mountain chain to the east near the modern day Appalachians, and a back side trough in what is now the east central US. This trough expanded and deepened as the continental collision continued, allowing sea water to intrude into the central mid-continent area. This sea was of moderate depth much of the Ordovician, but reached great depths during deposition of parts of the Maquoketa Formation. How do we know this? Why, because of the cephalopods of course!!

The inside of a cephalopod shell is divided into chambers by what are known as septa - little walls of aragonite secreted by the animal as it grew within its shell. The intersection of these chamber dividing septa with the inside wall of the shell is called the suture. Sutures tend to be simple in many Ordovician cephalopods, but can be complexly folded and fluted in more recent cephalopods such as ammonoids for instance.

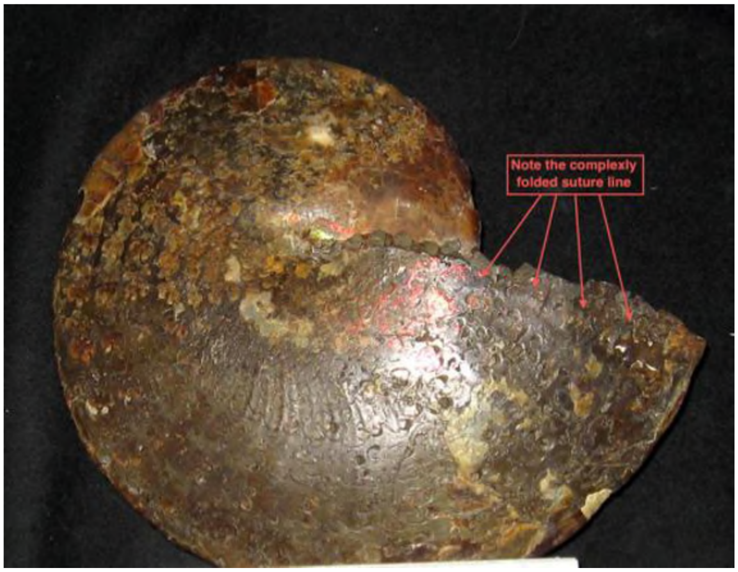

Figure 8. A specimen of one of the last widespread Late Cretaceous ammonoids - *Sphenodiscus*. Note the complexly folded suture line typical of many ammonoids, and compare it to the simple straight suture line in the representative Ordovician nautiloid *Oncoceras* (**Figure 9**). From Wikimedia Commons.

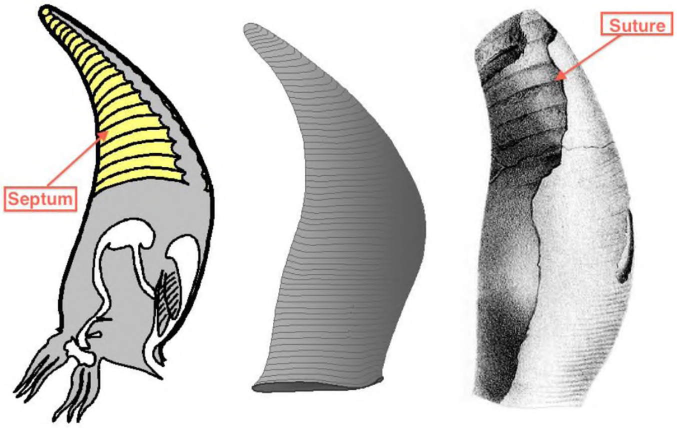

Figure 9. Diagram of the Ordovician nautiloid cephalopod *Oncoceras*. Note the relatively straight simple sutures made by the septa, compared with the complexly folded sutures in the ammonoid cephalopod *Sphenodiscus* (**Figure 8**). From Wikimedia Commons.

A world famous outcrop of the Elgin Beds of the Maquoketa Formation can be visited near the tiny burg of Graf in Dubuque County in eastern Iowa. Just north out of town, along a gravel road, there is an extensive exposure. At first glance it looks like any other ordinary sedimentary rock outcrop - interbedded soft shales and hard dolomite beds. Upon closer examination though, two very unusual layers jump out to greet your eyes. Two beds, separated by about a foot, contain countless numbers of the straight shelled nautiloid cephalopod *Isorthoceras sociale*; many of them "telescoped" one into the other.

Figure 10. Outcrop of the Elgin Member of the Maquoketa Formation near Graf, Iowa. Arrow marks approximate location of the *Isorthoceras sociale* layers. Photo by Charles Newsom.

Figure 11. Close-up shot of the *Isorthoceras sociale* beds at Graf, Iowa. Note the conspicuous concentrations of cephalopod fossils. Photo by Charles Newsom.

Raatz & Ludvigson (1996) were able to use measurements of implosions of the septa in *I. sociale* at Graf to estimate the water depth of the Maquoketa Sea. They showed that the water depth was in the 200 meter range - about 650 feet! These straight shelled nautiloids were classified as *I. sociale*, although I have later seen them referred to *Michelinoceras* and *Dolorthoceras*. I am not sure which of those names is currently recognized, so for purposes of this article, I will still refer to them as *I. sociale*.

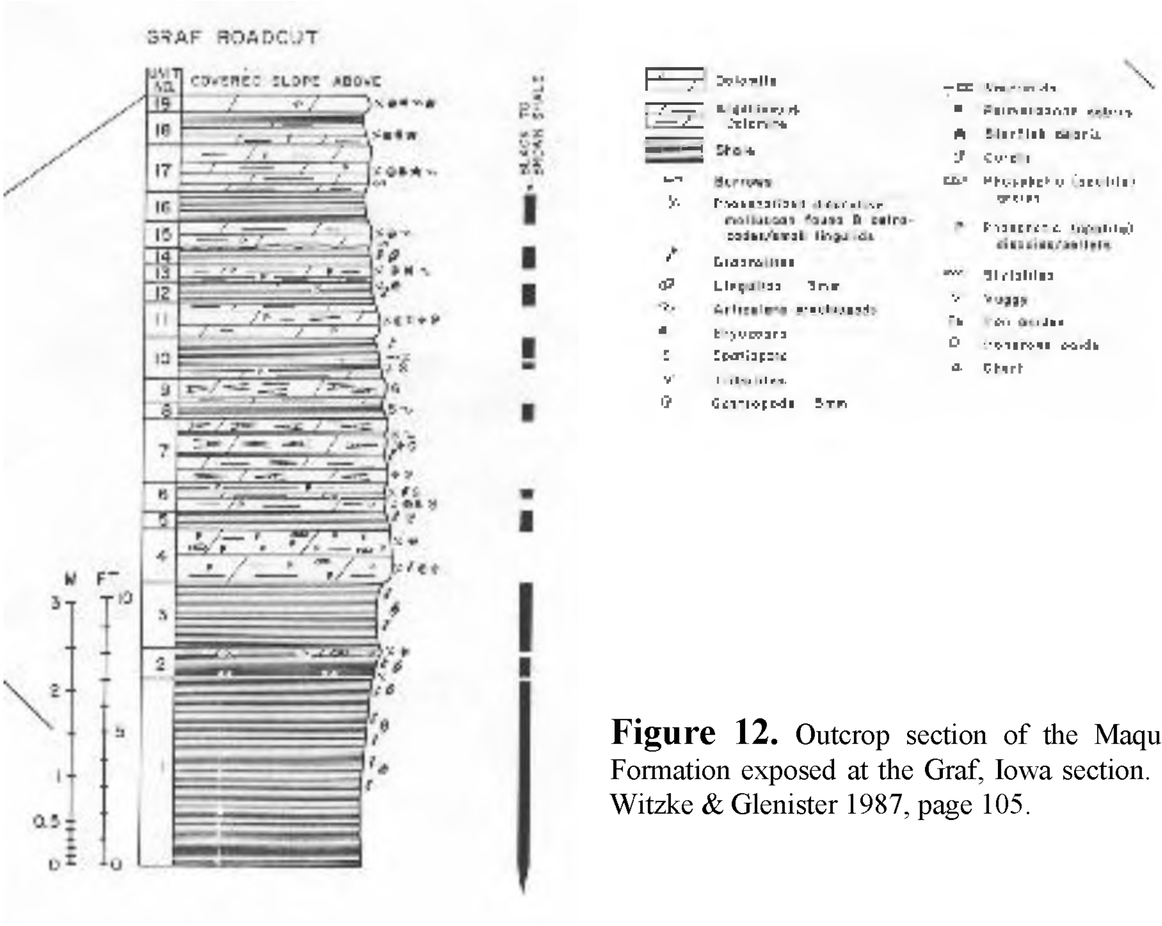

Figure 12. Outcrop section of the Maquoketa Formation exposed at the Graf, Iowa section. From Witzke & Glenister 1987, page 105.

Figure 13. *Isorthoceras sociale* fossil from Graf, Iowa. One shell is telescoped into another (H, N). Some imploded septa from the inner shell (A) are preserved, along with the first intact septum (B). Specimens such as this one allowed for determination of the water depth in the Maquoketa Seaway - found to be around 200 meters. From Raatz & Ludvigson 1996, page 149.

We can learn more than water depth from these beds though - they allow us a chance to postulate some behavior patterns for this long extinct group of cephalopods. What are some reasonable explanations for this concentration of cephalopod fossils?

One possibility is that there was a massive food web built up above the upwelling cold water current. This theory states that the nutrient rich water fed an algal bloom in the water column which fed lots of algae eaters, which fed the eaters of the algae eaters and so on up the food chain, which in the Ordovician was capped by nautiloids. So, over time, as individuals of *I. sociale* died and their shells slowly rained down on the sea bottom, the Graf cephalopod beds accumulated. Essentially the Graf cephalopod beds would be like a movie clip of life at the time - a movie taken over thousands or many tens of thousands of years. A perfectly logical explanation, but it may not be the one at work here. Similar later cephalopod beds in Iowa include a variety of cephalopod species and shell shapes, whilst the ones at Graf are dominated almost completely by *I. sociale*, nearly to the exclusion of all others.

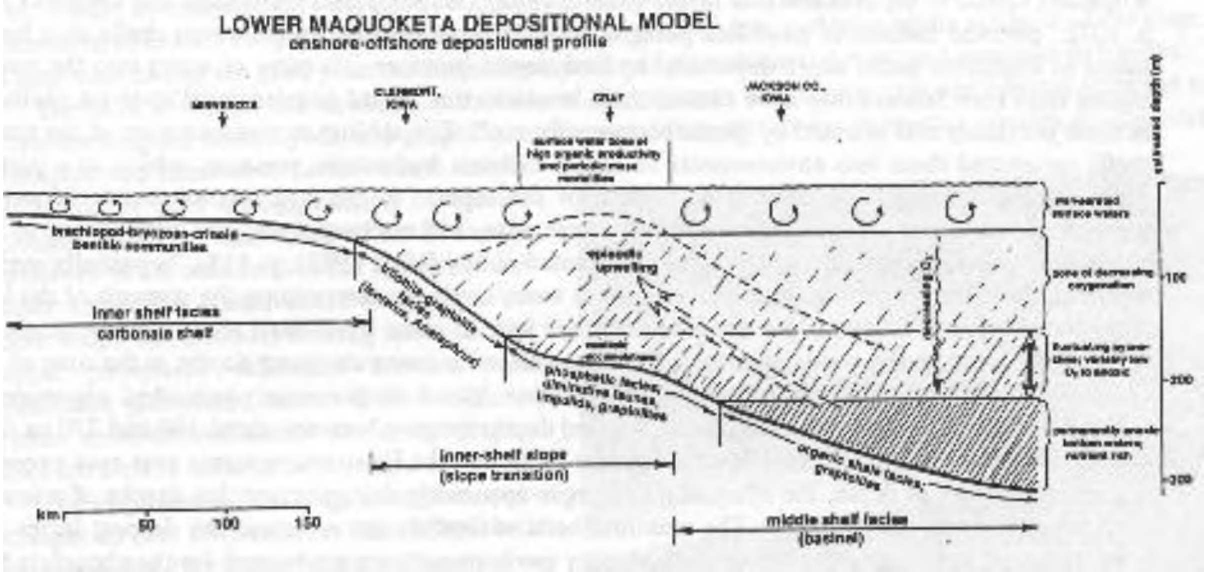

Figure 14. Depositional model for the Elgin Member of the Maquoketa Formation. Note the position of the Graf area near a zone of upwelling nutrient rich water. Also note the position of the Clermont area further north, in an area of relatively shallower water. From Witzke & Heathcote 1997a, page 33.

This leads to the other and potentially more intriguing explanation for the Graf cephalopod beds. This theory confers some behavioral traits on *I. sociale*. It is closely related to the group that eventually gave rise to the Bactritids - *Bactrites* and its kin are the ancestral group which gave rise to the more familiar Ammonoid and Coleoid cephalopods. Ammonoids are now extinct but the Coleoids are the most abundant cephalopods living today.

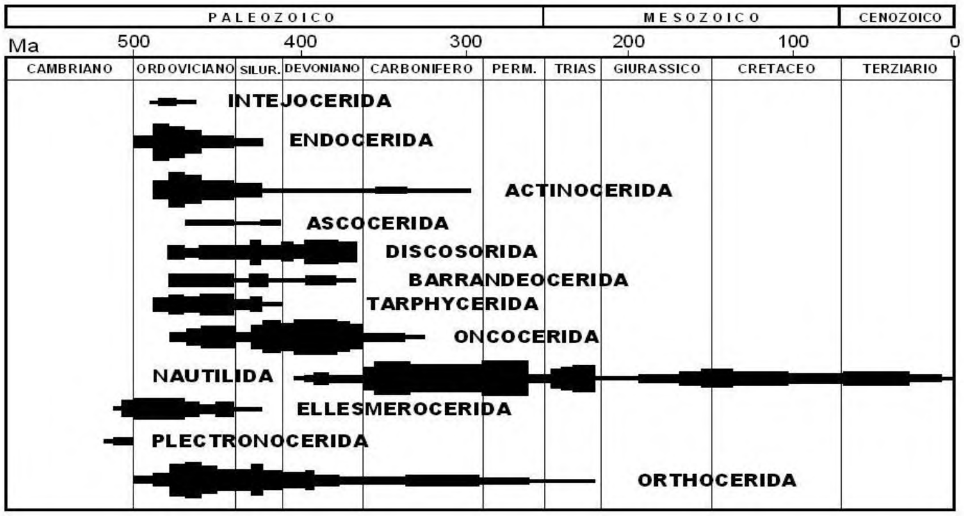

Figure 15. Nautiloid distribution chart. *Isorthoceras sociale* belongs to the Orthocerida, a long lived group which ranged from the Ordovician through the Triassic. It is thought that some portion of the Orthocerida gave rise to the later Ammonoid and Coleoid Cephalopods, through the Bactritids (see **Figure 16**). From Wikimedia Commons.

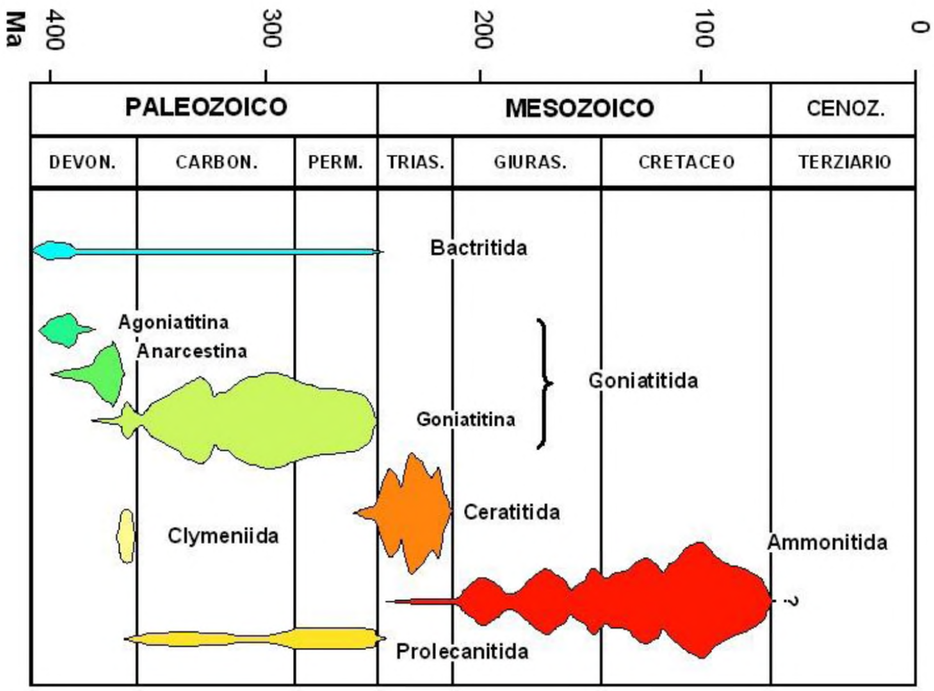

Figure 16. Ammonoid distribution chart. Note the position of the Bactritida, ancestral to the rest of the ammonoids. They also gave rise to the more familiar Coleoid Cephalopods - including modern squid, cuttlefish, and octopus. The Bactritids have their origins in the Orthocerida nautiloid group. From Wikimedia Commons.

Many modern Coleoids follow the "live fast, party hard, die young" strategy - they hatch in large numbers, reach reproductive maturity quickly, and then the adults often die after mass mating events - leaving ecological room for the next generation to exploit. Countless bodies of some modern squids wash up onshore after such events. In the fossil record, many ammonoid species also seem to exhibit this behavior - countless individuals of one species can often be found in a single layer of rock.

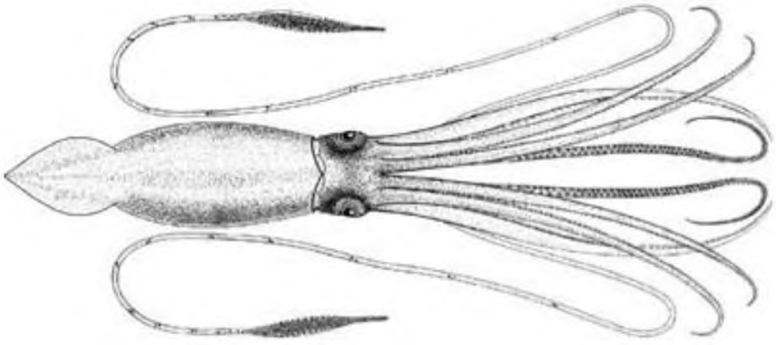

Figure 17. *Architeuthis*, a modern day Coleoid Cephalopod. From Wikimedia Commons.

The modern nautiloids represented by *Nautilus* & *Allonautilus* on the other hand, follow a very different pattern, one that has allowed them to persist nearly unchanged for roughly 375 million years. Female nautilus lay few eggs, and the juveniles hatch and immediately begin scavenging behavior, just like an adult. They do not reach reproductive maturity quickly, and can live for as many as 25 or even 30 years. They subscribe to the "slow and steady win the race" sort of life plan.

Figure 18. Shells of *Nautilus* and *Allonautilus*, the last living representatives of the Nautiloid Cephalopods. They are the only modern day cephalopods with an external shell, and more closely resemble the majority of fossil cephalopods than the Coleoid Cephalopods do. From Wikimedia Commons.

Perhaps the “live fast, party hard, die young” behavior reaches back further than the ammonoids. Could *I. sociale* have had the same sort of life pattern, all the way back in the Ordovician? Perhaps its members congregated around the algal bloom not only to feed, but also to mate, and then to die en masse. This theory would explain why *I. sociale* is almost exclusively the only fossil found in these two Graf beds. If this theory is correct, then the two *I. sociale* beds at Graf represent snapshots of life at the time - not movies. Perhaps you are looking at only centuries of accumulations, not thousands or tens of thousands of years.

The cephalopod fauna of the Maquoketa Formation is notably less diverse than that of the older Platteville Group interval. Sunleaf (1960) mentions only 14 species of cephalopods in the Maquoketa Fm. Granted that paper is now 50 years old, but if that number is even in the ballpark, the species diversity in the Maquoketa Fm pales in comparison to the 60+ species of cephalopod known to occur in the rocks of the Platteville Group (John Catalani pers comm).

Another feature of the Maquoketa cephalopod fauna is the dominance shown by straight shelled (orthoconic) forms over all other shell shapes. (However, this may simply be an anecdotal observation of this author.) Of the 14 species mentioned by Sunleaf (1960), 12 are straight (orthoconic) shells, one is bullet shaped (breviconic), and one is tightly (planispirally) coiled. This is a stark change from the diversity of shell shapes seen in the older Platteville Group faunas (John Catalani pers comm).

I can only begin to toss out possible explanations for the change in species diversity and shell forms seen as one goes up section from the Platteville into the Maquoketa. Perhaps the nautiloids were catastrophically hit by the extinction at the base of the Decorah Fm. They were to never again recover the species diversity seen in the Platteville Group. Perhaps climate change drove some species to extinction. Deepening seas may have removed some shallower water habitats that certain nautiloids had thrived in. Perhaps it was the combination of those factors, or others not yet thought of.

We are only left to wonder, and also to dream back to this wondrous time when nautiloids were rulers of the world’s oceans!!!!!!

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Receptaculitids the Forgotten Reef Builder

Thomas C. Williams

When one thinks of fossil reefs, typically one thinks of corals, sponges, bryozoans, and bivalves not receptaculitids. Receptaculitids, sometimes referred to as a mystery fossil, began in the Ordovician and existed into the Devonian and has no known living counterparts--maybe. Exact origin is still conjecture, based upon paleontologists' conclusions from looking at other fossils. Looking at this fossil, someone might think this could be a coral of some kind. *Receptaculites* were once called sunflower corals, but this is definitely proven not to be the case. Origins of this fossil are truly a mystery, but possible links to Chlorophyta (green algae) or possibly sponges are both considered possible. It is this link to algae, which is what appears to be the most accepted possibility or are they something in between? Questions arise because in terms of the fossil record, they kind just appear in the Ordovician. Maybe someday the true answer will be found with the discovery of their origin and disappearance from the fossil record. When alive, these important and impressive colonial organisms were sessile benthic living in marine environments and now as fossils are found in carbonate rocks of Ordovician age worldwide (see Figure 1).

Receptaculites oweni, now referred to as *Fisherites reticulatus* (Owen 1844), was the first receptaculitid described from North America by Owen in 1844 and was repeatedly referenced by Hall. This particular species was the largest of the receptaculitids reaching sizes up to 24 inches across being reported and is a key index fossil for the Ordovician time period. *Fisherites reticulatus* was the most common receptaculitid that occurred from the middle to late Ordovician and can be commonly preserved. Basic structure of receptaculitids is dish or globe like structure with an inner and outer layer. Overall the circular nature is centered on a central axis from which the organism radiates outward. The outer layer has hexagonal or rhombohedral shaped plates arranged in a clockwise pattern (see Figure 1). Inner layer is composed of tetraaxial spicules that can reveal a pillar like structure (see Figure 2). Receptaculitids in general structure do show considerable similarities to archaeocyathids and radiocyathids in their double-walled structure. This did present some interesting possibilities when trying to classify these organisms originally. The preservation of the dolomitic facies in the Galena Group has allowed these open pore spaces to be studied (see Figures 1, 2). This has allowed for perhaps an understanding of how these pore spaces with the columnar pillar structures were intended to function perhaps actually allowing for the passage of water through the organism or only for support (Finney 1994, Vonk 2005).

Paleoecology for this organism would seem to be one that would require sunlight to be available if the algae link is accepted since that is a requirement for life. During the middle Ordovician, at least in the middle of what is today North America, carbonate sediment was deposited with some interruptions of mud. The inner shelf of the Galena is similar of what exists today off the coast of Florida with a large group of organisms including corals and echinoderms that suggest open marine conditions. Deposits dominated by carbonates, some of which are pure especially the Wise Lake, with intrusions of more shale particularly in the eastern parts of the section. Galena deposits reveal that the environments of Iowa, Illinois, and Southeast Minnesota are inner shelf platform located in the photic zone. Dascylad green algae are also present in the shelf deposits are further indicator of this shelf environment being in the photic zone. Potassium bentonite deposition does show quieter conditions at least for a time which may have played into development of *Receptaculites* during quiet clear water periods. Absence of *Receptaculites* above and below the Galena carbonate formations could be an indicator that the potentially quieter conditions created by the inner shelf environment allowed for this organism development. The equator ran roughly on a line southwesterly to northeast and would have ran from what is today El Paso, Texas, to an area just west of Lake Superior creating a tropical ocean with well oxygenated water. Since receptaculites may have been algae, it is reasonable to assume that they possibly contributed heavily to oxygenation of the environment. However, many organisms that have evolved or thrive in tropical areas can be very susceptible to climatic and or geologic changes (Anderson, Finney 1994, Williams, Catalani 2009).

Receptaculitids of the Ordovician have been found extensively in the Galena Group throughout the Midwest in Illinois, Wisconsin, Iowa, southeastern Minnesota, and Missouri. However, rocks of the Platteville Group that precede the Galena have not reported *Receptaculites* in any of the units present in the fossil record. Therefore, one may conclude that these organisms were just plain not there yet or hadn't evolved to the form present in the Galena. This does seem to present one of the mysteries of this fossil it is not there and then it appears abundantly. Within the Galena, receptaculitids have found more numerously in three separate zones described as the lower, middle, and upper beds (see Figure 1). The Galena Group in the Midwest is typically a varying limestone and dolomite facies prevalent in northern Illinois. This facies appears to be primarily composed of carbonate type rocks with not a lot of shale, is something that appears to be a condition favorable to this species thriving (Vonk 1994).

Receptaculites oweni, now referred to as *Fisherites reticulatus*, is found in the Dunlieth, Wise Lake, and Kimswick Formations and are especially abundant in three specific but restricted stratigraphic zones (see Figure 3). Numerous numbers of specimens with sizes from 8 to 12 inches across reveal the importance of these reef builders in the Galena Group revealing their importance. Corals, brachiopods, sponges, and other fossils found from personnel observation are considerably smaller in the Galena than sizes of the *Receptaculites* up to one-half meter have been reported. This may indicate receptaculites as providing a substrate base from which other reef builders can also capitalize on, at least in the Galena. Moving more north into Iowa and Minnesota, the Galena is preserved mostly as calcitic limestone allowing fossilization to show the three dimensional structure of how the organism may have actually existed on the sea floor. Round, three-dimensional casts give a more true nature as to the reef building capability of the organism. A large specimen found by the author shows a low bowl shape but when in place on the sea floor would have been capable of providing stability in a reef community.

Other numerous places in North America in which receptaculitids are preserved include the Red River formation of Williston Basin near Winnipeg Canada, Panton Stone limestone Vermont, the Bighorn dolomite of Colorado and Wyoming, the Upham formation southwest Texas, the Lebanon limestone of Tennessee, Northwest Territory and Baffin Land Greenland. Of course as you move into the Cincinnatian age rocks corals reach much larger sizes which are plainly evident from examining the rocks of this age. It is not unusual to see massive coral heads and thousands of bryozoan fragments. So what happened to receptaculitids? Was it an environmental change or did the Richmondian invasion have something to with what one might describe as the disappearance of receptaculitids at least temporarily? This invasion, as it was called, allowed numerous new species of organisms into the area of the Galena deposition. Another possibility related to the disappearance of *Receptaculites* is large amounts of sediment which is evident from the rocks present of the Maquoketa Formation which is composed almost entirely of shale. Large amounts of shale do appear to be a limiting factor in the presence of *Receptaculites*. Prior to the Galena carbonates, the Decorah has no receptaculitids and has portions of the sea floor dominated by prasopora, a bryozoan. Then as you pass into the more carbonate units of the Kimswick receptaculitids appear and dominantly in places. The Galena shows at least 4 episodes of volcanic ash rich layers with potassium rich bentonite and other minerals proving a volcanic origin. With a total of at least 11 major episodes in the Ordovician, volcanic ash should be a consideration in any study of the paleoecological environment since it will affect the substrate upon which a sessile benthic organism depends. Source of the ash is suspected to be from an island arc system in what is now the Carolinas. The position of the island arc system is a considerable distance from the middle of the craton which would become North America. Therefore, for ash to actually be preserved in the Galena reveals that some of the volcanic events would be considered to be major eruptions. These types of eruptions are quite capable of producing kill zones. Did the dominance of the receptaculitids of Galena time eventually succumb to an influx of volcanic ash, or unfavorable sedimentation changes or possibly even predation? As the carbonate units of the Galena were replaced by an influx of finer shales of the Maquoketa formation, receptaculitids disappear. Any or all of these together could have easily at least temporarily removed receptaculitids from the fossil record allowing for other reef building organisms to take advantage of the opening. These forgotten reef builders did make a comeback but not to the dominance they showed in the Galena carbonate environments (Vonk 2005, Catalani, J., Williams, T.).

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Figure 1. Two *Fisherites reticulatus* found on a Minnesota Galena exposure. (Photo by John Catalani.)

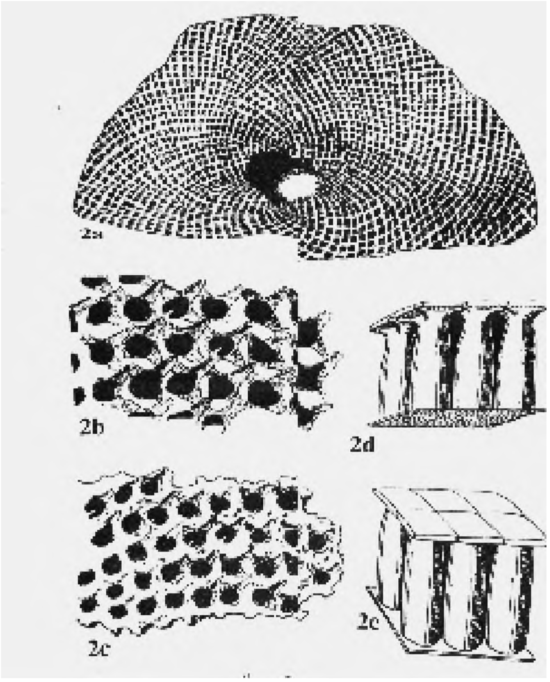

Figure 2. Diagrams showing column, pillar structure, and meroms of a receptaculitid.

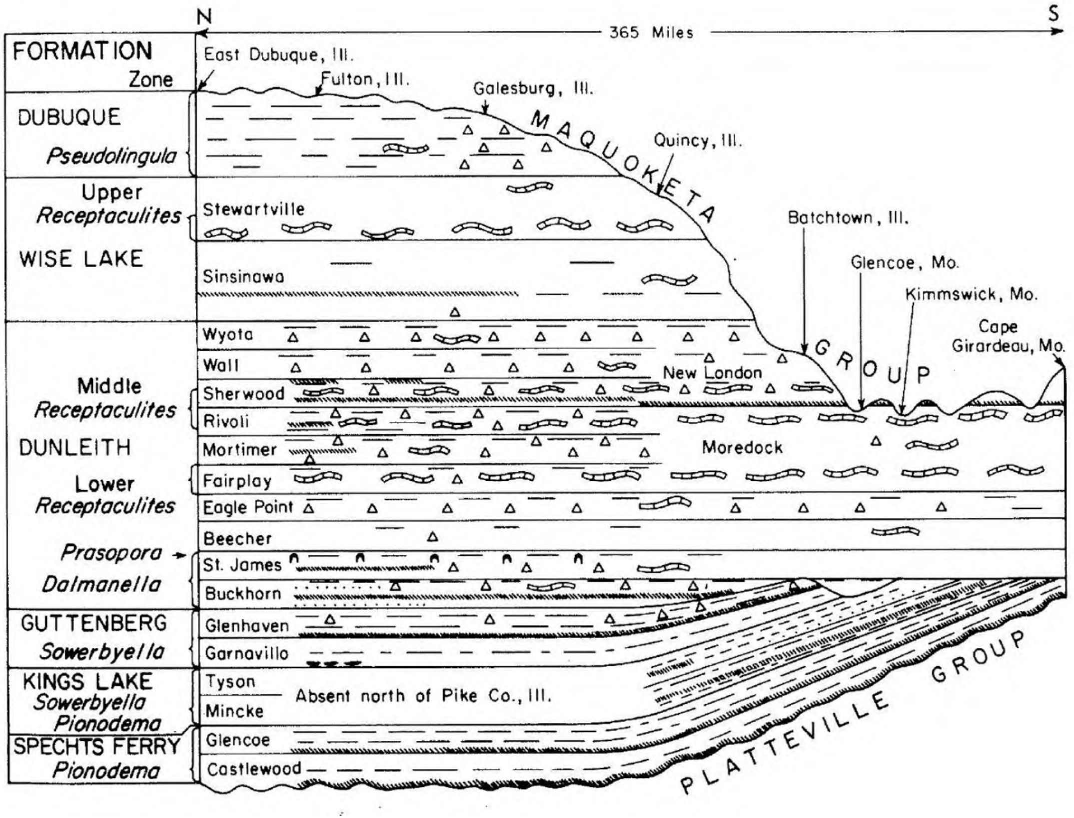

Figure 3. Galena stratigraphy for the Upper Mississippi Valley Region showing positions of the three Receptaculites Zones. (From Fig. O-24, p. 77, of Handbook of Illinois Stratigraphy, Illinois State Geological Survey, Bulletin 95.)

Fossils of the Van Buren Formation and the Cambrian-Ordovician Boundary of Missouri

Bruce L. Stinchcomb

Boundaries of some portions of the geologic time scale such as the K/T boundary (where the fossil record changes abruptly) are definitive and thus generally clear as to exactly where the boundary is. At the K/T boundary major groups of organisms disappear (ammonites, coiled oysters, dinosaurs, belemnites etc.). Other major stratigraphic boundaries such as that of the Silurian-Devonian are not so clear and distinct--such is also the case with strata near the Cambrian-Ordovician boundary and its fossils.

The Cambrian-Ordovician boundary in the Missouri Ozarks has traditionally been placed at the top of the Eminence Formation, a cherty dolomite where the chert sometimes carries what is distinctly an Upper Cambrian fauna including (most) of its trilobites. When detailed geologic work in the Ozarks after the Great War (WWI) began partially as a consequence of the availability of the motor car (Model T Ford), fossils were found in cherty strata similar to that of the Eminence Formation--but with some distinctly “new” additions--the most intriguing of which were small, peculiar cephalopods. It was realized that this sequence of Cambrian rocks in the Ozarks had some of the world’s oldest cephalopods and that specimens found in this strata, especially in an area around Potosi Missouri were the most distinct and abundant. (What were considered as cephalopods at the time, were also found in older, underlying, strata however these were found later to be monoplacophorans and not cephalopods). The zone or horizon which yielded these fossils was first referred to as the “Upper Eminence” due to the similar appearance of its cherts with those of the underlying Eminence Formation. Geologic work in the Current River region (now part of the Ozark National Scenic waterways), found the same horizon to occur around the Ozark town of Van Buren located on the Current River and the horizon was named the Van Buren Formation after that town. At this same time the Cambrian-Ordovician boundary was also placed at the boundary between the Eminence and Van Buren Formations. Earlier work in other parts of the Ozarks had placed this boundary near the top of the overlying Gasconade Formation from which strata delineating the Van Buren Formation had been derived. The validity of the Van Buren Formation being a distinct and recognizable formation (as is the case with most Phanerozoic strata), relied on its fossil fauna which included the before mentioned cephalopods.

Fossils of the Van Buren Formation represent a dilemma as to their belonging to either the Cambrian or the Ordovician period. There are the cephalopods, a faunal element which distinctly aligns the Van Buren with the Ordovician. Trilobites, which are usually an uncommon element in its fauna, are also considered to be Ordovician genera (trilobites are the fossils which many biostratigraphers “officially” use to determine where lower Paleozoic strata belong in the geologic time scale”. In addition to these, the author has found an early type of coral in the Van Buren and corals are also an Ordovician (and younger) organism. On the other hand mollusks other than cephalopods of the Van Buren have decidedly Cambrian aspects. Its gastropods are similar to those of the Eminence Formation as are its multiplated mollusks, the later, a problematic group which had its greatest diversity and abundance in strata just below and above the Van Buren Formation.

The Van Buren Formation "officially" came to an end when some members of the Missouri Geological Survey, in the late 1950's decided that the formation was no longer a valid one and its strata was again relegated to the Gasconade Formation. The reason for this "demotion" being that Van Buren strata could not be recognized in water well cuttings derived from subsurface geology. The fact remained however, that its surface outcrops (especially cherts), yielded fossils which were distinctly different from both the underlying Eminence Formation and the overlying Gasconade. Regarding where the Cambrian-Ordovician boundary should be placed, the late Jim Stitt of the University of Missouri-Columbia, on the basis of trilobites, drew the boundary near the very top of the Eminence Formation. He found that some of the trilobites found at the very top of the Eminence had Ordovician affinities. More recently James W. Hagadorn formerly of Amherst College and now with the Denver Museum of Natural History, on the basis of fossil track ways found in the Gunter Sandstone (A sandstone which occurs at the base of the Van Buren, and which he considers because of its trace fossils to be Cambrian in age), draws the Cambrian-Ordovician boundary above this sandstone. Track ways in the Gunter include *Climactichnites* (the Cambrian motorcycle track way) and *Protichnites,* possibly an aglaspid track way--both of which are diagnostic Cambrian trace fossils. Considering this, the Van Buren Formation is very close to being Cambrian in age.

In contrast to these fossils however, an entirely new element first appears in the Van Buren---the **cephalopod**. Primitive cephalopods of the order Ellesmeroidea first appear in the Van Buren and cephalopods are a decidedly **new element**--a mollusk characteristic of the Ordovician Period but **not** of the Cambrian. Cephalopods also represent a direction in evolution leading toward a sophisticated nervous system (The octopus, a cephalopod, being a fairly intelligent animal*). These early and undoubted cephalopods of the Van Buren are, the author believes, to be the oldest (undoubted) cephalopods known. Cephalopods (or cephalopod-like fossils) have been found in the Llano Uplift of the Texas Hill country but these, like others in Texas and New Mexico may be the same age as the Van Buren **or they may not be cephalopods.** Much heralded Cambrian ellesmeroid cephalopods are also reported to occur on El Paso Mountain (Franklin Mts.) near El Paso Texas, however specimens seen by the author, look just like those of the Van Buren Formation of Missouri. The Cambrian age for the cephalopod bearing strata of El Paso Mountain is shaky--the zone yielding them most likely correlates with the Van Buren Formation and possibly represents the same faunal zone as found in Missouri as both regions are in the Cambrian Laurentian faunal province of North America.

The other earliest cephalopod occurrence is in China! Besides problems with intercontinental correlation and the fact that Cambrian fossils of China represent a different faunal province, there is question as to these small, cone shaped fossils really being cephalopods. It may well be that Missouri's Van Buren cephalopods are the worlds earliest and first. It's also noteworthy that these interesting fossils occur in what generally is considered to be the earliest Ordovician strata and that they are abundant--especially in some areas of Washington County Mo., some 65 miles south of St. Louis. Also noteworthy is the fact that they occur associated with stromatolites--a mollusk-stromatolite ecosystem which was a dominant one in the Cambrian and essentially disappears after the Lower Ordovician.

*Proponents of exobiology and supporters of the appearance of intelligence in "other worlds" take note--cephalopods represent an entirely separate (from the vertebrates) evolutionary pathway leading to a sophisticated nervous system and consequent intelligence. They are an ancient group of invertebrates. Their occurrence in the Van Buren is probably the world's best and earliest occurrence of cephalopods which presumably evolved from monoplacophorans, a molluscan group also well represented in Cambrian strata of the Ozarks.

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Explanation of Figures:

1. Group of ellesmeroid cephalopods *Dakeoceras retrorsum* from the Van Buren Formation at Sand Springs, southeast of Potosi, Washington Co., Missouri.

2. Group of the gastropods *Sinuopea vera* and a cephalopod (*Dakeoceras* sp.) in the middle all associated with a “core” which formed between digitate stromatolites.

3. Group of gastropods *Sinuopea vera*. These are some of the earliest undoubted gastropods (snails) in the fossil record. The Van Buren Formation which yields them is considered early-most Ordovician in age--older gastropods found in the underlying Eminence Formation of the Missouri Ozarks are the **oldest of undoubted gastropods.** Sand Springs locality SE of Potosi Mo.

4. *Ectenoceras pergracile*. Elongate ellesmeroids (brevicones) from near the base of the Gasconade Formation (*Euomphalopsis* zone). These early cephalopods occur associated with large numbers of the gastropod *Euomphalopsis* where these mollusks are associated with siliceous sediments formed between stromatolite reefs. Gasconade Formation, 11 miles WSW of Potosi Mo.

5. A monoplacophoran feeding on a stromatolite. Early mollusks like those shown here are generally associated with stromatolites upon which they probably fed. Ellesmeroid cephalopods are also believed to have evolved from monoplacophorans (monoplacs) as an almost continuous series of fossil forms occur between the two groups---often it is difficult to determine if a fossil is a monoplac or is a cephalopod. As a consequence of this, a lot of confusion exists in the literature of these two groups especially those near the Cambrian-Ordovician boundary. Artwork by Guy Darrough. The early Ordovician (lower Ordovician) was still a time of dominance of stromatolites in the fossil record. This **stromatolite dominated ecosystem,** a paleoecological throwback to deep into the Precambrian, became uncommon after the lower Ordovician.

6. Reconstruction of two early living ellesmeroid cephalopods. Whether these animals had an eye is conjectural---however modern cephalopods have a highly sophisticated eye similar to that of the vertebrates. Artwork by Virginia M. Stinchcomb.

7. Gastropods (*Sinuopea*) and small ellesmeroid cephalopod *Burenoceras* sp. (top) Van Buren Formation, Sand Springs locality SE of Potosi Mo.

8. *Climactichnites* sp. The "motorcycle track" fossil track way from the Gunter Member of the Van Buren Formation near Williamsville Mo. *Climactichnites* is a puzzling and distinctively Cambrian fossil. It occurs in sandstone beds deposited in intertidal environments where it may have fed on moneran mats (cyanobacteria) which formed on the sand surfaces which were preserved as sandstone beds and which can exhibit "old elephant skin", a pattern formed from these mats of cyanobacteria.

9. Group of early mollusks:

1. A kirengellid monoplacophoran of the genus *Kirengella* sp. These are one of the elements of the Van Buren Formation which has Cambrian affinities. It is also a fossil which might suggest that the Van Buren Formation should be considered Cambrian in age. Note the ring of multiple muscle scars on this fossil---this is one of the distinctions which separate monoplacs from gastropods.

2. A hypseloconid monoplacophoran. These elongate monoplacs are very close morphologically to primitive ellesmeroid cephalopods.

3. A Shelbyocerid monoplac. These fossil mollusks, like hypseloconids, are elongate however unlike hypseloconids they have an end (apex) which contains chambers like a cephalopod but with no siphuncle. In earlier literature they were confused with and often considered to be cephalopods---they are most characteristic of the latest Cambrian.

4. An early gastropod (*Sinuopea*). Gastropods are more typical of the Ordovician than they are of the Cambrian. Gastropod-like fossils occur throughout Cambrian rocks but all of these except for those of the very latest Cambrian are questioned as to their being actual gastropods---many paleontologists considering them to be representatives of extinct molluscan classes.

5. *Dakeoceras retrorsum*. This is a nice specimen (internal mold) of this early cephalopod showing the phragmocone (chambered region of the shell) and the living chamber (bottom). Notice the similarity of this to the monoplacs. Cephalopods are an element of the Van Buren Formation which give it a very Ordovician "flavor". From the Van Buren Formation south of Potosi Mo.

10. Paleontological zones in the Lower Ordovician Van Buren and Gasconade formations of the Missouri Ozarks.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

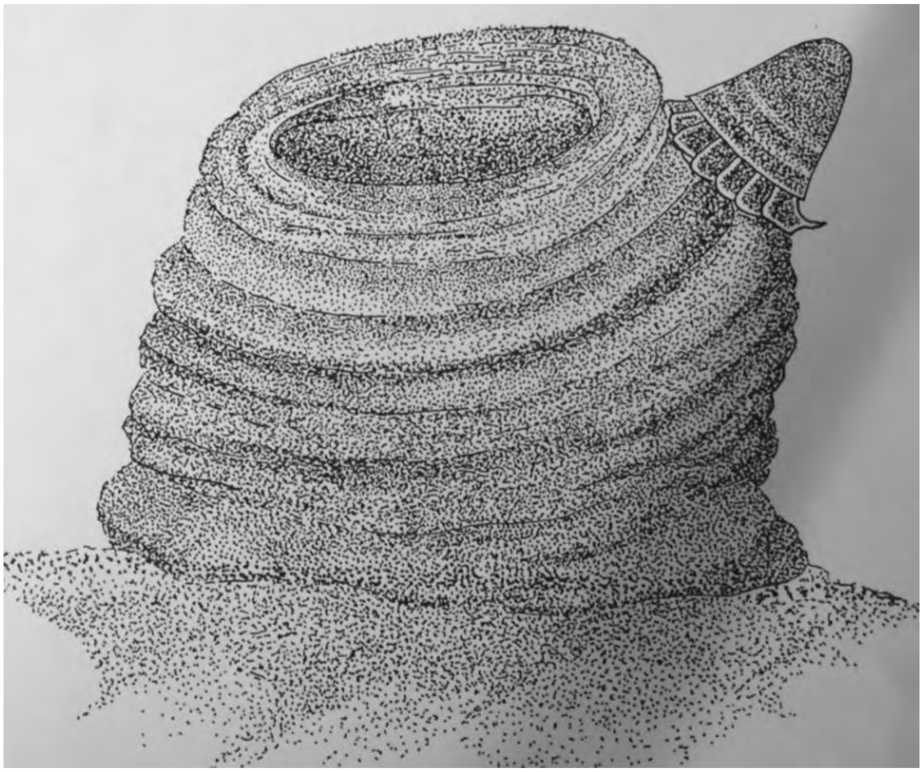

Figure 5.

Figure 6.

Figure 7.

Figure 8.

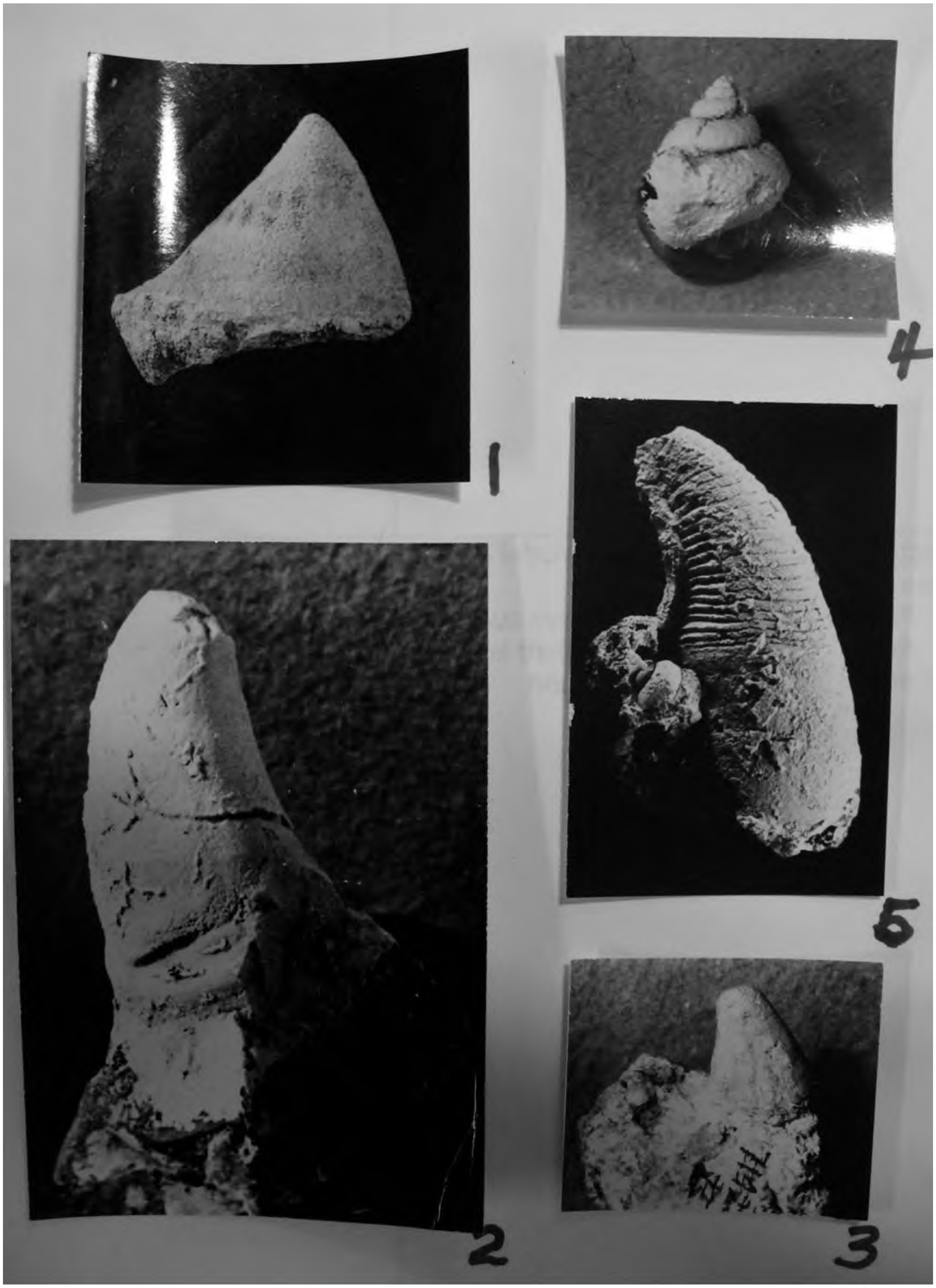

Figure 9.

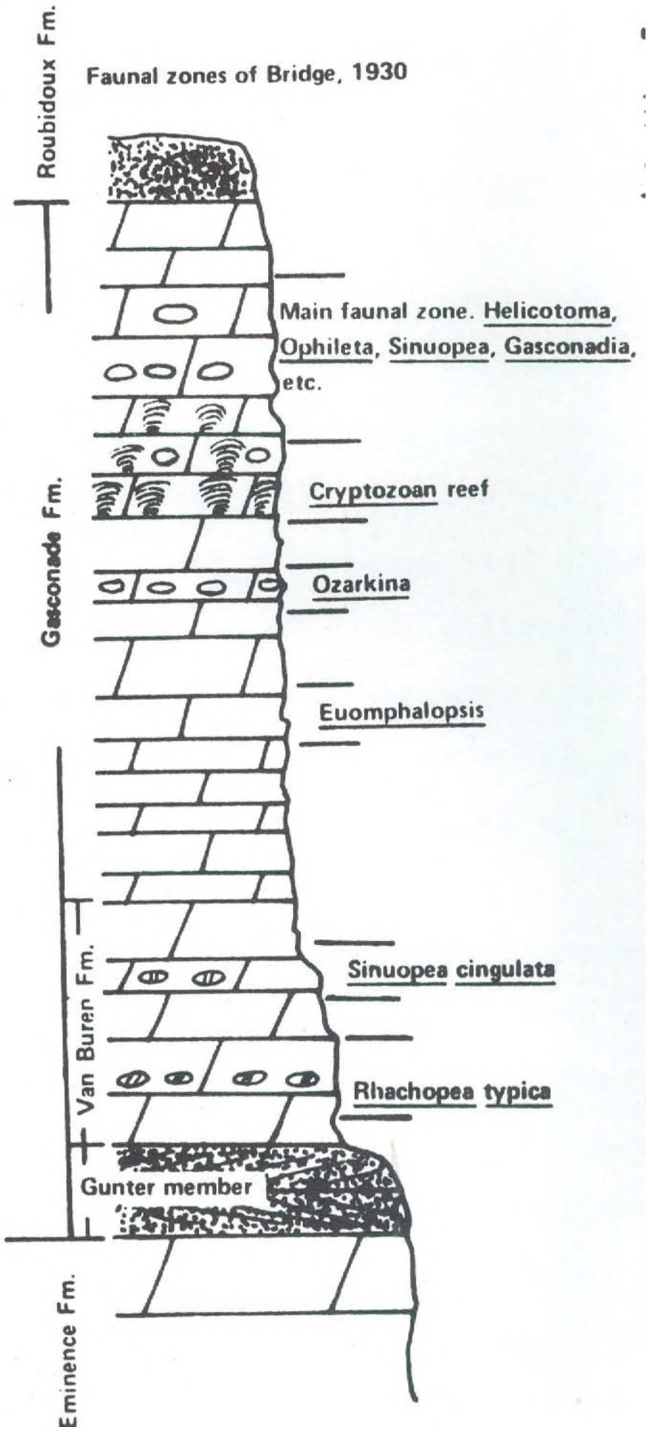
Faunal zones of Bridge, 1930
Roubidoux Fm.
Main faunal zone. Helicotoma, Ophileta, Sinuopea, Gasconadia, etc.
Cryptozoan reef
Gasconade Fm.
Ozarkina
Euomphalopsis
Sinuopea cingulata
Van Buren Fm.
Rhachopea typica
Gunter member
Eminence Fm.

Figure 10.

Ordovician Trilobite with Possible Calcified Muscles

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Trilobites are without a doubt the most popular invertebrate fossils of all time. Usually just the upper surface of their exoskeleton is preserved. Under exceptional circumstances, legs and antenna may be fossilized but this is rare and limited to a few special deposits. Even under special circumstances internal anatomy is generally lacking.

Back in the 1980's I answered an advertisement in a geological magazine for Bolivian fossils. The address put me in touch with a Bolivian business major attending college in Louisiana. Over a two year period the student sent me many boxes of fossils including conulariids, brachiopods, straight cephalopods, and, of course, trilobites. All of the fossils were in bulk and when they arrived many were eroded or fragmentary. This does not mean they all were "duds"; one or two were spectacular and others showed features useful for classroom purposes.

Of the trilobites he sent, the most common were Asaphids preserved in lenticular nodules that had been gathered in Ordovician sediments in Cocachambamba Province. They were 3 to 7 inches in length and represented 4 or so genera. A few of them showed odd color patterns on the glabella that were symmetrical. The patterns were shown best just under the flaked off exoskeleton and may well represent calcified muscle attachments.

The specimen illustrated here shows what may be muscles that ran the hyposoma and/or the first few paired appendages on the underside of the animal. The markings are not color patterns and they do not line up with elevation differences on the cephalon (apodems), indicating that they are more likely to be muscles. A second specimen is in the Carnegie Museum Section of Invertebrate Fossils and a third is in a teaching collection in Buffalo, New York.

Check your fossils for similar markings; some may be dark in color or pyrite... you could find additional indications of internal anatomy that have not been recognized before!

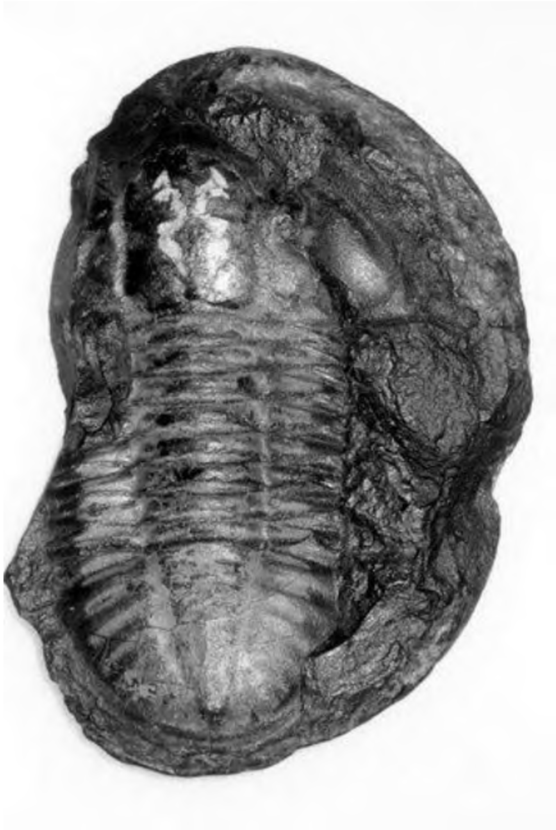

Figure 1

Figure 2

Caption: cf. Hoekaspis sp. Ordovician Trilobite cephalon showing possible muscle preservation. Trilobite is 3.75 inches