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CRINOIDS

A LOVE OF FOSSILS BRINGS US TOGETHER

CRINOIDS

M.A.P.S. Digest

EXPO XXXI EDITION

MID-AMERICA PALEONTOLOGY SOCIETY

A LOVE OF FOSSILS BRINGS US TOGETHER

Western Illinois University
Western Hall
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April 3, 4, 5, 2009

John Catalani and Chris Cozart, Editors

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Preface

As you can see, the Board decided to return to the old format for this year's EXPO Edition. 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 crinoid-related topics contributed by our members and our guest speaker, William Ausich. We would also like to thank William Ausich for delivering the keynote address.

ABOUT THE COVER

Photo submitted by John Moffitt

The cover photo is of a new Pennsylvanian crinoid discovered by George Wolf, Jr. at the Lake Brownwood, Texas spillway site. The specimen is being donated to a repository.

Introduction to Crinoids

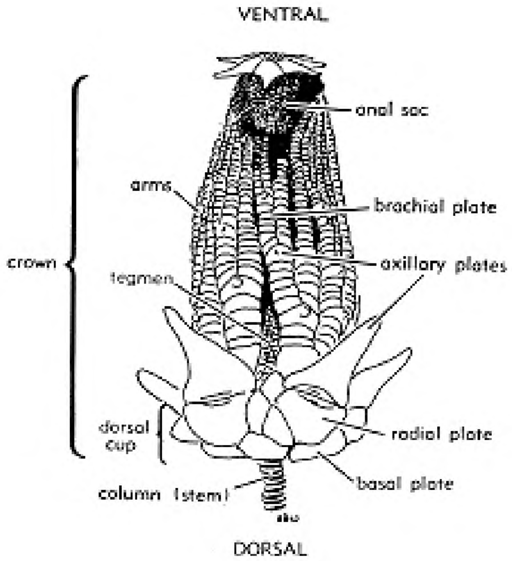
Chris Cozart

Crinoids are one of the life forms most sought after by fossil collectors. Their desirability as fossils stems from their beauty and rarity as a fully articulated specimen, and from their widespread occurrence throughout the fossil record. Over 1,000 genera of crinoids have been described, with over 160 living.

Definition

A crinoid is an organism that is assigned to class Crinoidea, a class within the Phylum Echinodermata. Echinoderms are a group of sea dwelling animals that have external skeletons made up of calcareous plates, a water vascular system, and tube feet. Many echinoderms also exhibit a pseudo pentameral or five-sided radial symmetry. This five-sided symmetry may be expressed as five or multiples of five. A modern starfish is a good example of these characteristics.

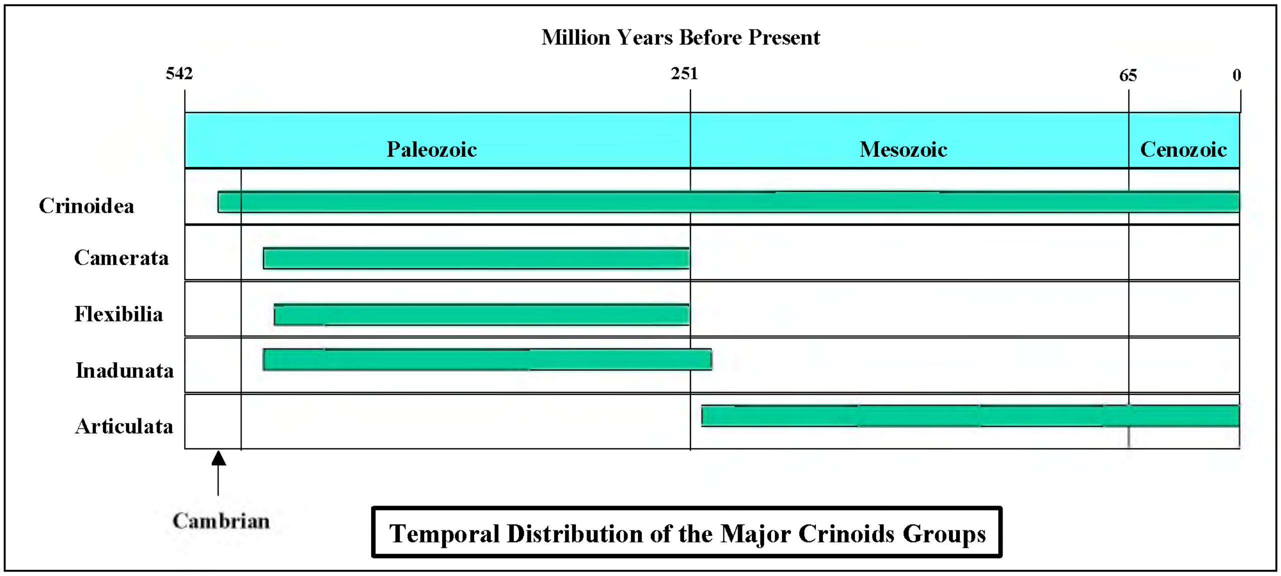
The characteristics, that, taken together, make a crinoid unique from other Echinoderms, are in their specific body plan and life style. The crinoid body has a calyx, made up of a ball or cup shaped group of plates located below arm attachments, collectively called the cup, and a flat to highly domed group of plates located above the arm attachments called the tegmen. The cup and tegmen together form the calyx, which houses the internal organs of the crinoid. The Arms that extend from the Calyx have food grooves on the inside surface of the arms, with pinnules attached to the arm plates. Tube feet attached to the pinnules act to collect and direct food to the food grooves on the inside surface of the arms. Most fossil crinoids have a stem or column that connects the calyx to a holdfast structure. The holdfast may either be a “root” structure that cements to a hard substrate, or an anchor or grappling structure. Other crinoids have cirri that attach to the base of the Calyx that function as legs and permit the crinoid to be free ranging.



KGS Image

Evolution

Crinoids first appeared by the middle Cambrian. The earliest know crinoid is *Echmatocrinus* from the Burgess Shale of British Columbia. Until recently, crinoids have been placed in four major groups: The Inadunates, Camerates, Flexibles and Articulates. The Inadunate and Camerate crinoids are first know from the early Ordovician. The Flexibles appear to have evolved from the Inadunates by the middle Ordovician. Both the Camerates and Flexible crinoids became extinct at the end of the Permian. The Inadunates survived briefly into the lower Triassic and appear to have given rise to the Articulate crinoids. The articulate crinoids persist today.



Temporal Distribution of the Major Crinoids Groups

Life Style

In life, crinoids are filter feeders that either attach themselves to the sea floor with a cementing holdfast, or hop along the sea floor using an anchor to stabilize them, or drift from place to place and grapple onto other structures. Some have been drifters, such as Uintacrinus in the Cretaceous, and others have attached themselves to floating logs for support. There have been entire colonies found in the Jurassic of Holtzmaden Germany that display this lifestyle. Many modern crinoids walk on short cirri that attach to the base of the calyx.

Individual crinoid species are adapted to specific ecological niches. Mature adults feed in specific zones. Some crinoid lay on the bottom. Most Paleozoic crinoids fed some short distance above the seafloor, the distance determined by the length of its column. Since different species had different column lengths, various species of crinoids could inhabit the same area at the same time, much like various species of plants share the same ground in a forest, forming various "stories" of vegetation. Likewise crinoid gardens could support different species of crinoids feeding at different levels.

Some species in a garden may have had columns of only a few inches or less, while others might be as tall as 10 feet.

The diversity of species in a given crinoid habitat is driven by factors such as the amount of sediment suspended in the water, the strength of currents at various levels above sea bottom, the nature of the substrate, presence of predators, etc.

Reproduction

Crinoid reproduction is understood from study of only a couple of modern crinoids. The reproduction habits of these modern crinoids may or may not be good indicates of fossil crinoid reproductive modes. However, they are generally consistent with the reproductive habits of other Echinoderms.

Most crinoid reproduction appears to be sexed, though some hermaphroditic reproduction may have been observed. Male crinoids expel gametes into the sea, which encounter eggs that have been expelled by female crinoids. The fertilized eggs become free swimming larvae, with bilateral symmetry. After a brief period (days – weeks) the larvae settle to the bottom and metamorphose into the adult stage. The settled larvae begin secreting their calcite skeletons and develop the adult 5 sided water vascular system. Sexual maturity is achieved in one to two years.

For more information about crinoids, please see:

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Moore, R.C., and C. Teichert (eds.). 1978. Treatise on Invertebrate Paleontology. Part T, Echinodermata 2. The Geological Society of America and University of Kansas Press, Boulder Colorado and Lawrence, Kansas.

THESE ARE NOT THE CRINOIDS YOUR GRANDDADDY KNEW!

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INTRODUCTION

The *Crinoid Treatise on Invertebrate Paleontology* was published in 1978 (Moore and Teichert, 1978), and this represented a pivotal juncture in the study of crinoids. During the 1970's crinoid paleontology research shifted from only asking "What is the crinoid fossil record?" to also include questions such as "Why did the crinoid fossil record unfold as it did?" and "What does it mean?" Of course, the title above is wrong, because these are the same crinoids that my grandfather first showed me. However, crinoid research since 1978 has concentrated much more on the biology of living and ancient crinoids, functional morphology, preservation or taphonomy of fossil crinoids, phylogeny, evolutionary history, and various paleobiological questions aimed at understanding the large-scale evolutionary trends of this important group of fossils.

Thirty years later, we are beginning to write the *Revised Crinoid Treatise*. It will not only include crinoids known in 1978, but the new volumes will include an incredible number of new crinoids and a summary of the biological and paleontological advances in our understanding of crinoids. This short contribution will outline briefly some of the recent changes to the basic classification of crinoids and outline research needed to unravel the macroevolutionary history of Paleozoic crinoids.

CRINOID CLASSIFICATION

The *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1978) codified a crinoid classification scheme that was outlined in the 1940s by Raymond C. Moore and Lowell R. Laudon (1943, 1944) (Table 1). However, immediately following its publication, questions about the 1978 classification began to emerge. This is the disconcerting aspect of committing the incredible effort required to summarize what we know into a compendium, such as the *Treatise*. Summarizing all that you know immediately points out what you do not know. However, rather than a problem, this is one of the primary strengths of a *Treatise* volume, because it sets the research agenda for the next generation. So it was with the 1978 *Crinoid Treatise*. I acquired my formal training during the 1970s when the *Treatise* was in preparation and in press. My generation took the accumulated knowledge of the 1978 *Treatise* and concentrated on the biology, paleoecology, phylogeny, classification, taphonomy, and paleobiology of crinoids. However, it is critical to mention that these more "trendy" research approaches have never displaced the need for fundamental discovery and description of new faunas. This is more critical now than ever, especially for faunas that complete temporal and paleogeographical gaps in the crinoid fossil record.

A biological issue that has emerged in the past few decades is the viewpoint toward classification. Changes in classification can be frustrating – "Why do they keep changing the names?" However, these changes record a quest to develop a classification based on the evolutionary history of organisms. The goal is to group together organisms that share common ancestry rather than simply subdividing life into groups that look similar. Of course, the evolutionary history of a group of organisms is only an interpretation of the available data, and different workers may, and commonly do, have contrasting interpretations. Further, one of the exciting aspects of paleontology is that new discoveries can revolutionize our thinking. This is especially true for phylogenetic relationships.

With the *Revised Crinoid Treatise* underway, the entire classification of crinoids is under review. In the 1978 *Treatise,* the class Crinoidea was subdivided into four subclasses: Camerata, Inadunata, Flexibilia, and Articulata. The Camerata were divided further into the order Diplobathrida (with two circlets of plates beneath the radials) and Monobathrida (with one circlet of plates beneath the radials). Similarly, the Inadunata were divided into the order Cladid (with two circlets of plates beneath the radials) and the order Disparida (with one circlet of plates beneath the radials) (Table 1).

Changes at these subclass and order levels are underway. A consensus has not been reached in all cases, and alternative hypotheses are emerging (Table 2). There is agreement on one fundamental change in the classification of crinoids. The "Inadunata" is not a natural evolutionary grouping of taxa. Therefore, the "Inadunata" was eliminated, and the disparids and cladids, which are not closely related, are elevated to the subclass status (subclass Disparida, subclass Cladida) (Kelley, 1982, 1986; Simms and Sevastopulo, 1993; Ausich 1998a, 1998b).

In a similar manner, the classification of the cladid crinoids has been changed. In 1978 there were three cladid suborders, the Cyathocrinina, Dendrocrinina, and Poteriocrinina, with the Poteriocrinina being those cladid crinoids with pinnules (fine arm branches alternating from every arm plate). However, we now know that pinnulate cladids evolved many times from different ancestors, so the former suborder Poteriocrinina is not a natural evolutionary grouping with a common ancestor. This has led to the elimination of the Poteriocrinina (McIntosh, 1986; Sevastopulo and Lane, 1988; Simms and Sevastopulo, 1993; Ausich, 1998a), and the subclass Cladida now has only two primary subdivisions, the orders Cyathocrinida and Dendrocrinida (combination of the 1978 Dendrocrinina and Poteriocrinina) (Table 1). Recognizing the multiple evolutionary origins of the former Poteriocrinina is one thing. Unraveling the complex evolutionary history of the new Dendrocrinida is a considerable challenge and is one of the major tasks that must be completed for the *Revised Crinoid Treatise*.

Other proposed changes include the classification of the earliest crinoids, about which we know the least. Most specialists no longer recognize the Burgess Shale *Echmatocrinus* as a crinoid, and the corresponding subclass is eliminated from the Crinoidea as conceived by Moore and Teichert (1978) (Ausich and Babcock, 1998; but see Sprinkle and Collins, 1998). Also, the Coronata, previously an order in the Inadunata are now considered a "blastozoan" and are more closely related to blastoids and rhombiferans than to crinoids. The exact position of the Hybocrinida also needs to be determined. The 1978 Treatise also listed the Class Hemistreptocrinoidea, and this group is no longer recognized (Arendt and Rozhnov, 1995).

New Ordovician crinoid subclasses proposed since 1978 include the Aethocrinea (Ausich 1998b) and the Protocrinida (Guensburg and Sprinkle, 2003). The Aethocrinea is a grouping of Early and Middle Ordovician crinoids that have three circlets of plates below the radial circlet, thus they are four circlet crinoids (typical crinoids have a total of two or three plate circlets). The concept of the Aethocrinea is not universally accepted. The Protocrinida includes a group of newly discovered, highly unusual Early Ordovician stalked echinoderms with numerous, irregular circlets of plates and a style of calyx growth unique among crinoids. The position of these organisms on the crinoid phylogenetic tree is uncertain.

Perhaps, these changes and alternative classification schemes appear a bit arcane, and one wonders who really cares about such things? However, today's phylogenetic approach to classification actually records the unfolding of the evolutionary history of a group of organisms. This approach not only gives us names to call groups of organisms; but it also enables us to solve the "who, when, where, and why" of evolutionary history.

CRINOID EVOLUTIONARY FAUNAS

Baumiller (1994) and Ausich et al. (1994) identified three distinct macroevolutionary faunas during the Paleozoic (Figure 1). During the Ordovician, crinoid faunas were typically characterized, both in dominance and diversity, by diplobathrid camerates, disparids, and hybocrinids (Table 1) (Figure 2). Also, other groups of pelmatozoans, such as rhombiferans, paracrinoids, or diploporans, commonly co-occurred with Ordovician crinoids. This is the Early Paleozoic Crinoid Evolutionary Fauna (CEF). The end-Ordovician extinction event was the second most devastating collapse known in the marine biosphere. Along with many other organisms, crinoids suffered severe extinctions; and when the Silurian crinoid faunas recovered they had a very different composition. This new fauna was the beginning of the Middle Paleozoic CEF. The Middle Paleozoic CEF existed from the Early Silurian through the middle Mississippian, and these faunas were commonly dominated by monobathrid camerates, cladids, and flexible crinoids (Figure 3). Finally, during the Middle Mississippian, the Late Paleozoic CEF emerged with assemblages dominated by only cladid crinoids (Figure 4).

In recent years, a primary focus of crinoid research has been to develop an understanding of the Ordovician origination of crinoids, the transitions between Paleozoic CEFs, and the origination of the subclass Articulata, which are the post-Paleozoic crinoids.

RESEARCH QUESTIONS

In order to fully understand the evolutionary history of crinoids, we need to understand the transitions between the CEFs. How and why did these transitions occur? What was the evolutionary tempo and mode during the transitions? Are there commonalities among the transitions or are each of these a unique episode in Earth history? Emphasis on these boundary intervals in no way diminishes the importance of learning more about crinoids between boundaries, because commonly the faunas and their adaptations between boundaries were ultimately responsible for the survival or declines during the periods of crisis and change.

Crinoid origins.—A traditional view is that the dominant evolutionary trend among Paleozoic crinoids is the reduction in the number of plates in the calyx. This is true in many, but not all, cases. A corollary of this view is that the oldest crinoids must have had many calyx plates. This is an area of active research, and a consensus among crinoid workers does not exist. Various interpretations are based on differing approaches to understanding morphology and marvelous, new Early Ordovician faunas. The addition of the Aethocrinida and Protocrinida mentioned above reflect two alternative views of early crinoids. In part, what is needed to resolve this question is even more new Early Ordovician crinoid faunas. Learning more about the morphologic diversity of early crinoids will certainly help. It is also important to understand the echinoderms from which crinoids arose. Rhombiferans, "eocrinoids," and edrioasteroids have all been argued to be the direct ancestor of crinoids. Understanding the morphology of the direct ancestor of crinoids is key to unraveling early crinoid evolutionary history.

End-Ordovician extinctions.—In 1978, the largest gap in our knowledge of Paleozoic crinoids was between the Upper Ordovician (for example the Cincinnatian faunas) and Middle Silurian faunas (such as the Waldron Shale and the dolomite faunas of the Great Lakes region). This was a worldwide concern, because the end of the Ordovician was a major glacial epoch. Large southern hemisphere glaciers grew, and sea level in the oceans fell accordingly. As a result, there are very few rocks anywhere in the world that record latest Ordovician to earliest Silurian shallow marine faunas. The only solution was the discovery of new faunas so that we can understand the transition between the early Paleozoic CEF and the middle Paleozoic CEF. A focused effort yielded amazing results. In North America, Brian Witzke (1981), Jim Eckert and Carl Brett (2001), I (Ausich, 1984, 1986a, 1986b, 2005), and others have done much to fill this gap, with important new faunas from Iowa, New York, Ontario, Ohio, and Quebec. Approximately 140 Early Silurian genera are now known, whereas only 19 percent of these were recognized in 1980 (Figure 5). Now that new faunas have been discovered, the focus of current research has changed to understanding the character of this macroevolutionary transition, and preliminary results suggest that it was a complex transition of adjustment between evolutionary faunas, from diplobathrid and disparid crinoids to the cladids, monobathrids, and flexibles of the middle Paleozoic CMF. Crinoids did suffer a mass extinction (Peters and Ausich, 2008), but the complete faunal transition took considerable time to be completed.

Middle Mississippian transitions.—In contrast with the previous evolutionary transition which was noteworthy because of the lack of data, understanding the middle Mississippian transition between the middle Paleozoic CEF and the late Paleozoic CEF has been hampered by too much information. By 1980 we knew 92 percent of the Lower Mississippian crinoid fauna from a total of approximately 1000 (Fig. 6). There are many species that need to be combined, and many generic definitions are not precise. The middle Mississippian transition occurred largely between the late Osagean and early Meramecian. For those familiar with the Mississippian stratigraphy in the Mississippi River Valley, this is between the lower and upper parts of the Warsaw Formation. In contrast to the end-Ordovician, this transition was not caused by a mass extinction. Even more surprising is that this change occurred in association with the all-time maximum crinoid diversity (Kammer and Ausich, 2006). Rather than mass extinction, this change was an interval of relatively rapid evolutionary turnover (Ausich et al., 1994). Although this transition affected other crinoid groups, to a great extent, this transition was a shift between the two major groups of pinnulate crinoids, monobathrid camerates to pinnulate cladids. The task at hand now is to correctly identify the genus assignment of all Mississippian crinoids, so that their true temporal and geographic distribution is known. Unfortunately, this work will result in the generic reassignment of many familiar crinoids, including placement into several new genera.

Rise of modern crinoids.—The end of the late Paleozoic CEF is the most poorly understood of these changes but, arguably, the most important. Advanced, pinnulate cladids dominated late Paleozoic faunas. How did the post-Paleozoic fauna evolve at the close of the Permian occur? This is the modern fauna composed of the articulate crinoids that still dominate today's oceans. A similar theme is repeated for this interval – not enough faunas are known, and this change occurred in association with mass extinctions. The end-Permian was the most significant collapse of Earth's biosphere known. As many as 82 percent of genera went extinct at the close of the Paleozoic (Erwin, 2006).

Current research concerning this interval of crinoid history needs to determine the oldest articulate crinoids. How far, if at all, did the articulate lineage extended into the Paleozoic? Do all of the post-Paleozoic Articulata share a common ancestor? Alternatively, was the articulate condition evolved in more than one lineage of Permian crinoids, thus rendering the Articulata not a single evolutionary grouping?

CONCLUSION

Today, paleontologists are asking very different questions than they did in previous generations. Regardless, robust answers can only be achieved with the discovery of new fossils. New faunas during critical intervals of change need to be discovered. Further knowledge of existing faunas also needs to be expanded to better understand their paleoenvironmental distribution, detailed morphology, and ontogeny, which will provide the framework with which to understand episodes of macroevolutionary change.

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Table 1. Order-level classification from Moore and Teichert (1978).

- Class Crinoidea
- Subclass Echmatocrinea
    - Order Echatocrinida
- Subclass Camerata
    - Order Diplobathrida
        - Order Monobathrida
- Subclass Inadunata
    - Order Disparida
        - Order Hybocrinida
        - Order Coronata
        - Order Cladida
- Subclass Flexibilia
    - Order Taxocrinida
        - Order Sagenocrinida
- Subclass Articulata
    - Order Millericrinida
    - Order Cyrtocrinida
        - Order Bourgueticrinida
        - Order Isocrinida
        - Order Comatulida
        - Order Unitacrinida
        - Order Roveacrinida
- Class Hemistreptocrinidea
    - Order Hemistreptcrinida

Table 2. Order-level classification from Moore and Teichert (1978).

- Class Crinoidea
  - Subclass Protocrinoidea
    - Order Protocrinoida
- Subclass Aethocrinidea
  - Order Aethocrinida
- Subclass Camerata
  - Order Diplobathrida
    - Order Monobathrida
- Subclass Cladida
  - Order Dendrocrinida
    - Order Poteriocrinida
  - Subclass Disparida
    - Order Eustenocrinida
    - Order Maennilicrinida
    - Order Tetragonocrinida
    - Order Homocrinida
    - Order Calceocrinida
    - Order Myelodactyla
    - [note additional disparid orders need to be names]
- Subclass or Order Hybocrinida
- Subclass Flexibilia
  - Order Taxocrinida
    - Order Sagenocrinida
- Subclass Articulata
  - Order Millericrinida
  - Order Cyrtocrinida
    - Order Bourgueticrinida
    - Order Isocrinida
    - Order Comatulida
    - Order Unitacrinida
    - Order Roveacrinida

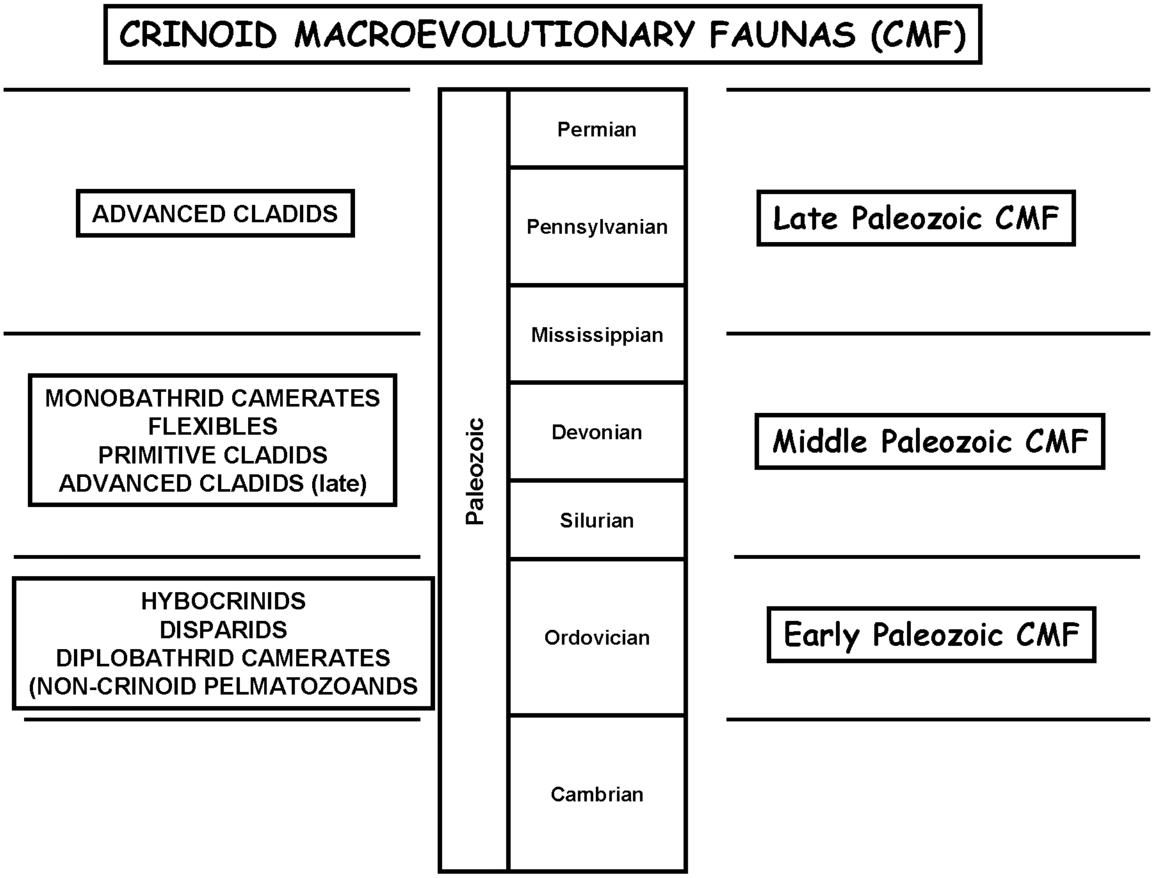

Figure 1. The three Paleozoic Crinoid Evolutionary Fanuas (CEF).

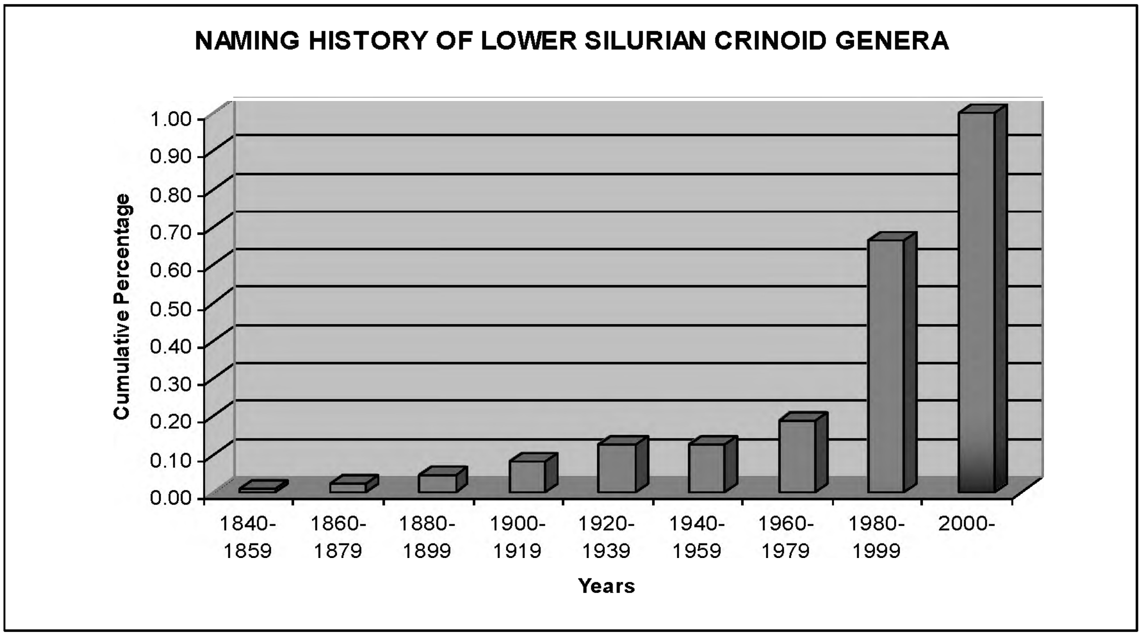

Figure 2. Cumulative percentage of the naming of Early Silurian crinoid genera.

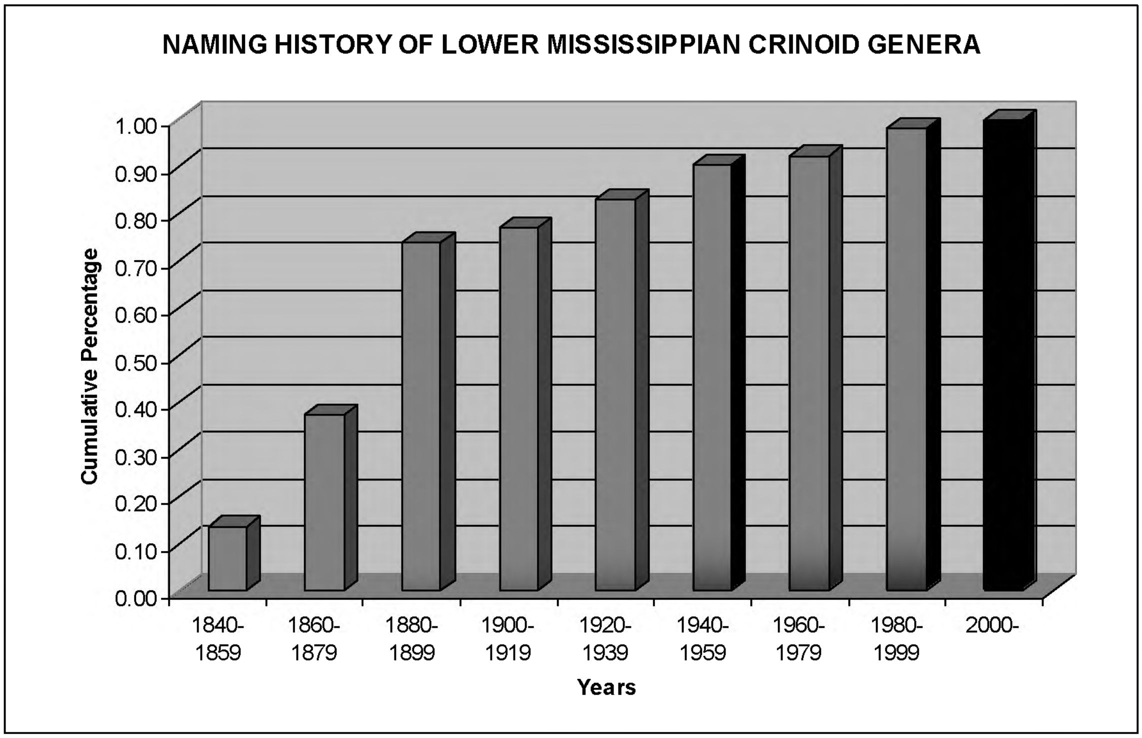

Figure 3. Cumulative percentage of the naming of Middle Mississippian crinoid genera

Figure 4. *Iocrinus subcrassus* Meek and Worthen – a representative disparid from the Early Paleozoic CEF. Specimen from the Upper Ordovician (Cincinnatian) of southwestern Ohio.

Figure 5. *Onychocrinus exsculptus* Lyon and Casseday – a representative flexible from the Middle Paleozoic CEF. Specimen from the Middle Mississippian of Indiana.

Figure 6. *Aesiocrinus* Miller and Gurley – a representative advanced cladid from the Late Paleozoic CEF. Specimen from the Pennsylvanian of Kansas.

150 YEARS OF COLLECTING CRINOIDS AT THE UNIVERSITY OF IOWA PALEONTOLOGY REPOSITORY

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INTRODUCTION

The University of Iowa Paleontology Repository is home to over 1 million fossils from all geological ages and with worldwide coverage. A large part of this collection is what I like to refer to as the Midwest Crinoid Collection. It contains more than 50,000 specimens collected over the last 150 years by well known fossil collectors and paleontology researchers including Samuel Calvin, Frank Springer, Charles Belanski, Lowell Laudon, Harrell Strimple, Christina Strimple, Calvin Levorson, Arthur Gerk, Amel Priest, and Glenn Crossman. By far the largest volume of material is the Glenn Crossman Collection bequeathed to the Repository in 2002. It contains over 1000 specimen lots, is valued at approximately $100,000 and weighs 10 tons!

HISTORICAL COLLECTIONS

The Paleontology Repository grew out of the University of Iowa (then State University of Iowa, hence our SUI acronym) Cabinet of Natural History which was created by an 1855 Act of Legislature to house specimens collected during geological surveys of Iowa. The first official surveys were done by David Dale Owen between 1839-1851, as part of a federally sponsored reconnaissance of 11,000 square miles of mineral lands in Wisconsin, Minnesota, and Iowa (Prior 1996). Crinoid specimens collected during that time and published in Owen's reports (Owen and Shumard 1852), including holotypes (specimens used to define a new species) of crinoids such as *Platycrinus burlingtonensis, Cyathocrinus iowensis and Megistocrinus evansii* from Burlington, Iowa, are in the Field Museum (Golden and Nitecki 1972).

In total, the Midwest Crinoid Collection contains nearly 3000 type specimens that are either primary types, or figured or mentioned in over 160 scientific papers. The earliest published crinoid specimen is SUI 3423 (figure 1) collected from the Pennsylvanian of SW Iowa by Charles White, State Geologist from 1866-1869, and described by White and Assistant State Geologist, Orestes St. John as the holotype of *Hydreionocrinus verrucosus* (White and St. John 1868).

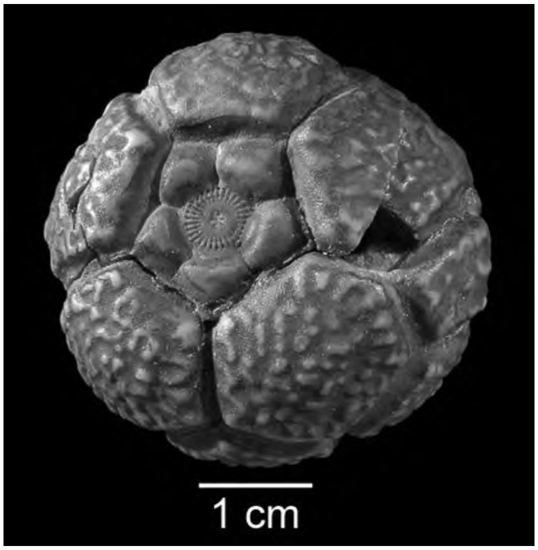
Few specimens from the early geological surveys (Owen, Hall, White) remained or were deposited at the University and when Samuel Calvin (1840-1911) was recruited in 1873 as Acting Professor of Natural Science and Curator of the University Cabinet, he was dismayed at the lack of good specimens available for teaching. Calvin made his personal collection available and obtained funds

($150!) from the University to collect specimens from Canada, New York, Lake Erie, Massachusetts, Long Island, New Jersey, Ohio and Indiana. Under his direction the collection was firmly developed. The Paleontology Repository Archive contains Calvin's original catalogue of his early collection, and includes records of *Eucalyptocrinus*, *Saccocrinus*, *Rhodocrinus* and *Glyptocrinus* specimens from the Silurian of Racine, Wisconsin, and Waldron, Indiana, but only one specimen from Iowa – *Agaricocrinus americanus* which Calvin notes as a "Head with stem attached" from the "Burlington Group," Burlington. Calvin later used photographs of many specimens, including crinoids from Burlington, to illustrate a laboratory book now referred to as Calvin's Plate Book. The Paleontology Repository has two student copies from 1898 and 1904 with the students' class notes written next to each photograph. Matching up Calvin's photos and catalogue records with Repository specimens would make an interesting project.

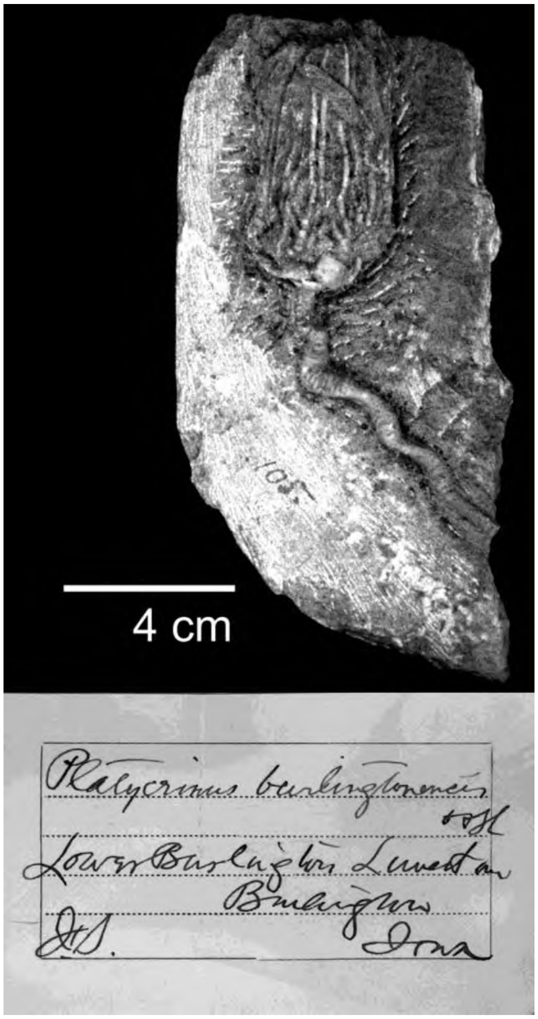
Frank Springer (1848-1927) was one of the great crinoid workers of the late 19th and early 20th centuries along with Charles Wachsmuth, and their "rival" Francis A. Bather (Ausich and Kammer 2001). Springer was born in Wapello, Iowa, graduated with a law degree from the University of Iowa in 1866, and while still a student, studied geology and paleontology with White and St. John at the Geological Survey office (no geology classes were available at the University at that time). While professionally an attorney, Springer collected and studied crinoids with Wachsmuth in his spare time, and spent the latter part of his life conducting research on crinoids at the Smithsonian (Anderson and Furnish 1983). His magnificent crinoid collection and library were donated to that museum, but he also donated his Iowa non-type specimens to the University of Iowa (figure 2). A selection of these is on display at the Des Moines Historical Society Museum in Burlington.

Two other historical collections are the Belanski and Laudon collections. Charles Herbert Belanski (1897-1929) was an authority on Devonian fossils and the Midwest Crinoid Collection contains hundreds of thousands of his specimens including, for example, several species of *Megistocrinus* from the Cedar Valley Limestone of Iowa, all with meticulous locality and stratigraphic data. Many of Belanski's specimens are labeled "type" but Belanski died in 1929 at the age of 32, due to effects of mustard gassing he had suffered in WWI and they were never published. Belanksi was a protégé of University of Iowa professor A. O. Thomas, who encouraged him to study paleontology and hired him as curator in the University's museum in Old Science Hall.

Lowell R. Laudon was a University of Iowa graduate (BS 1928, MS 1929, PhD 1930) who became an expert in Mississippian crinoids and a faculty member at the Universities of Tulsa, Kansas and Wisconsin- Madison. Fox Network anchorwoman Greta Van Susteren, a graduate of Wisconsin-Madison, claims that Laudon's field class was the best course she ever took (Dott 2007)! Holotype specimens of thirty-three new crinoid species from Iowa that Laudon described are housed in the Paleontology Repository (Laudon 1933, 1936, Laudon and Beane 1937), along with thousands more specimens of all types of fossils that Laudon donated while a student. On his retirement in 1975, he donated half of his collection to the Paleontology Repository, including over 40 boxes and 21 drawers of "Mississipian crinoids etc." (Laudon, pers. comm.1976). He donated the remainder of his collection to Wisconsin-Madison.



1) (above) SUI 3423 *Hydreionocrinus verrucosus* (White and St. John, 1868). Pennsylvanian, Iowa.



Platycrinus burlingtonensis
O&S
Lower Burlington Limestone
Burlington
J.S. Iowa

2) (right) Frank Springer specimen with original? label. *Platycrinus burlingtonensis* Owen and Shumard, 1850. Mississippian, Burlington Limestone, Burlington, Iowa.

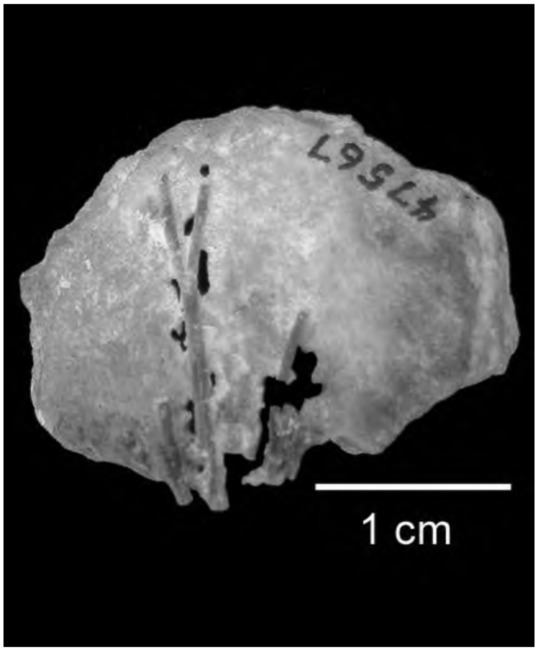
THE STRIMPLE CONNECTION

A large part of the pre-2000 crinoid collection was acquired for the Paleontology Repository by Harrell Strimple, curator from 1962 to 1980, through his collaboration with local collectors such as Amel Priest of Peru, Iowa, Cal Levorson of Riceville, and Art Gerk of Clear Lake, and through his work with University of Iowa students such as Dennis Burdick and Terry Frest. Strimple was one of the most productive self-trained paleontologists of all time, publishing nearly 300 scientific papers and making a major contribution as an author of the Treatise on Invertebrate Paleontology (Crinoidea) (Anderson and Furnish 1983). The Midwest Crinoid Collection contains 1470 specimens, including 147 holotypes, that are cited in Strimple's publications, (e.g., Strimple 1962, 1975; Strimple & Moore 1969, 1971, 1973; Burdick and Strimple 1971, Warn & Strimple 1977; Frest & Strimple 1977; Frest et al. 1979; Brower & Strimple 1983; Lewis & Strimple 1990).

Strimple often named new species after local fossil collectors, e.g., *Rhodocrinites beanei* after Bernice H. Beane, *Calceocrinus gossmani* after Brian Gossman, *Cremacrinus crossmani* after Glenn Crossman, and *Cremacrinus gerki* after Art Gerk (Strimple 1965, Brower and Strimple 1985).

The reputation Strimple gave the Paleontology Repository as a suitable place to deposit collections was continued by Julia Golden (Collections Manager, 1980-2003) and under her stewardship the collection received its largest crinoid donations from Crossman, Gerk, Levorson, C. Strimple, and Priest.

3) SUI 47553 *Cremacrinus gerki* Brower and Strimple, 1983. Ordovician Dunleith Fm. Near Decorah, Iowa.



4) SUI 47567 *Cremacrinus crossmani* Brower and Strimple, 1983. Ordovician Galena Group. Near Owatonna, Minnesota.

Arthur V. Gerk and Calvin O. Leverson were two Iowa collectors who worked closely together and with Harrell Strimple. Both collected a wide range of fossil taxa from the Devonian Lime Creek, Shell Rock and Cedar Valley Formations, Mississippian Gilmore City Formation, and the Ordovician Makoqueta and Galena Groups (e.g., Strimple and Levorson 1971, 1973). Among the thousands of specimens they donated to the Paleontology Repository are exquisite and unusual Ordovician echinoderms (Anderson and Furnish, 1983). Their records of the stratigraphy of the different formations they collected from are remarkable for their detail and professionalism. Levorson and Gerk were jointly awarded the Harrell L. Strimple Award by the Paleontological Society in 1987.

The Amel Priest Collection contains over 500 specimen lots, mostly crinoids from the Burlington and Gilmore City Formations. Priest was an avid collector who worked closely with Strimple. Part of his collection is at Luther College in Decorah, Iowa.

THE CROSSMAN AND C. STRIMPLE BEQUESTS

Since 2000, two major crinoid collections have been bequeathed to the Paleontology Repository. Glenn Crossman collected fossils for more than 20 years and amassed a huge collection predominantly of Paleozoic echinoderms from sites within Iowa and nearby southern Minnesota, with a significant collection from one site in Illinois. In particular, Crossman's collections have been the focus of research by Dr. James Brower (Syracuse University), who has described many new species in the *Journal of Paleontology* based on the collections (Brower 1992, 1994, 1997, 1999). Many of Crossman's previously donated specimens are types (104 paratypes, 5 holotypes, 34 figured non-types).

The holotypes from Crossman's previous donations are:

Echinoid:

SUI 42700 *Bothriocidaris maquoketensis* Kolata et al., 1977. Ordovician, Fort Atkinson Formation, from Fort Atkinson, Winneshiek Co., Iowa.

Crinoids:

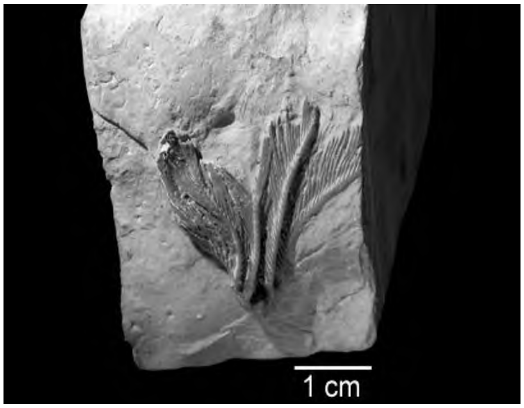
SUI 52177 *Drymocrinus strimplei* Brower, 1997. Upper Ordovician, Maquoketa Formation, from near Ossian, Fayette Co., Iowa.

SUI 80031A *Caleidocrinus (Huxleyocrinus) gerki* Brower, 1992. Middle Ordovician, Dunleith Formation, from Burr Oak, Winneshiek Co., Iowa (collected by Brower & Crossman).

SUI 80157 *Euptychocrinus skopaios* Brower 1994. Middle Ordovician, Dunleith Formation, from Pederson Quarry, Fillmore Co. Minnesota.

Rhombiferan:

SUI 80258 *Pleurocystites strimple,* Brower, 1999. Middle Ordovician, Dunleith Formation, from Burr Oak, Winneshiek Co., Iowa.



L-R: 5) SUI 5277 *Drymocrinus strimplei,* Upper Ordovician, Maquoketa Fm. Near Ossian, Iowa. 6) SUI 80031A *Caleidocrinus (Huxleyocrinus) gerki* Ordovician, Dunleith Fm. Burr Oak,Iowa. 7) SUI 80157 *Euptychocrinus skopaios*, Ordovician, Dunleith Fm. Pederson Quarry, Minnesota.

Whenever notification of a bequest is received, immediate action is necessary to secure funds to assess, pack, transport, unpack, house, organize, curate and care for the collection, even if the bequest has been planned for some time. Glenn's bequest was no exception. Julia Golden and I travelled to Riceville, with Julie's husband, Stephen, to look at the collection and see how much material there was, what quality it was, whether it was appropriate for the Paleontology Repository collection, and plan how we were going to get it back to Iowa City. Julie knew it was a big collection, but I think we were both amazed at the extent of it. Boxes and boxes of material on shelves, tables, and in cabinets in three buildings (house, garage and barn)! We made a very basic inventory and took photographs. Fortunately, we had a grant from the National Science Foundation for which we were able to apply for a supplement to move the collection back to Iowa City. The size of the collection meant that it was not feasible to get student volunteers to Riceville for a day or two and Julie opted for a professional moving crew. Unfortunately, the Repository did not have immediate space for the collection! Luckily the Iowa Geological Survey had just built an addition to their Oakdale campus facility and we were able to store the collection on open shelving there temporarily (temporarily meaning three years in this case).

The Crossman Collection consists of 900 trays (beer flats) of material, 250 slabs and 150 bulk collections (sacks, buckets, and boxes). The bulk of the collection is Paleozoic echinoderm material, with a few samples of trilobites, brachiopods, vertebrates and plants. Our first task was to organize the collection. Our supplemental grant employed graduate students for a semester and over the summer to physically organize the collection stratigraphically, and then grade the material. Danielle Shapo and Tin Wai Ng organized the entire collection in stratigraphic order, which meant looking through every box to find labels and locality numbers marked on specimens, and interpret abbreviations or look up locality numbers in Glenn's card index. Danielle assigned a GC number to every beer flat, slab, sack and specimen tray and created an inventory of the collection noting identification (if any), geologic age, and collecting locality. Then she went through the collection again and assigned preparation grades to the specimen lots as follows:

GRADE 4: prepared, identified, with full locality and stratigraphy information.

GRADE 3: prepared, unidentified, with full locality and stratigraphy information.

GRADE 2: unprepared, unidentified, full locality and stratigraphy information.

GRADE 1: unprepared, unidentified, missing some information.

GRADE 0: unprepared, unidentifiable (fossil not visible), with or without information.

8) Left. Part of the Crossman Collection in Glenn's garage at Riceville.

9) Above. A typical drawer of curated specimens in the UI Paleontology Repository.

This scheme allows us to tackle the curation of the collection in a systematic way. First of all we curated grade 4 material. This was very easy as all the information was available. We extracted the grade 4 material and organized it by taxon, age and identification in cabinets in our Oakdale campus storage facility, so that we could determine how much space we would require to incorporate it into our Trowbridge Hall collection. At this current time we estimate 4 double door cabinets will be required.

Meanwhile, in 2003, we received another large bequest (>1000 specimen lots, but smaller in volume than the Crossman bequest) from the estate of Christina Strimple, the widow of late Repository curator, Harrell Strimple. Christina Cleburn had been introduced to crinoids by B. H. Beane and later discovered a significant crinoid locality in the La Salle Limestone (Pennsylvanian) of Illinois and through that discovery met Harrell. Harrell joked that people said he married Christina to get her crinoids, but that in reality she married him to get them back (Anderson and Furnish 1983). Again, time was of the essence dealing with Christina's bequest, and fortunately we had enough funds in our National Science Foundation grant to pay for professional movers to bring the collection from Christina's house in Iowa City to the Survey building at Oakdale. Prior to moving the collection we visited Christina's house, made an inventory, bagged up specimens that were in disintegrating boxes in the basement, and determined where we would put the collection. Once the collection was moved, we made it available to an appraiser of the family's choice, who gave them a financial appraisal for tax purposes. As the receivers of the bequest, we were not involved in the appraisal any further as this would have been a conflict of interest. We were able to accommodate the C. Strimple collection in the Repository (individual specimens that had been stored in cabinets) and the Oakdale campus storage facility (basement and bulk samples). Rocks and minerals that were not within the Repository's collection scope, were accepted by Geoscience faculty for teaching.

Next we started acquiring additional space for the Crossman collection in our Oakdale campus storage facility. This involved two years of negotiations with University Facilities and the College of Dentistry who occupied the rooms we wanted. Finally we persuaded Dentistry to reorganize their facilities and vacate a 4-room complex. In the meantime we also applied for a new grant from the National Science Foundation to digitize parts of the Paleontology Repository collections and, among other things, to complete an inventory of the C. Strimple, Crossman, and Priest collections. Through this grant we were able to purchase temporary shelving for the Crossman Collection and hire students to move it from the Survey building to the Oakdale campus storage facility during the Fall/Spring of 2006/2007, taking care to keep the collection in the order it had been organized in the Survey building. This was no easy task, and could not have been done without the help of many student volunteers who gave their time, muscles and vehicles, in exchange for ice cream and a lunch or two.

Students employed under our Computerization grant have made inventories of the Crossman, C. Strimple and Priest Collections, and the Crossman inventory which was completed first has been made available to several researchers, including Jim Brower who is now studying some *Pleurocystites* specimens from the collection. Forest Gahn (Brigham Young University, Idaho) and Colin Sumrall (University of Tennessee) have visited the Paleontology Repository several times and have helped organize and identify specimens and lithologies in the C. Strimple and Priest collections. Compared to the Crossman Collection, these two collections pose the greater challenge for documentation as many specimens don't have any labels at all. For fossil specimens to be of any real use to paleontology researchers, they must have at least good locality data. Stratigraphic data is very desirable but often can be deduced from the locality, and identifications can be made by specialist researchers. Only occasionally, when localities are known for a very diagnostic lithology or suite of fossils, can locality be deduced, and even then there is always slight doubt that can tinge the specimens' usefulness for research. If donors are known to have collected from specific localities, this can narrow down possibilities, but doesn't help much with specimens exchanged with other collectors or purchased material. In cases where there is no information, and after consultation with specialist researchers (e.g., the specimen is not rare/exceptional preservation/research interest), specimens with no data may be transferred to the teaching collections (we have 3 grades of teaching collection), donated to other schools for their teaching collections, or used in the Millie and Sam Fossil Hunt sand box. The Paleontology Repository will not sell the specimens or use them for anything other than educational purposes.

NEXT STEP: IDENTIFICATION, PREPARATION AND INVESTIGATION

The Crossman Collection is now organized, inventoried, and has temporary labels giving as much information as is available. The next step is to catalogue individual specimens. This means assigning a unique number to each specimen, entering identification, locality, age, and collector data in the specimen catalogue, photographing new species or outstanding specimens and making all the information available on-line. We can start this immediately for Grade 4 specimens, but need specialist help with identifying most of the material, and also need to prepare specimens where necessary. Grade 4 specimens need to be incorporated into the collection stored in the Paleontology Repository, which requires major reorganization of the existing echinoderm collection to accommodate them. Our next goal is to acquire funding for a new project: "Development of the Midwest Crinoid Collection." For this project we will need to hire at least one graduate student and an undergraduate student to assist with organization and cataloguing; bring in crinoid researchers to identify species and lithologies, and purchase museum-standard storage for specimens currently stored on open-shelving at the Oakdale campus storage facility. Since there's no way we can accommodate the entire collection in the Paleontology Repository in Trowbridge Hall we need to upgrade our Oakdale campus storage to allow better access to, and organization and preservation of, specimens. We hope to develop a preparation area with equipment and a fume hood, and learn preparation techniques, by training at the Field Museum. An outreach component of this project could be a series of summer workshops for students and enthusiasts to learn or practice specimen preparation and crinoid identification. This will be the third grant these bequests have been included in, illustrating how a donation can grow into a very large project that can include students, researchers, enthusiasts, school children and the public. Watch this space!

ACKNOWLEDGEMENTS

Thanks to UI Museum Studies student Brittany Maltas for estimating the number of crinoid specimens in the Midwest Crinoid Collection, and to Geoscience undergraduate Alex Wall, for photography.

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A Crinoid Bank in the Mississippian of Eastern North America

Thomas Williams

Crinoids were virtually not all that long ago thought of as being extinct. However, if you were to go diving in places such as the Great Barrier Reef, the Straits of Florida, the Bahamas, Figi, Truk atoll, the Red Sea, and other suitable areas you will find living crinoids. Crinoids in these areas are found associated with reefs, in lagoons, and in deeper waters over 300 feet. Occasionally, such as in the Straits of Florida crinoids have been found living on bare rock basically all by themselves. They look similar to what is preserved in the fossil record but do differ with some crinoids having up to thirty two arms and some only five arms (Hess, Ausich, Brett, Sims 1999).

The Chesterian age units of Eastern North America are made up of significant amount of limestone and shale's and geologically make up a number of former carbonate platforms. (Pashin 1993 and others) In the eastern portion of North America the carbonate platforms occurred in Northern Alabama, Kentucky, Indiana and Illinois. The carbonate platform in Northern Alabama has been described as a bank which is a part of a reef complex extending across the northern portion of the state. As described by Selley 1985 a bank is a, "A carbonate buildup which is a syn-depositional topographic high of non-resistant wave material, e.g. an oolitic shoal, a coquina bank, or a mound of crinoid debris." More simply put a reef is a buildup of biological skeletons and related material which can include crinoidal debris. Reefs and reef type deposits which a bank is are typically found in the Paleozoic shallow tropical seas in neritic environments of normal marine conditions. Overall, you tend to find Paleozoic crinoids and their associated fauna in continental shelf waters meeting that have specific requirements for their survival. However, today's crinoids prefer colder deeper water environments (Bailey 2007, 1977).

Reef environments today occur for the most part occur in shallow tropical seas in settings such as the Great Barrier Reef of Australia or the Bahamas in the Caribbean. There is a known exception off the coast of Norway which occurs in colder deeper water. Reefs typically have four basic parts that include a back reef/shelf lagoon, the reef flat itself which can include growing reef rock and a reef front and a fore reef. (Seeley 1985). Pieces of a reef can be assembled with these basic parts or include other entities such as barrier islands. Today we classify reefs into three basic types; fringing reefs, barrier reefs, and atolls. Barrier reefs are long structures separated by a lagoon from the land. Fringing reefs are long structures that stretch out parallel to the coast but with little or no space to the land. The third is what is referred to as an atoll which is a circular structured reef usually involving an island or some sort of structure such as a volcano. This type of structure is common in the Pacific ocean today. Atolls contain a large lagoon inside of the circular structure. The circular structure can be built up into low level islands or structures just below the surface. (Seeley 1985) It is the lagoons and the off shore environments with the right conditions that provide habitat for crinoids past and present (Bailey 1978, 2007).

Paleo-Ecological conditions for crinoids

Crinoids are suspension feeder organisms in other words filter feeders. These are organisms as defined by Bailey 2007 as, “organisms that filter or sieve microscopic food from fluid usually water. Most marine or suspension feeder consumes small plankton (microscopic algae, animals and plants or organic detritus). Some of the materials may be living, others may be dead or decayed; other particles may be feacel debris.” Crinoids as filter feeders have living space limitations as a result of this survival mechanism which places their position in the fossil record as well. This helps us in the study and collection of crinoids by knowing where we may encounter them in the fossil record.

Open marine conditions begin with the salinity content of the ocean itself which typically will means a salinity content of greater than 30% salinity, however the water must become too saline over 40%. This type of salinity classification is referred to as ultra-haline. The creation of brine or brackish water environment through either restrictive conditions or the introduction higher salinity or freshwater will create unsuitable conditions. Paleozoic crinoids also needed relatively warm above 20 degrees Celsius for optimum conditions. This probably for the most part limited them the euphotic zone the top 100 meters of the neritic zone. This area is part of what is called the continental shelf also were the light requirements of the euphotic zone will also apply (Bailey 2007, Paleoecology WIU class notes 1978).

Turbidity is simply the amount of material suspended in the water which includes both organic and in organic debris. Water that is too turbid inhibits light penetration even in shallow water. Turbidity is a problem for filter feeding organisms especially sessile forms or life forms with slow mechanisms for transport themselves out of the cloud. Typically crinoids are going to be found in clear water with low turbidity. Therefore an influx of too much silt and clay can over whelm the filter feeders perhaps even resulting in rapid burial of the crinoids present. This may even cause an oxygen deficiency in an area causing an even faster burial (Bailey 2007, Paleoecology WIU class notes 1978).

Typical organisms associated with crinoids include organisms such as corals both colonial and solitary, bryozoans, and other miscellaneous fauna. These three groups of animals are sessile types of organism with similar living requirements and thrive along with crinoids. However, they too are bounded by the same kind of conditions and are commonly found intermixed with crinoids. One could conclude from this that introducing water and materials outside this narrow tolerance range to these organisms causes their elimination from this particular area at least temporally.

Geologic Time Frame and Deposition Environments of the Platform

During this time of the Mississippian, Northern Alabama and areas that stretched through out the Midwest of what is now the United States the former Laurentia continent of the Paleozoic Era. This area was in tropics with shallow warm water near the equator similar to exists. Tectonic influences included the up rising of the Appalachian Mountains from the collision of Africa and the North American/Laurentia continents to the east. Other more local influences such as, the Nashville dome, the Ouachita mountain, and farther north the continued formation of the Illinois and Michigan basins.

It was the rising of the mountains any other tectonic activity that provided possible sources of the necessary sediment for the formation of the carbonate platform/bank that were formed. The carbonate platform of Northern Alabama appears to have depositional environments that have been created as a result of two orogenic belts, the Appalachian and Ouachita. (Pashin 1993) A platform or bank with clastic and carbonate tidal flats began in Kentucky and followed the orogenic belts into Alabama but thins rapidly to the southwest of this area (Chestnutt and Ettleson text fig. 4 bul. 330) (Pashin 1993).

Moving outward from the tidal flat areas, the environment grades into the Bangor-Glen Dean formations sand belt that is a platform or bank which contains a lagoon and shoals areas, see figures 1 and 2. The lagoonal environments that contained the shoals created good conditions for crinoids and other echinoderms. Shoal type environments provided more stable substrates for crinoids stem attachment. In addition, shoals provide the necessary currents required for filter-feeding organisms see figure1. These areas tended to be of higher energy and have access to nutrients being carried up from deeper water. The crinoids living on these shoals would be controlled to some point by the wave base action from the open ocean. Fossil evidence from different types of deposits show that crinoids may have been present in more shallow areas such as intertidal zones and shallower portions of the lagoon. This is provided enough water and nutrients were present to sustain life in shallower water. However, from fossil evidence crinoids appear more commonly in certain zones that provided the best combinations for entire crinoid banks to develop. Larger crinoids in particular would need some depth below the wave base where actions from waves couldn’t smash them to bits or repeatedly tear them up. However, the fossil record reveals crinoids regenerated arms when this occurs, therefore, crinoids in a more rugged area are possible. So their best areas of existence in a certain place would constitute a balance of the all of the factors present (Chestnutt, Ettensohn 1999).

Out side of the Glen Dean-Bangor sand belt grades into the open marine areas of the Hartselle-Hardinsburg formations which contain various geologic materials from sandstones to shale’s. Throughout this area barrier islands existed composed of units such as the Hartselle. These islands essentially were large sand bars as evidence from large sandstones of the Hartselle formation. In other cases these sands would simply create a sand bar below keeping the open ocean from directly crashing into lagoon shoal areas providing some level of protection, however, sand bars do migrate. It is evident from the units contained within the Bangor that influxes of shale and sand were relatively common in places. In other places no shale is present, yet the limestone is still highly fossiliferous with crinoid material but very massive in places as well (Thomas 1972 Tull 1980).

Stratigraphy of the Alabama Carbonate Platform

The Bangor limestone is Mississippian in age and part of the Chesterian series in northern Alabama. In general area of this crinoid bank the Bangor overlies the Hartselle formation. Bangor limestone in much of Alabama is overlain by the Pennington fm, but towards the west in many places it is not present. In northwestern Alabama the lower Cretaceous gravels unconformably overlie the Bangor and towards the southwest of the Bangor limestone platform, where tongues of the Floyd shale become more common (Burdick 1982, Thomas 1972).

In Alabama as described by Thomas 1972, “The Bangor Limestone is primarily a bioclastic limestone and oolitic limestone. Other constituents include micrite, shaly argillaceous limestone, calcerous clay shale, and in Northeast Alabama fine grained earthly dolostone.” Included within the limestone are, “…small reef like masses of corals” that occur throughout the sequence. Oolitic and bio-clastic limestones with some shales inter-bedding dominate the area of the carbonate platform where crinoids have been found in Alabama. The massive oolitic limestones tend be at least fifty feet in thickness and contain the lots of reef-like coral masses. These limestones decrease in thickness toward the Warior basin in the west where the Floyd Parkwood formations are deposited. (Thomas 1972 and Pashin 1993) According to Pashin 1993, “Southwestward thinning of the Bangor and passage of oolitic grainstone into wackestone and shale suggests that agitated environments of the platform were bordered on the southwest by a carbonate ramp where lower-energy biomicrite shale prevailed.” Also deposits of paleo-sols in this area reveal island formation in the platform and show what Pashin describes as “shoaled bank rim”. (Burdick 1982, Pashin 1993)

The Hartselle units have been described in places is as quartz arenite which means that it is almost made up entirely of quartz and probably beach sand. These deposits have also been responsible for off shore barrier islands in places thus helping to create the overall setting for the formation of this off shore crinoid bank. As the sea advanced towards these barrier islands the carbonate facies of the Bangor limestone were deposited. This carbonate platform and bank would create a substrate favorable for organisms requiring an environment in which calcium carbonate was able for the formation of shells and exoskeletons. The crinoid bank described here, is in the lower part of the Bangor and equivalent to the Glen Dean of Illinois and Indiana as noted from work by Horowitz and Butts. (Smith 1967)

Crinoids in the Bank

Specimens preserved here reveal a fantastic preserved fauna in situ living position showing crinoids from immature to full size adults. Stem length reveals the longest stem encountered was five feet in length belonging to an *Onychocrinus pulaskiensis*. Numerous stems up to lengths of three feet were encountered throughout the entire excavation attached to *Onychocrinus*, and *Culmicrinus*. Though good specimens were not recovered of large *Phalcelocrinus*, they were present. The large stems of *Onychocrinus* in many cases provided a base for stems of other crinoids to wrap themselves around in particular inadunates and small camerate crinoids. The deposit also revealed that the crinoids were tiered in three to four layers. The larger *Onychocrinus, Culmicrinus, Phacelocrinus* and perhaps some of the *Aphelecrinus* made up the top layer. Next layer was composed of inadunates such as *Phanocrinus bellulus*, smaller *Aphelecrinus*, and immature crinoids of the top tier. The lower tiers would be composed of again smaller crinoids which didn't get large to begin with. Towards the substrate, the stems large siri are present and perfectly preserved which were used to anchor the specimens to the substrate. Siri are extremely fragile extensions extending from the more robust stem to assist in anchoring the crinoid. With the excellent preservation of the siri on so many specimens it only goes to reinforce that this once prominent crinoid bank was buried very quickly.

Conclusion

The rock units here in Alabama show that he crinoids were living on this crinoid bank in a number of possible locations. Included in this would be crinoids living behind the barrier island complex in the lagoons in a somewhat shallower more protected positions, possibly limiting larger growth opportunity. Other deposits of this time frame in Kentucky Indiana and Illinois reveal crinoids of similar kinds and sizes, but these deposits reveal more agitation in deposition. Limitations such as agitation will limit the size of the crinoids to a certain extent and favors transportation of material including the fossils. This could also just be a factor of the fossil record and preservation. However, crinoids at least one place of the Alabama crinoid bank are found in all sizes from immature to fully developed. These crinoids preserved and described here were killed off by an incursion of black micritic mud turned into soft shale 4 to 6 inches in thickness possibly brought up from depth by a large storm given the extensive network of preservation of crinoids in situ. This shale formed a seal thus preserving these fossils in situ as noted by the extensive network of attached stems to complete crinoid crowns that can be found.

In addition, this mud incursion could have created an oxygen deficient condition making a more rapid burial possible increasing preservation. Placement of this crinoid bank on this outer portion toward more open ocean would mean crinoids would have the chance get larger with optimum conditions present. The seaward locality on this part Carbonate Platform in Northern Alabama probably represents the optimum conditions for crinoid development as well as preservation.

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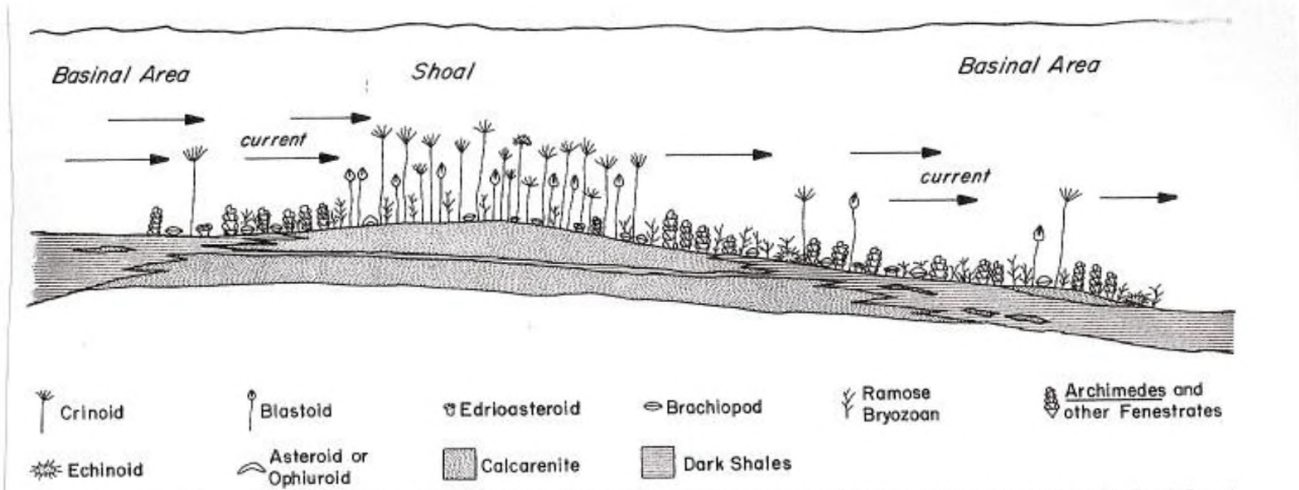
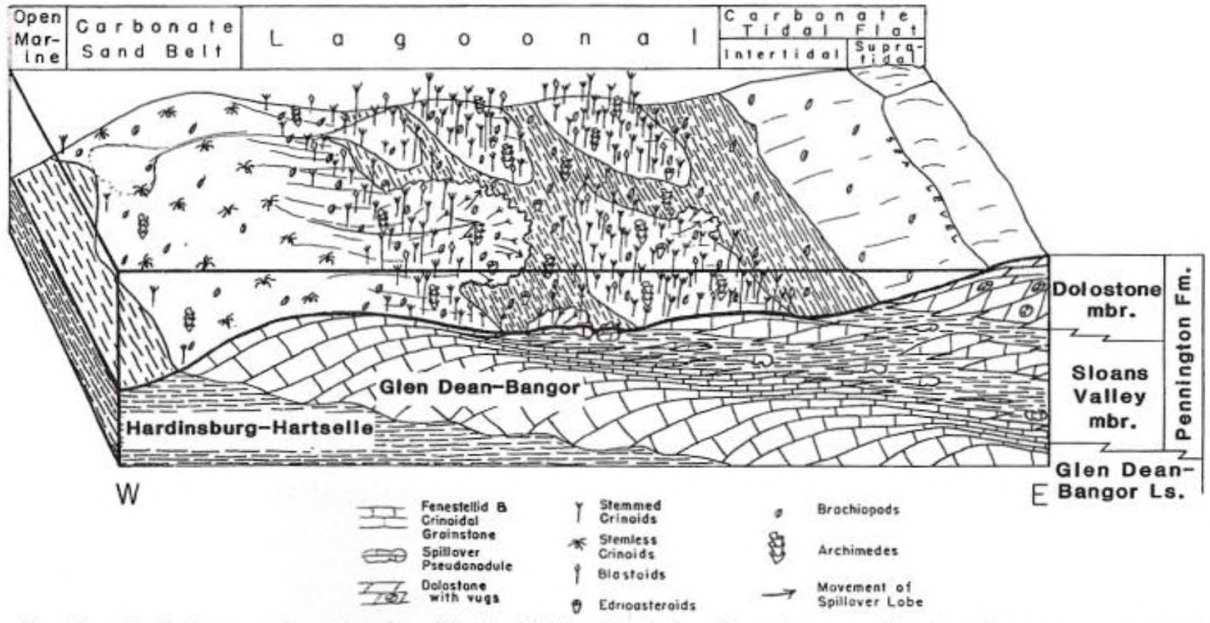


Text-figure 9.—Schematic reconstruction of carbonate shoals and nearby muddy basinal areas in the Sloans Valley lagoon showing inferred stratification of suspension feeders and relative positions of common organisms on and near shoals.

Figure 1 Chestnutt D.R. Ettensohn F.R., 1988



Text-figure 6.—Environmental reconstruction of the late Middle and early Late Chesterian progradational continuum represented by the sequence of units from the Hartselle–Hardinsburg through the dolostone member of the Pennington Formation in south-central Kentucky.

Figure 2 Chestnutt D.R. Ettensohn F.R., 1988

Some Crinoids from the Bangor Fm.

Onychocrinus sp.

Onychocrinus sp.

Phanocrinus bellulus

Zeacrinites sp.

Coon Dog Dig, Bangor Formation, Upper Mississippian

The Crew Larry, Tom, Carol, Wendy and Dennis

The crew removing cover shale

The crew examining the crinoid bed

Larry examining crinoid bed

Tom tracing a stem into the cover shale

Wendy performing touch up gluing

Coon Dog Dig, Bangor Formation, Upper Mississippian

Larry and Wendy preparing area for epoxy gluing

The crew working preparing specimens

Epoxy glued area next to next slab.

Area in preparation, close up of above photo.

Martin sawing glued slab

Lifted out slab Onychocrinus with stem

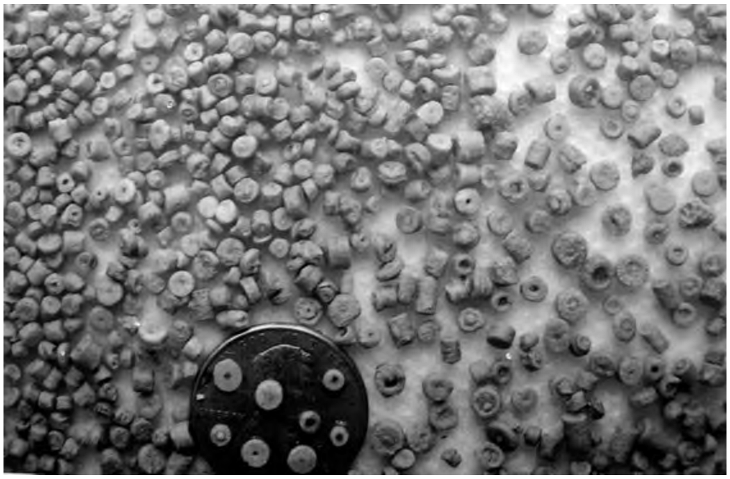
Cambrian crinoids
Bruce Stinchcomb

True crinoids—that is an echinoderm with a stem and a holdfast (pelmatozoan) which is not a cystoid or a paracrinoid—are rare or non existence in the Cambrian Period, that period of geologic time which held the first "flowering" of invertebrate animals, many possessing distinctive hard parts. Two questionable crinoid-like fossils are known from the famous Middle Cambrian Burgess Shale otherwise Cambrian crinoids are unknown! Crinoids (as well as most other echinoderms), when they die disarticulated and their hard parts, consisting of the head (calyx) and stem (pelma), scatter but may also the concentrate and form so called crinoidal limestones. Crinoidal limestones are particularly common and widespread in the late Paleozoic Mississippian Period (Lower Carboniferous) where sizeable beds of limestone can be almost entirely composed of their disarticulate hard parts. The well known Burlington and Keokuk limestones of the Midwest U S being good examples as well as Lower Carboniferous limestones of other parts of the world such as found in the Urals of Russia and the Brooks Range of northern Alaska.

Middle Ordovician limestones can also contain pelmatozoan fragments similar to those of later periods of the Paleozoic Era; Ordovician "crinoidal" limestone (pelmatozoan limestones) do have crinoids as a major contributor however disarticulated plates and stems of cystoids and paracrinoids are also major contributors. Crinoid-like fragments, including stem fragments similar to those found in Ordovician limestones also occur in Upper Cambrian limestones such as the Flathead Formation of Wyoming and the Bonneterre Formation of Missouri. In limestones of these Cambrian formations can occur pockets of what look very much like crinoid stem fragments—their being from true crinoids is doubted although they do look like small crinoid stems. For one thing, complete crinoids are unknown from localities where complete, articulated Cambrian echinoderms do occur. Both the Spence Shale of southern Idaho and the Wheeler Shale of western Utah yield excellent complete echinoderms but crinoids have not been found. What is found (and desirable) are eocrinoids, a class of stemless crinoid-like echinoderms which went extinct after the Cambrian and **cystoids**—an extinct phylum of echinoderms which have a stem. Cystoids represent a sizeable category of echinoderms which supplied the raw material in the 1980's and 90's for a number of "new" classes (viz. body plans) of echinoderms., Echinoderm classes proposed included "new" classes like the homostealians and the stylophorans. These (presumed) echinoderms (stylophorans have been placed as an extinct phylum by some paleontologists) lack a pelma (stem) and were apparently free swimming. Cystoids on the other hand, have stems which were often attached to hard grounds. The issue of Cambrian echinoderms is still a "muddy" one as well as a complicated one.

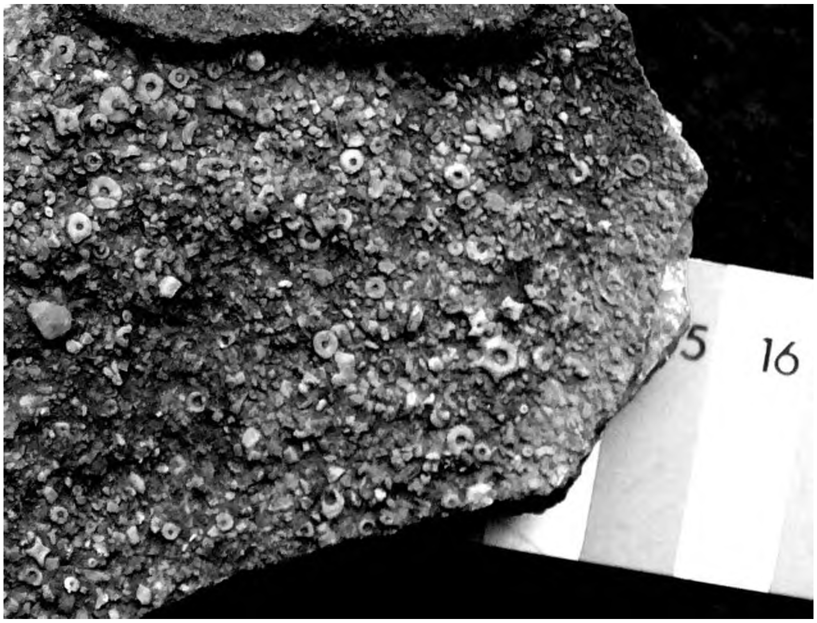
My interest in these fossils was tweaked by the finding a Cambrian stemmed echinoderm which resembled a crinoid as well as finding various "crinoid" stem-rich limestone pockets in Cambrian age rocks. In many ways the Cambrian Period was a strange, archaic world whose fossils are representative of body plans different from those of later geologic time. Fossils shown here are (presumably) not crinoids—rather they are echinoderms, probably cystoids representative of that time designated as **B C**—that is **before crinoids**.

#1. Unidentified-stalked Cambrian echinoderm. This fossil was tentatively placed as a crinoid? in my 2008 book “Paleozoic Fossils”; It is most likely an undescribed stalked cystoid from the Davis Formation, Ste. Francois Co., Missouri.

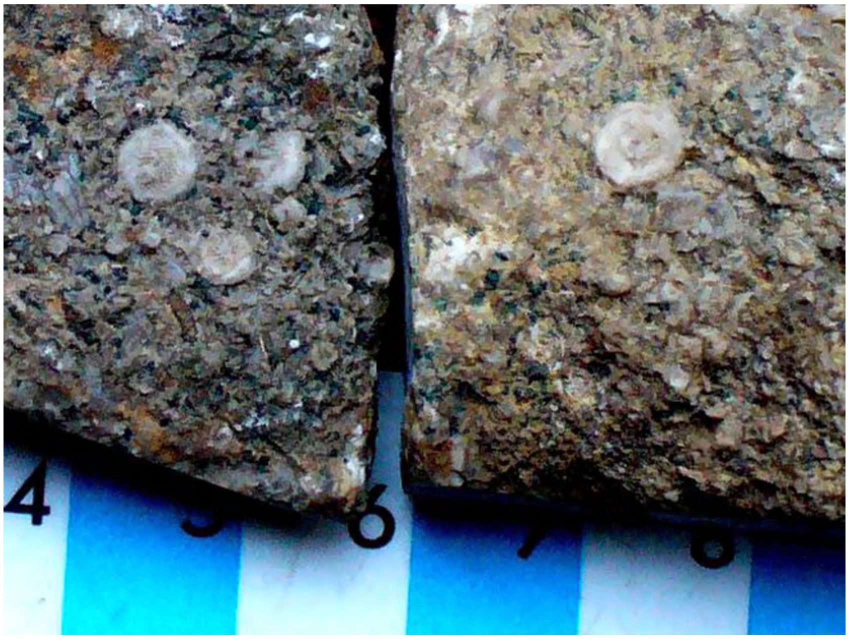


#2. “Crinoid stem fragments”. Cambrian age rocks were scoured when a huge rush of water spilled from a failed pumped-back-electrical storage facility, (Taum Sauk Reservoir) in southern Missouri. Exposed in this potential catastrophe were shale beds which yielded these small crinoid stem like fossils. If these fossils were Ordovician or younger they would be considered as crinoid stem fragments—being Cambrian in age they probably are from some sort of cystoid. Bonneterre Formation, East Fork of Black River, Missouri.

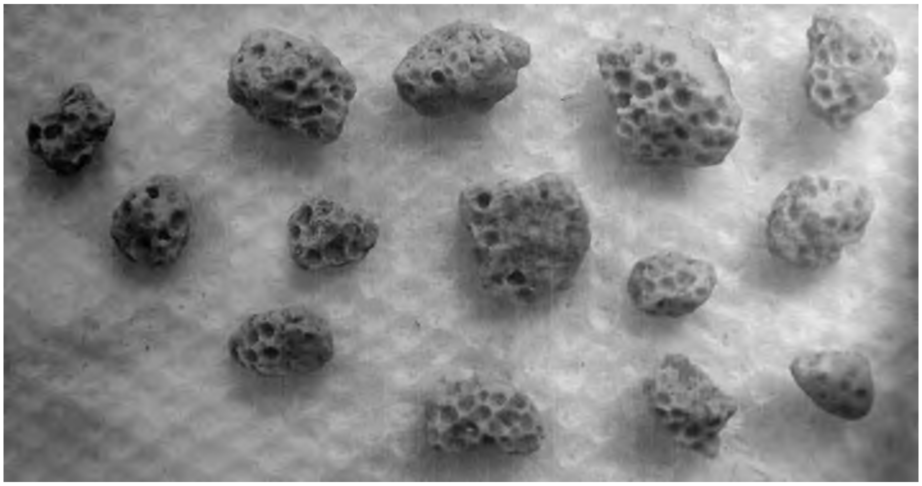
#3. Holdfasts. These button-like holdfasts (Echinoderm pelma attachment structures), can locally be abundant on what are referred to as hardgrounds (hard limestone surfaces which existed on the ancient sea floor). The crinoid-like stem fragments of the previous picture may have been attached to something like these. Crinoid stem holdfasts usually resemble the root of a plant rather than having a button-like shape like these. Davis Formation, Ste Francois Co., Missouri.



#4. Crinoid like stem fragments from the Big Horn Mountains of Wyoming. The Flathead Formation of Wyoming's Big Horn Mountains can locally contain limestone beds full of these fossils. Such fossils, if younger than the Cambrian, would be considered as being from crinoids. As with the Bonneterre fossils these, if they were younger would be considered as parts of crinoid stems. They are probably from cystoids — stemmed echinoderms which predated the crinoids back in B C—that is, **before crinoids**.



#5. Peculiar crinoid stem-like fossils from the lower Bonneterre Formation Ste. Francois Co., Missouri. These look like crinoid stems except that they have small perforations in them. They may be a type of sponge or again they may be parts of peculiar cystoids—a number of small, odd fossils occur in the Bonneterre Formation.



#6. *Kinsabia* sp. A small coral-like fossil associated with "crinoid stem" like fragments from the Bonneterre Formation of Missouri.

CRINOID COLLECTING IN THE BURLINGTON LIMESTONE

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GATHER YE CRINOIDS: A FOREWORD

The opening lines of Samuel Calvin's (1897) memoir of Charles Wachsmuth state that "Burlington, Iowa, has long been classic ground to the paleontologist, particularly to the student of that special branch of paleontology which deals with the most beautiful of all the fossil forms, the crinoids."

As a son of Burlington and a student of her crinoids, there are few experiences more personally fulfilling than the discovery of a bone-white crown in soft, orange-tinted encrinite. Moreover, there are few acts more humbling or provocative than contemplating the origins, relationships, and fate of such objects.

I desire that my tombstone will include the phrase "Gather crinoids while ye may," a twist on Robert Herrick's famous poem, "To the Virgins, to Make Much of Time." Not only do I gain great satisfaction by collecting crinoids, I'm moved by the histories of those who collected before me, and I hope to leave a legacy for those who follow.

Hearing the conversion stories of fossil enthusiasts is among my favorite aspects of MAPS and paleontology generally. Accordingly, this contribution includes a slight indulgence: my own introduction to crinoids and that of my historical heroes, Charles Wachsmuth and Frank Springer. I'll also share some observations on the Burlington Limestone and its crinoids that, I hope, will increase your knowledge and enthusiasm for the most diverse crinoid-bearing formation in the world.

With the exception of the first few sections, much of this paper is taken directly from my contribution to the 64th Annual Tri-State Geological Field Conference Guidebook (Witzke et al. 2002). Because it originally received very limited distribution, and because many MAPS members might find its content helpful, I decided to reprint it here with the final edits that never made it to press and a few additional modifications. Generally, that publication (Gahn 2002) provides a simple, yet accurate framework for recognizing and recording fossil occurrences in the Burlington Limestone. For this contribution, I had hoped to prepare a series of plates that illustrate the composition of the crinoid and blastoid biozones of the Burlington Limestone, but other obligations interfered. However, for those not familiar with the crinoid and blastoid species of the Burlington Limestone, Shimer and Schrock's (1944) *Index Fossils of North America* should provide an adequate introductory visual reference.

To anyone who has a question about the Burlington Limestone or its echinoderms, I welcome you to contact me. I'd be especially grateful to receive images of particularly remarkable specimens that you've collected or purchased. Although the Burlington Limestone has been heavily collected for over 150 years, many of the described species are known from just a few specimens, and new species are still being found. For example, *Cyathocrinites deroseari*, one of the most recently described Burlington crinoids (Kammer and Gahn 2003), was based on two specimens collected at a single locality by Doug DeRosear. Doug kindly donated the only known crown (and holotype) to the Smithsonian so it could be formally named. I purchased the second specimen, a small calyx, from Doug at a MAPS EXPO for $5! I'm also very interested in specimens that record biotic interactions, such as regenerated arms, drill holes, and infesting gastropods and ophiuroids.

At the end of this contribution (Appendix), you'll find a table that includes a working list of all the crinoid and blastoid species in the Burlington Limestone, their stratigraphic distributions, and relative abundances. Not only do I hope that you'll find it useful, I would appreciate receiving any reports of discoveries that would increase our understanding of species distributions in the Burlington Limestone.

Forget the rosebuds, gather ye crinoids while ye may!

BORN ON THE BURLINGTON

I'll never forget Thanksgiving, 1990. That's the day I found my first crown. I was a senior in high school, and the crinoid was *Eratocrinus elegans*. It was a slightly compressed crown with a partial stalk, and it glistened like a beacon as it lay wet in a southeast Iowa creek. Filled with a sense of wonder and accomplishment upon seeing the prize, I launched my rock hammer into the air and exclaimed aloud "Oh glorious day!" Though overly dramatic, even borderline cheesy, those words adequately express the way I feel every day I spend on the Burlington Limestone.

My conversion to crinoids began months prior to that cool November day when *Eratocrinus elegans* engraved that moment on my memory. In part, the satisfaction that I felt then was the culmination of a many-months search for a near perfect Burlington crown.

I began my junior year at Burlington Community High School excited to take a year-long geology elective. I couldn't have known how it would change my life or the debt of gratitude that I would owe its teacher, Sherman Lundy. One day Mr. Lundy introduced the class to the geology and paleontology of Burlington, Iowa. He placed an overhead on the projector that contained extraordinary images of creatures that he explained were once prolific in ancient seas that covered Burlington. Crinoids? I remembered seeing their remains in the bluffs, creeks, and even building stones around town, but I didn't know them by name, and I had no idea that crinoids were animals. Even more astounding was the fact that their columnals supported a complex feeding structure on one end and a plant-like root on the other. I was in awe and determined to learn more about them.

The semester was nearly over when Mr. Lundy introduced the class to crinoids. Before its end, I asked him if I could borrow a rock hammer and if he could offer some advice on where I might find a complete specimen. It wasn't far into summer break before I laid out a plan, stowed food and water into a pack, and readied myself for my first crinoid hunt.

The next morning I awoke to a heavy rain that tested my resolve. Determined, I threw on my pack, pulled a raincoat over my head, and started riding my bike toward a nearby outcrop. Tunnel-vision set in as I started looking intently at the rocks. Every beautiful grain in that limestone had my attention, and it wasn't long before I noticed the freely-weathered fossils in the wet soil. I started collecting and examining every columnal, and after a few hours a curious round ball caught my eye—my first calyx! As the hunt intensified, I forgot about the rain, my lunch, and the rest of the world. In fact, it grew dark before I could pull myself away, and it was my mom who had to do that. I told her where I was going and she had come to find me. It wouldn't be the last time I strained twilight for just one more specimen.

By the end of the summer I had a small shoebox full of crinoids, but even then I wasn't sure what I was looking at. Surprisingly to me, the calyxes that I had collected weren't all the same. In my inexperience, I expected a crinoid to be a crinoid, but clearly, there were different kinds of crinoids. The concept of diversity in deep time was slowly growing in my mind, but it was soon to rise up like a vast forest.

Near the beginning of my senior year I revisited Mr. Lundy with my small box of crinoids. I think he was amazed that I went to look for them at all, but he was even more surprised by the number of specimens. He referred me to a few books at the Burlington Public Library where I found the 1897 *North American Crinoidea Camerata* by Charles Wachsmuth and Frank Springer. I began by opening the third volume that contains 83 lithographic plates. I was humbled and captivated: humbled by my now seemingly insignificant box of specimens and captivated by the astounding diversity of the crinoids so beautifully illustrated on those pages. I even recognized a few of them and was able to assign a name to the first crinoid calyx that I had collected: *Azygocrinus rotundus*. That first rainy day of collecting I'd also found specimens of *Abatocrinus laura,* and *Macrocrinus verneuilianus*. However, there were so many species that I hadn't found, many of which were beyond imagination and absolutely remarkable.

Equal to the awe generated by examining the illustrations was the sense of wonder inspired by the text. Many of the specimens were collected, and the publication under consideration was written, in my hometown! I enjoyed a newfound respect for Burlington and her crinoids. From that evening I knew that I would spend the rest of my days considering these extraordinary animals. Moreover, I was enthralled by the histories of Wachsmuth and Springer. Who were these men, and what compelled them to dedicate their lives to crinoids?

WACHSMUTH & SPRINGER

The story of Charles Wachsmuth has been told in many places, but in one publication that should have celebrated his life, he wasn't even mentioned. The year Wachsmuth died, Hamilton Kirk Watkins (1896) published an illustrated celebration of the semicentennial of Burlington, Iowa. The work addresses the history of the city and highlights many of its prominent citizens. It opens with a few lines from Henry Wadsworth Longfellow's *A Gleam of Sunshine*:

Let me review the scene,
And summon from the shadowy Past
The forms that once have been.

Ironically, this poem, which could so fittingly apply to the paleontology of the city, doesn't mention Wachsmuth or his work, both of which were world renowned well before Burlington's semicentennial.

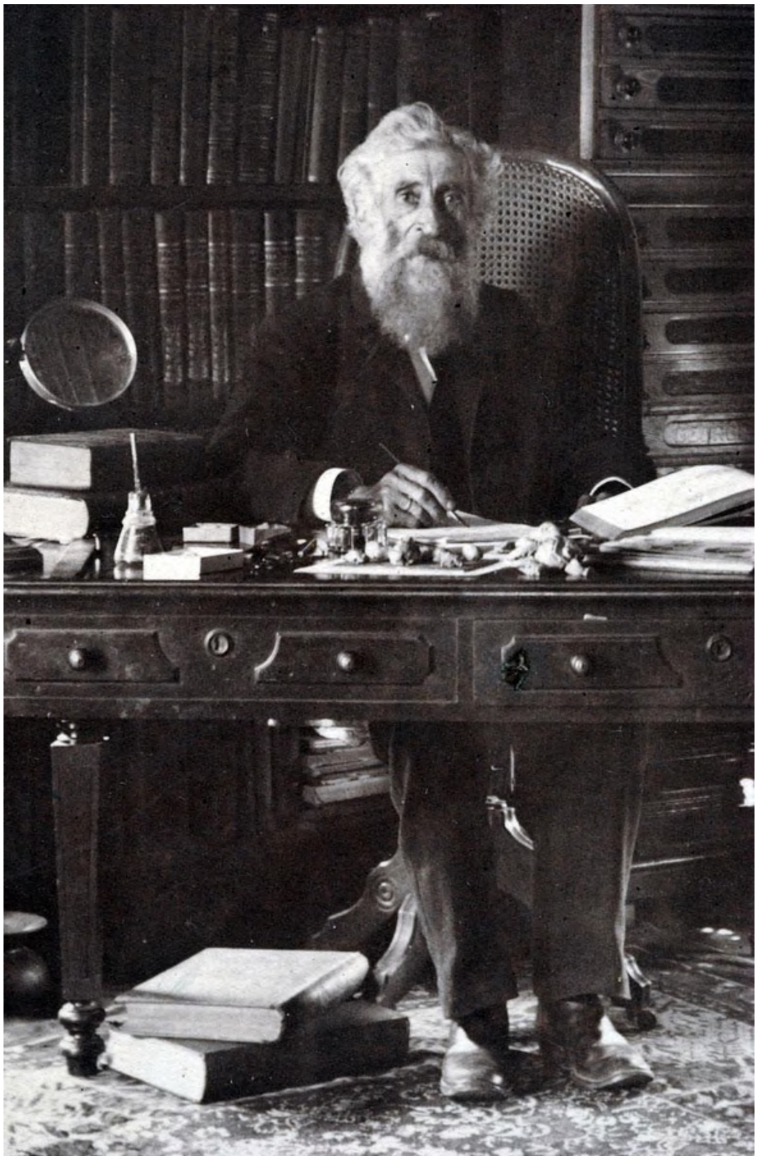


Figure 1. Charles Wachsmuth (1829-1896).

Charles Wachsmuth (Figure 1), a native of Hanover, Germany, was born on September 13th, 1829 (this year marks his 180th birthday). He immigrated to the United States in 1852, and by 1855 he had settled and married in Burlington, Iowa where he and his wife operated a small grocery store, *Wachsmuth & Rose*. Since his youth, Wachsmuth struggled with poor health. His physician, Otto Thieme, was a Burlington crinoid enthusiast, and "the first who began their systematic study after the few obtained by Owen's expedition in 1848-49" (Springer 1820). When Wachsmuth sought his medical advice, Dr. Thieme prescribed a heavy dose of crinoid collecting! Wachsmuth took his medicine, and "it did not take long for him to develop into an enthusiastic collector, so that days at a time were spent in quarries and ravines around the city, his wife often looking after the store" (Keyes 1897). Likewise, British crinoid specialist and colleague Francis Bather wrote that the "magnificent remains contained in the Burlington Limestone, especially the fossil crinoids, soon aroused in him the enthusiasm that ceased only with death" (Bather 1896).

Aldo Leopold (1949), famed conservationist and Burlingtonian, recalled Wachsmuth at work:

"When I was a boy, there was an old German merchant who lived in a little cottage in our town. On Sundays he used to go out and knock chips off the limestone ledges along the Mississippi, and he had a great tonnage of these chips, all labeled and catalogued. The chips contained little fossil stems of some defunct water creatures called crinoids. The townspeople regarded this gentle old fellow as just a little bit abnormal, but harmless. One day the newspaper reported the arrival of certain titled strangers. It was whispered that these visitors were great scientists. Some of them were from foreign lands, and some among the world's leading paleontologists. They came to visit the harmless old man and to hear his pronouncements on crinoids, and they accepted these pronouncements as law. When the old German died, the town awoke to the fact that he was a world authority on his subject, a creator of knowledge, a maker of scientific history. He was a great man—a man beside whom the local captains of industry were mere bushwhackers. His collection went to a national museum, and is name is known in all the nations of the earth."

Among the "great scientists" that visited Wachsmuth was Louis Agassiz, the celebrated Swiss naturalist and founder of Harvard's Museum of Comparative Zoology. In 1864, Agassiz decided to visit Wachsmuth and his collection while on a speaking tour. Coincidently, on that same speaking tour, Agassiz spoke at the University of Iowa on "the coral reefs of Iowa City" (Caffey 2006). His presentation deeply impressed another future crinoid specialist, Frank Springer, to whom we'll soon return.

While in Burlington, Agassiz invited Wachsmuth to visit him in Cambridge, and by 1865 the Wachsmuths had sold their business in Burlington and accepted Agassiz's invitation to visit Harvard before traveling to Europe on an extended vacation. In England, they visited the British Museum of Natural History. Bather (1896) mentioned that Wachsmuth arrived at the museum "with one of his magnificent Burlington specimens in either pocket."

In addition to Agassiz, Fielding Meek and Henry Worthen, from the Geological Survey of Illinois, learned of Wachsmuth's collection and made arrangements to study it. Nearly every Burlington crinoid species described and illustrated by Meek and Worthen (1868, 1873) was collected and prepared by Charles Wachsmuth, whose contributions were graciously acknowledged (Meek and Worthen 1873):

"Through the kindness of Mr. Charles Wachsmuth, of Burlington, Iowa, we have recently had an opportunity to examine some unique and exceedingly interesting specimens of Carboniferous

Crinoids,…but, before proceeding to do so we avail ourselves of this opportunity to express our thanks to Mr. Wachsmuth for the zeal, industry, skill and intelligence he has brought to bear, in collecting and preparing for study, such an unrivaled series of the beautiful fossil Crinoidea of this wonderfully rich locality [Burlington]. Some idea of the extent of his collection of these precious relics may be formed, when we state that of the single family Actinocrinitidae alone, after making due allowances for probably synonyms, he must have specimens of near 150 species, or perhaps more, and many of them showing the body, arms, and column."

"It is also due to Mr. Wachsmuth, that we should state here that he is not a mere collector only, but that he understands what he collects, and knows just what to collect, as well has how to collect."

Wachsmuth had collected and catalogued nearly 400 Burlington crinoids by the late 1860's. It's also clear that his collection included other echinoderms: blastoids, echinoids, and ophiuroids. Moreover, he had begun thinking, and even writing, about their morphology and taxonomy. In their publications, Meek and Worthen (1868, 1873) referred to a manuscript written by Wachsmuth and even used a genus, *Nipterocrinus*, which was proposed by him as the name for one of his undescribed specimens. As indicated by Calvin (1897), "to a mind as gifted as Wachsmuth's the more purely intellectual questions of morphology, derivation, and natural relationships became invested with the keenest interest." Yet Wachsmuth remained "a man of simple, unobtrusive habit, scarcely known outside a narrow circle of intimate friends."

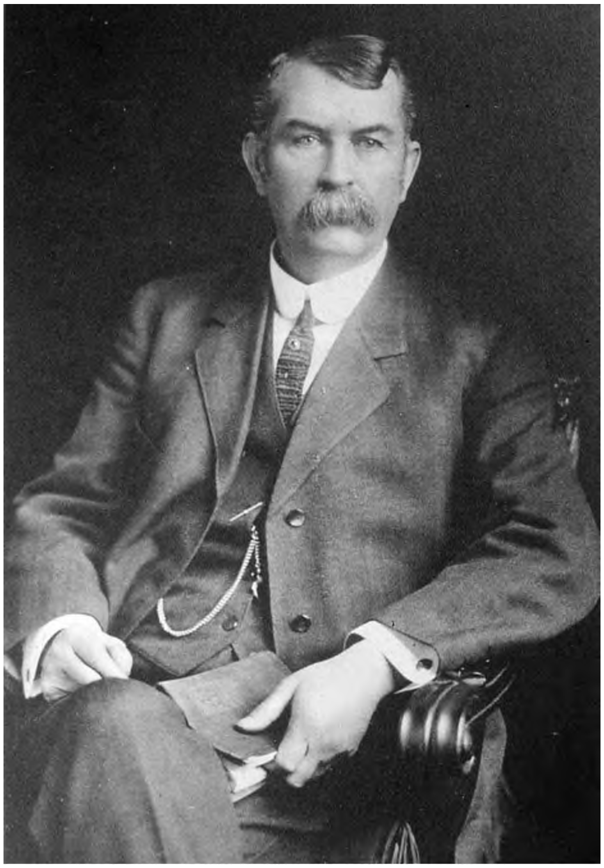


Figure 2. Frank Springer (1848-1927).

Within Wachsmuth's circle of intimate friends was Frank Springer (Figure 2). Springer was born on June 17th, 1848 in Wapello, Iowa. Early in life he decided to pursue a law degree at the University of Iowa, which he completed in 1867. While attending the University of Iowa, Springer was not only inspired by a geology lecture from Louis Agassiz, he became enthusiastically engaged in the study of geology and paleontology. In fact, during his later years at the University of Iowa, Springer worked under the direction of Charles White and Orestes St. John, independently studied fossils in the collections of the geological survey, and cared for the collections while White and St. John were engaged in fieldwork (Keyes 1896). During his early foray into paleontology, he seemed particularly drawn to the remains of fossil fish.

After graduating from the University of Iowa in 1867, Springer accepted a position in the law office of Henry Strong, Burlington, Iowa (Caffey 2006). According to Springer's personal field notes, his interest in paleontology continued to mature, and he traveled throughout southeast Iowa and eastern Illinois searching for fossils, often with Orestes St. John. By 1869, it is clear that Springer had met Charles Wachsmuth and that the two men had begun collecting fossils together by 1871. Wachsmuth's knowledge and passion for crinoids further shaped Springer's paleontological interest and ambition, and between them a collaborative friendship developed that would reverberate through the world of science.

Although Springer was compelled to abandon his pursuit of law for a life devoted to paleontology, he lamented that "it won't pay. Science is so little appreciated in this country that one can hardly make a comfortable living who devotes himself to it" (Caffey 2006). Ultimately he decided to press forward with his career in law, and in 1873 he left Burlington for Cimarron, New Mexico, where he was offered a lucrative position with the Maxwell Land Grant and Railway Company. However, his forward-looking choice was made with the intent of securing a comfortable future so that he might devote his later years to his now beloved crinoids.

Springer's move to New Mexico hardly severed his newly formed bond with Wachsmuth or his burgeoning interest in crinoids. On April 23rd, 1873, just a few months after he left Burlington, Springer wrote to Wachsmuth, "I have thought of you frequently. Especially on Sunday, when I have often wished I could go by telegraph and spend the day with you…I need not tell you how much I enjoyed the time we spent together." He then at length explained his early experiences in New Mexico, and closed with "I should like to know all about your fossilizing, your collections, etc…I see by the paper you have had plenty of rain, and I expect you have found some good things already."

Later that same year, Louis Agassiz made a second visit to Wachsmuth and his crinoids in Burlington. According to Keyes (1896), Agassiz "was greatly surprised at the enormous growth of the collection since he had last seen it, and, struck by the beauty and perfection of the specimens, he intimated that he was anxious to procure the collection for Cambridge, at the same time expressing a desire to have Mr. Wachsmuth go with it and take charge of all the crinoids in the museum." Agassiz was granted both wishes: he received the collection and Wachsmuth went to Harvard. However, Wachsmuth remained in Cambridge only until Agassiz's death in December, 1873, following which, he and his wife traveled through "Italy, Greece, Turkey, Arabia, and Africa" (*The*

Hawkeye, February 11th, 1896).

Before Agassiz's death, he encouraged Wachsmuth to publish his own work and ideas rather than allowing the fruits of his labor pass to other researchers. According to Keyes (1896), it was Agassiz who encouraged Wachsmuth "to publish the results of his observations under his own name, on the ground that he was doing a great injustice to himself by placing them in the hands of others."

Agassiz wasn't alone in his encouragement of Wachsmuth. Perhaps because of his concern for Wachsmuth following the concurrent loss of his collection and mentor, Springer wrote him (March 18, 1874) extolling his qualities as a scientist and pleading that he publish his discoveries, "You have laid the foundations of the most important investigations by far, that have ever been undertaken in this field. You have struck out in an original path, and you bring to the subject a knowledge which no one else can command. I have sometimes thought that you did not fully appreciate the immense advantage you possess in prosecuting such investigations in your unequalled familiarity with the formations in which the fossils occur, your intimate knowledge of the character of the rocks, the mode of occurrence, and association of the various forms, their distribution, and succession in the different beds. The more I see of paleontological work, the more firmly I am convinced that such knowledge is absolutely essential to reliable results. All this you possess in a preeminent degree…it is no mere flattery or compliment to say that no man living is prepared to do the work you have begun so well as you, and from no other source can we at present hope for so much of real scientific value on the subject as from you. If you will pursue the work to its legitimate result, you will but accomplish the wishes of your most sincere friends. I remember how slow you were in beginning original work and your disposition to allow others to reap the credit of your observations and benefit from your knowledge, and this makes me constantly fearful that you may tire of the work and throw it aside. You have worked too long and stored up too much knowledge of crinoids to permit it to rest without some lasting monument, some permanent result. You owe it to the scientific world, to give it the benefit of your observations, and you owe it to yourself to secure the fame and credit which justly belongs to you. If you don't do yourself justice in this respect, I shall continue to grumble."

Wachsmuth may have returned to Burlington without a crinoid in his collection, but he certainly hadn't lost his drive to collect. Within a few years, he had amassed a new collection that exceeded the first in quality and quantity of specimens. Moreover, and perhaps because of the encouragement of his friends, he spent the rest of his days publishing the results of his investigations. In addition to authoring nearly 100 pages of text on fossil crinoids as the sole contributor, Wachsmuth and Springer jointly published almost 2000 pages from 1877 to 1897. Most highly acclaimed were the *Revision of the Paleocrinoidea* (published in four parts between 1880-1886) and the *North American Crinoidea Camerata* (1897).

Although the names "Wachsmuth & Springer" are conjoined in the annals of science, the intellectual credit for most of their work belongs to Wachsmuth. Springer's obligations in New Mexico allowed him little time for research, which was an ever-present source of frustration and contention between them. Generally, their working relationship might be characterized by Wachsmuth collecting, studying, and writing while Springer provided editorial and financial support. In Springer's own pen, "our work is the result of an undertaking in which Wachsmuth furnishes the brains and I the money, and both, I think, a fair equivalent of enthusiasm" (letter from Springer to A. Agassiz, February 15, 1888).

Regardless, Springer played a very important role in their collaboration. Not only was he a source of encouragement for Wachsmuth, but his editorial labors were significant. Wachsmuth was much less concerned about style and grammar than he was about the science, and Springer strove to make their contributions clear and concise so that the science might be better received and understood (Caffey 2006).

Springer's financial contributions were also significant. Not only did he often cover the costs of figure preparation and publication, he offered to pay for the construction of a small fireproof brick building behind Wachsmuth's home at 111 Marietta Street, Burlington, which still stands today (Figure 3). That building was used to store not only a growing library, but their research collection. In fact, Springer also contributed by acquiring books and crinoids from throughout the world to increase their reference materials. Finally, Springer was no intellectual light-weight. His limited contributions to manuscript generation were not due to a lack of understanding of the subject matter. Without a doubt, he not only carefully scrutinized Wachsmuth's style and grammar, but his science. Frank Springer was a very capable crinoid paleontologist. Wachsmuth and Springer's final work was the *North American Crinoidea Camerata*. Heralded as "one of the master-pieces of American science" (Keyes 1896), it is arguably their greatest work from the perspective of both natural history and artistic achievement. Alexander Agassiz, the son of Louis Agassiz and his successor in Cambridge, agreed to publish the monumental three volume, 897-page work as a Memoir of the Museum of Comparative Zoology. Wachsmuth mailed the manuscript to Cambridge on September 15th, 1894, but Wachsmuth died on February 7th, 1896, and sadly, the *Camerata* wasn't published until May, 1897. Wachsmuth never saw the crowning achievement of his life's labor.

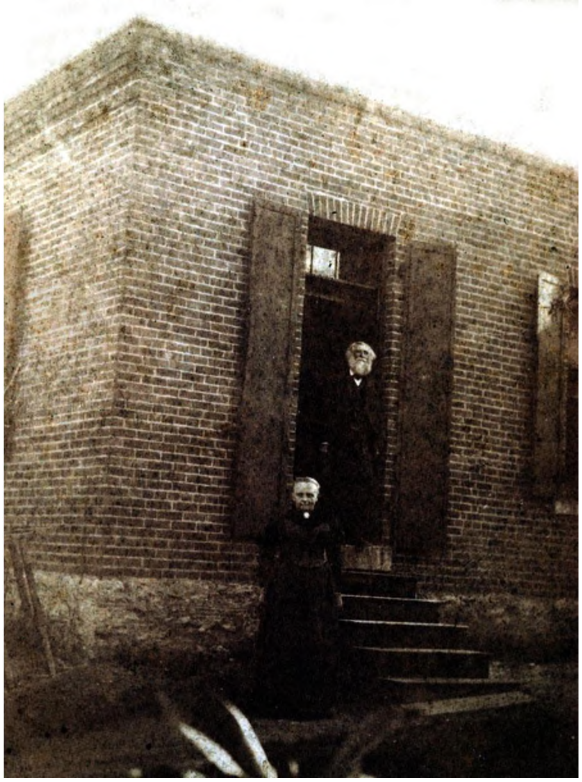


Figure 3. Charles and Bernhardina Wachsmuth standing outside of the crinoid museum and library at 111 Marietta Street, Burlington, Iowa.

Springer continued to edit the proofs after Wachsmuth's passing, and lamented the loss of his friend in a note at the beginning of the *Camerata*, "It is a source of extreme regret that my learned colleague and long-time friend, Dr. Charles Wachsmuth, did not live to see the publication of this Monograph, to which he had devoted so many years of assiduous labor. His keen powers of observation, sagacious judgment, and indefatigable energy have left their impress upon the works which have been brought out by us. While his death is a loss to Science not easily repaired, it is none so great—aside from his family—as to the friend with whom he had worked in pleasant collaboration for so many years."

The death of Charles Wachsmuth was pronounced in newspapers (including the New York Times) and scientific journals throughout the literate world. It marked the end of an era in crinoid paleontology. However, there was more than one Wachsmuth in "Wachsmuth & Springer."

Charles married Bernhardina Lorenz, also an immigrant from Hanover, Germany, on June 3, 1855. Not only was Mrs. Wachsmuth a steadfast spouse of nearly 40 years, she was an accomplished crinoid collector. Bernhardina Wachsmuth is one of the strongest, and perhaps most unrecognized, female figures of 19th century paleontology. Before continuing further, it should be noted that her first name appears in at least 4 different spellings in the published literature: Bernandina (Bather 1869; Calvin 1897), Bernhardine (Howe et al, 1915; which is also the name given on her tombstone), Bernhardina (Springer 1920) and Bernardina (Caffey 2006). Here I tentatively use Springer's spelling. Based on written correspondence between them, it's clear that they were very close, although Springer generally referred to her simply as "Mrs. W-". Moreover, Springer was demonstrably attentive to small details, and I believe that he would have been especially so in the proper naming of *Wachsmuthicrinus bernhardinae* Springer 1920 (Bernhardina discovered the holotype).

Bernhardina's contributions to crinoid paleontology have been noted by several authors, but none more tenderly than by Frank Springer (1920), "One other acknowledgement remains, not so easy to fittingly express, and that is in relation to Mrs. Bernhardina Wachsmuth, widow of my old friend and associate, Charles Wachsmuth. It is rendered doubly difficult by the fact that the demise of this venerable woman, pending the publication of these lines, compels me to substitute words of affectionate remembrance for those of grateful recognition….Although my residence and business affairs were in New Mexico, I continued my scientific researches at such intervals as my time and other occupations would permit in the little museum in the beautiful city of Burlington, Iowa. The manifold kindness, the solicitude for my personal comfort, and the intelligent interest in my work which were at all times exhibited by Mrs. Wachsmuth, could not be adequately characterized by the ordinary expressions of gratitude."

"But I wish here to record my appreciation of one of the finest characters I have ever known. She was her husband's untiring companion and helpmeet through all is long years of study and battling for health, not only in a material way, but intellectually. While without a technical knowledge of geology and paleontology, she was always an intense lover of nature, and a keen observer as well; so she became an ardent and skillful collector, and for the last 20 years of his life accompanied Wachsmuth in all of his travels and collecting journey, tramping cheerfully over mountains and searching among glades and outcrops with an energy that never flagged. Many splendid specimens that enrich this great collection were of her finding. She not only rejoiced in their discovery with the zest of the successful collector, but apprehended their scientific importance as contributions to the problems that were under investigation."

As indicated by Calvin (1897), "The world of science owes a large debt to Mrs. Wachsmuth."

After Charles Wachsmuth's death, the collection and library of Wachsmuth and Springer remained with Bernhardina at 111 Marietta Street, Burlington. Springer visited as often as time would allow, and as his business obligations waned, he found more time to study crinoids. Working without his friend and collaborator, Springer demonstrated his proficiency as a crinoid specialist. As he advanced in age, he began to worry about the fate of the collection and library that remained in Burlington. After much deliberation, he ultimately decided to send it to the Smithsonian for safekeeping. Springer continued to work diligently on fossil crinoids until his death on September 22nd, 1927. Among his last contributions to the crinoids of the Burlington Limestone was his *Crinoidea Flexibilia* (1920) in which he described 6 new Burlington species, and *Unusual Forms of Fossil Crinoids* (1926) in which he described two. Recently, an exceptional biography of Springer was written by David Caffey (2006). Anything more that I could say about him is better and more thoroughly examined in that wonderful book.

Although the story of Wachsmuth and Springer has been told before, I gain inspiration, even comfort, in its retelling. Perhaps it is because we share a common geographical and geological heritage, or possibly it is because I associate their names with the singularity of my "crinoid conversion" in the Burlington Public Library. Whatever the reason, I revere them and share in the passion they had for crinoids and the Burlington Limestone.

THE BURLINGTON LIMESTONE

Following the first geological survey of Iowa, Wisconsin, and Minnesota (1848-49), Owen and Shumard (1850, 1852) were the first to name crinoids and blastoids from the "encrinital layers of the sub-carboniferous limestone at Burlington, Iowa" (Figure 4). Later, Owen (1852) named these crinoidal limestones the "Encrinital Group of Burlington," for the limestones exposed along the bluffs of the Mississippi River in the vicinity of Burlington Iowa, and the "Reddish-brown Encrinital Group of Hannibal," for similar grainstones exposed in the vicinity of Hannibal, Missouri; however, he believed that the crinoidal limestones of Hannibal were stratigraphically younger than those exposed in Burlington. The same strata were referred to as the "Encrinital limestone" in the first geological survey of Missouri (Swallow 1855; Shumard 1855); but Swallow (1855) recognized that Owen's (1852) "Encrinital Groups" of Burlington and Hannibal were actually part of the same geologic formation. Hall (1857) concurred with Swallow and formally named the "Encrinital limestone" the "Burlington limestone," for the well-exposed encrinites of Burlington, Iowa.

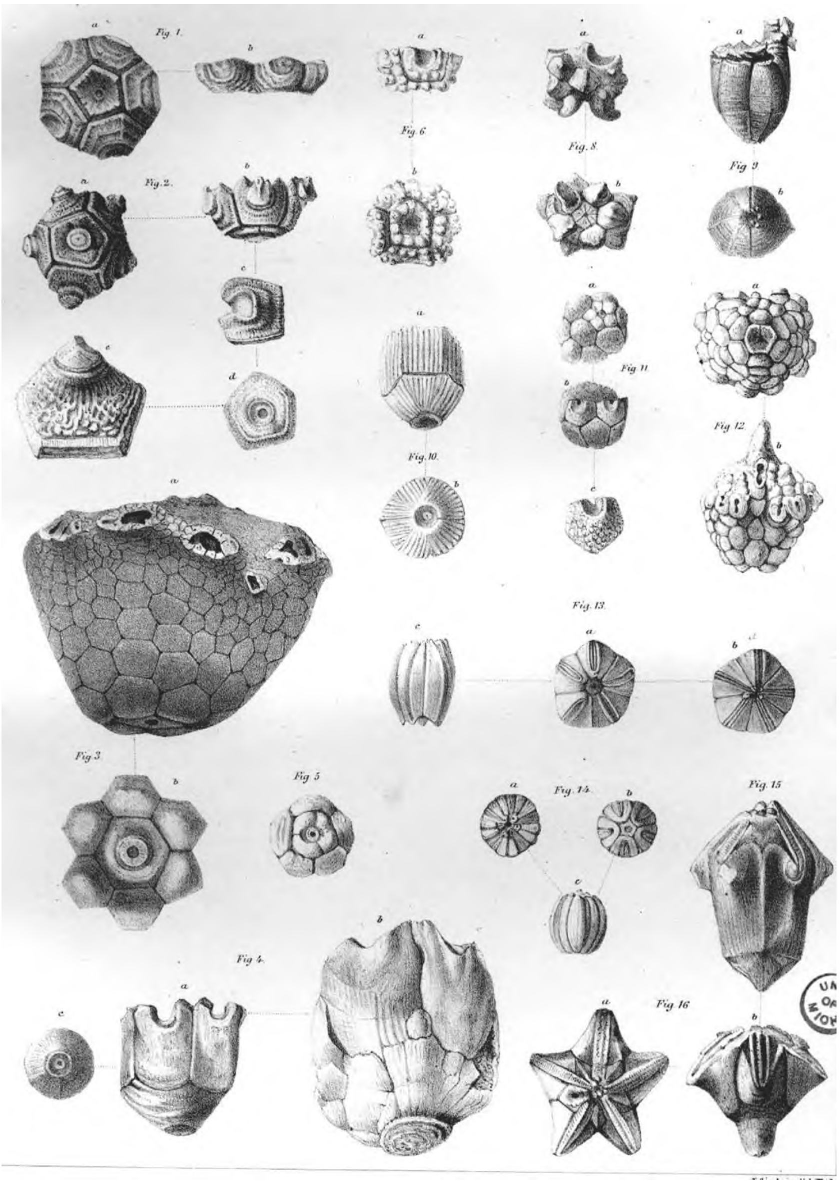


Figure 4. The first published plate of Burlington crinoids (Owen and Shumard 1850).

Since the 1850's, the Burlington Limestone has received much attention from stratigraphers, economic geologists, and paleontologists, with the latter paying particular attention to the extremely high concentration of crinoidal material. Furthermore, many researchers noted that the Burlington was not uniform in its lithologic or biotic composition and began subdividing the formation based on these differences (White 1860, 1870; Niles and Wachsmuth 1866). The purpose of the remaining portion of this contribution is to present an historical account of attempts to divide the Burlington Limestone lithologically and paleontologically and discuss confusion that has arisen around the position of these boundaries. Moreover, I hope to provide a framework within which, any Burlington collector or researcher will be able to easily recognize the primary faunal associations. Because crinoids and blastoids are the most abundant fossils in the Burlington, this work follows the lead of White (1860), Niles and Wachsmuth (1866), Rowley (1908), Laudon, (1937, 1973) and others in focusing on the distribution of these pelmatozoan, or stalked echinoderms, as biostratigraphic markers. Understanding faunal assemblages and the stratigraphic ranges of each species is essential for documenting multi-scale spatiotemporal paleoecological and evolutionary patterns. That these distributions are clearly understood for the pelmatozoans of the Burlington Limestone is particularly crucial as it represents the most diverse concentration of stalked echinoderms in the geologic record. Therefore, I also provide a culled listing of currently recognized crinoids and blastoids from this formation, which includes their occurrence and relative abundance. Finally, I propose recommendations for reporting the stratigraphic occurrence of paleontological samples from the Burlington Limestone and suggest directions of future research.

HISTORICAL DIVISION OF THE BURLINGTON LIMESTONE

White (1860) was among the first geologists to recognize that the Burlington Limestone could be naturally divided based on lithological and paleontological criteria. He described three divisions of the Burlington, including: 1) a basal crinoidal limestone, 2) alternating layers of limestone, mudstone, and chert and 3) and an upper crinoidal limestone. White (1860, 1870) referred to the lower two portions as the "lower division," and called uppermost portion the "upper division" of the Burlington Limestone. White (1870) also suggested that "…the accession of silicious material to the waters of that epoch resulted in or at least was followed by the extermination of all the species of crinoids then existing…," suggesting that the interbedded chert and dolomitic mudstone of the "lower division" formed a significant paleontological boundary between the two crinoidal limestones. Niles and Wachsmuth (1866) proposed to divide the Burlington Limestone into two distinct geological formations based on these paleontological differences, naming White's "lower division" the "Lower Burlington limestone," and the "upper division" the "Upper Burlington limestone." However, White (1870; who was at the time, the state geologist of Iowa) rejected the formal division of the Burlington Limestone into two separate formations based on his observations that the distinction between the two divisions could only be recognized locally. Nevertheless, Niles and Wachsmuth (1866), as well as many subsequent workers, reported the occurrence of Burlington Limestone species as occurring in the informal "lower" or "upper" Burlington Limestone.

The practice of dividing the Burlington Limestone into lower and upper divisions and reporting species in relation to their boundaries is still a common practice (see Gahn and Kammer 2002); but it does not adequately (or accurately) reflect the natural divisions within this formation. There has been considerable confusion concerning the placement of the lower-upper Burlington boundary by various authors resulting in its inconsistent application. This confusion is centered in the lithological variability of White's (1870) second division of the Burlington Limestone, which is roughly equivalent to the Haight Creek Member (Harris and Parker 1964) (Figure 5).

The Haight Creek Member is typically characterized in southeast Iowa by having abundant layers of interbedded chert and dolomitic mudstone. However, the Haight Creek Member also contains layers of crinoidal packstone and grainstone that can vary in abundance from being sparse to the dominant lithotype. The Haight Creek Member often contains a thick encrinite near its middle and top that is very similar to the crinoidal limestones of the underlying Dolbee Creek and overlying Cedar Fork Members (Harris and Parker 1964). This “middle grainstone” was noted by Van Tuyl (1922, p. 121) and further discussed by Witzke et al. (1990, p. 16). The Haight Creek Member carries a unique pelmatozoan assemblage that is more similar to the fauna of the Cedar Fork Member than that of the Dolbee Creek Member.

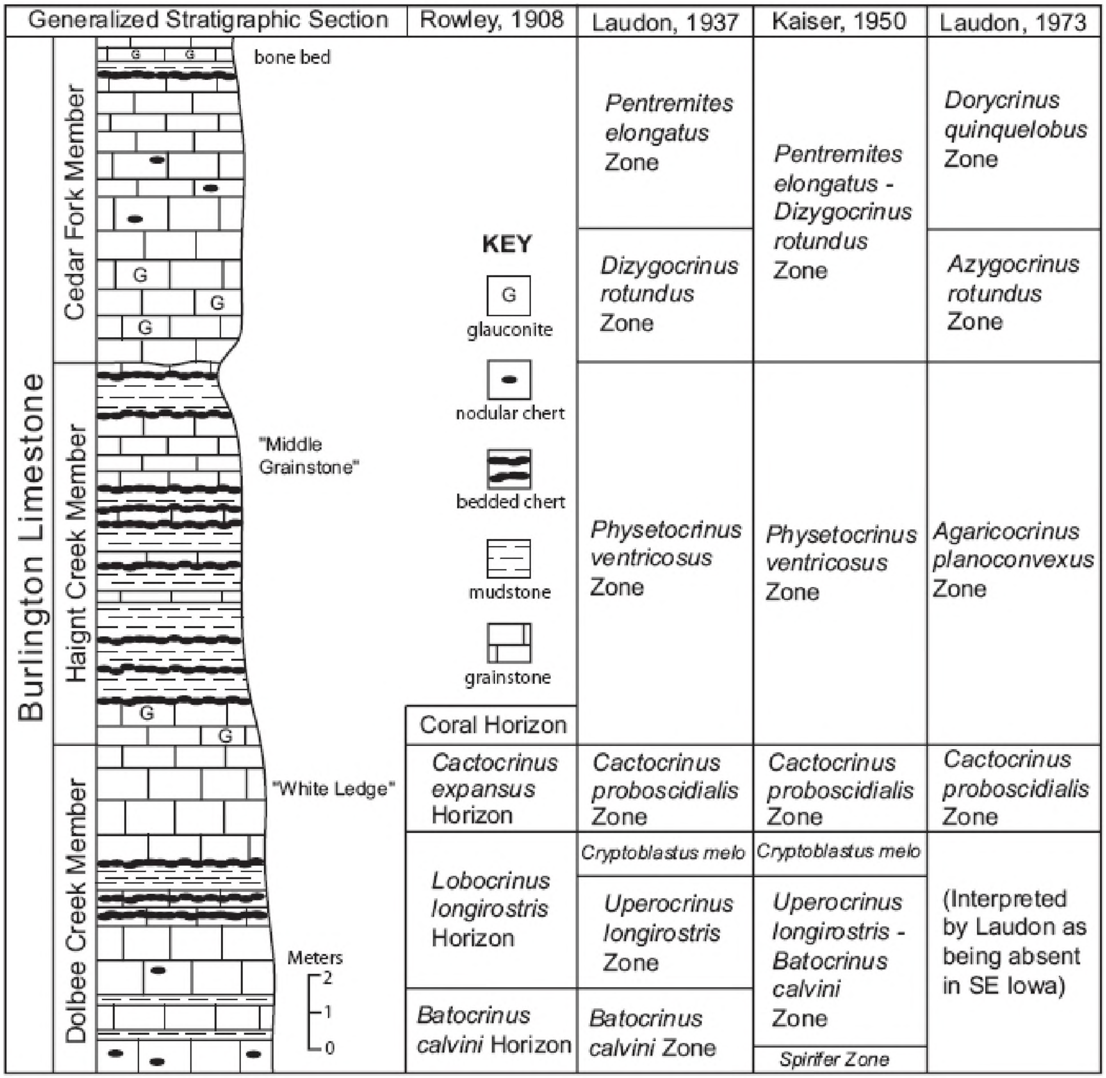


Figure 5. Historical biozonation of the Burlington Limestone. Faunal zones of Rowley (1908), Laudon (1937, 1973), and Kaiser (1950) are plotted against a generalized section of the Burlington Limestone. The zonation proposed by Rowley (1908) was based on the Burlington section at Louisiana, Missouri. The zonation proposed by Laudon (1973) is a composite group of biozones created from Burlington sections in Hannibal, Missouri and southeast Iowa. The zonation proposed by Kaiser (1950) was based on several Burlington sections in southwest Missouri. The second zonation proposed by Laudon (1973) was restricted to southeast Iowa.

The currently accepted interpretation of the lower and upper Burlington places their boundary at the base of the Cedar Fork Member, with the entirety of the Dolbee Creek and Haight Creek Members being confined to the lower Burlington (Van Tuyl 1922; Laudon 1973; Witzke et al. 1990). Nevertheless, the fauna from the Haight Creek grainstones were most commonly assigned to the upper Burlington. This unfortunate circumstance results in a paleontologically defined lower-upper Burlington boundary that conflicts with the recognized lithological lower-upper Burlington boundary.

However, it is quite possible that White (1860, 1870) and Niles and Wachsmuth (1866) originally placed the lower-upper Burlington boundary at the base of the "middle grainstone." White (1870) suggested that the lower and upper Burlington divisions are approximately equivalent in thickness, which would be consistent with a lower-upper Burlington boundary at the base of the "middle grainstone." Niles and Wachsmuth (1866) recognized the alternating layers of chert and mudstone of the Haight Creek Member as being part of the lower Burlington, and delineated the lower-upper Burlington boundary by "the uppermost stratum of chert, which attains any considerable extent and thickness." This is a particularly enigmatic boundary definition as thick, persistent chert beds can be present locally in the vicinity of Burlington, Iowa at the base of the middle grainstone of the Haight Creek Member and at the base of the Cedar Fork Member (and even extending into the lower beds of the latter). Wachsmuth and Springer (1897) refer to many of the typical representatives of the Haight Creek fauna as occurring in the "lower part of the Upper Burlington limestone," confirming the practice of assigning these beds to the upper Burlington on paleontological grounds. More recent studies have also variably placed the lower-upper Burlington boundary. For example, Van Tuyl (1922, p. 121, horizon 2) assigned strata equivalent to the Haight Creek Member to the lower Burlington, including the "middle grainstone" in Burlington, Iowa. However, in Augusta, Iowa, he assigned the "middle grainstone" to the upper Burlington, possibly because he was able to collect what he interpreted as an "upper Burlington" fauna from these strata (Van Tuyl, 1922, p. 132, horizon 3). Furthermore, Moore (1928, p. 171) assigned strata that was equivalent to the Haight Creek Member almost wholly to the upper Burlington. Understanding the placement of the boundary between the lower and upper Burlington Limestone by those who originally defined it is difficult enough, but the inconsistent use of these divisions on local and regional scales makes the distinction between the lower and upper Burlington essentially meaningless; and therefore, I recommend ending the formal use of these divisions.

Rowley (1908) made the earliest attempt to further subdivide the Burlington Limestone into discrete biozones (Figure 5). He separated the lower Burlington strata of Louisiana, Missouri into four zones including, in ascending order: 1) the *Batocrinus calvini*, 2) *Lobocrinus longirostris*, 3) *Cactocrinus expansus*, and 4) Coral Horizons. Laudon (1937) expanded Rowley's (1908) work by establishing seven "life zones" in the Burlington. He retained Rowley's division of the Dolbee Creek Member, but separated out the upper five feet of the *Lobocrinus longirostris* Horizon (which he named the *Uperocrinus longirostris* Zone) in Hannibal, Missouri, and called this interval the *Cryptoblastus melo* Zone. Moreover, Laudon renamed Rowley's *Cactocrinus expansus* Horizon as the *Cactocrinus proboscidialis* Zone (probably because *C. expansus* is not a formally defined species; Rowley may have actually been referring to *C. exerptus* (Hall) or *C. extensus* Wachsmuth and

Springer, but this is uncertain), and renamed Rowley's "Coral horizon" the *Physetocrinus ventricosus* Zone, which he extended to include the full extent of Haight Creek-equivalent strata. Laudon also established two "life zones" in the Cedar Fork Member, including the *Dizygocrinus rotundus* Zone and the overlying *Pentremites elongatus* Zone.

The "zones" recognized by Rowley (1908) and Laudon (1937) were based exclusively on exposures of the Burlington Limestone in southeastern Iowa and northeastern Missouri. However, Kaiser (1950) applied the same zonation scheme to the Burlington Limestone of southwestern Missouri, albeit with a few changes. He recognized an additional horizon at the base of the Burlington Limestone that he referred to as the "Spirifer zone." He was also unable to distinguish between the *Batocrinus calvini* and *Uperocrinus longirostris* Zones or the *Dizygocrinus rotundus* and *Pentremites elongatus* Zones, and thus combined them.

The most recent echinoderm zonation scheme for the Burlington Limestone was proposed by Laudon (1973) for exposures in southeast Iowa, exclusively. The lowest zone that he recognized was the *Cactocrinus proboscidialis* Zone; believing that the underlying zones were not deposited in southeast Iowa (see Laudon 1937). Inexplicably, Laudon changed the name of the overlying *Physetocrinus ventricosus* Zone to the *Agaricocrinus planoconvexus* Zone, even though they are exactly equivalent. He also changed the *Dizygocrinus rotundus* Zone to the *Azygocrinus rotundus* Zone (after Lane's 1963 amendment of *Dizygocrinus*), and the *Pentremites elongatus* Zone to the *Dorycrinus quinquelobus* Zone (without a clear reason for doing so).

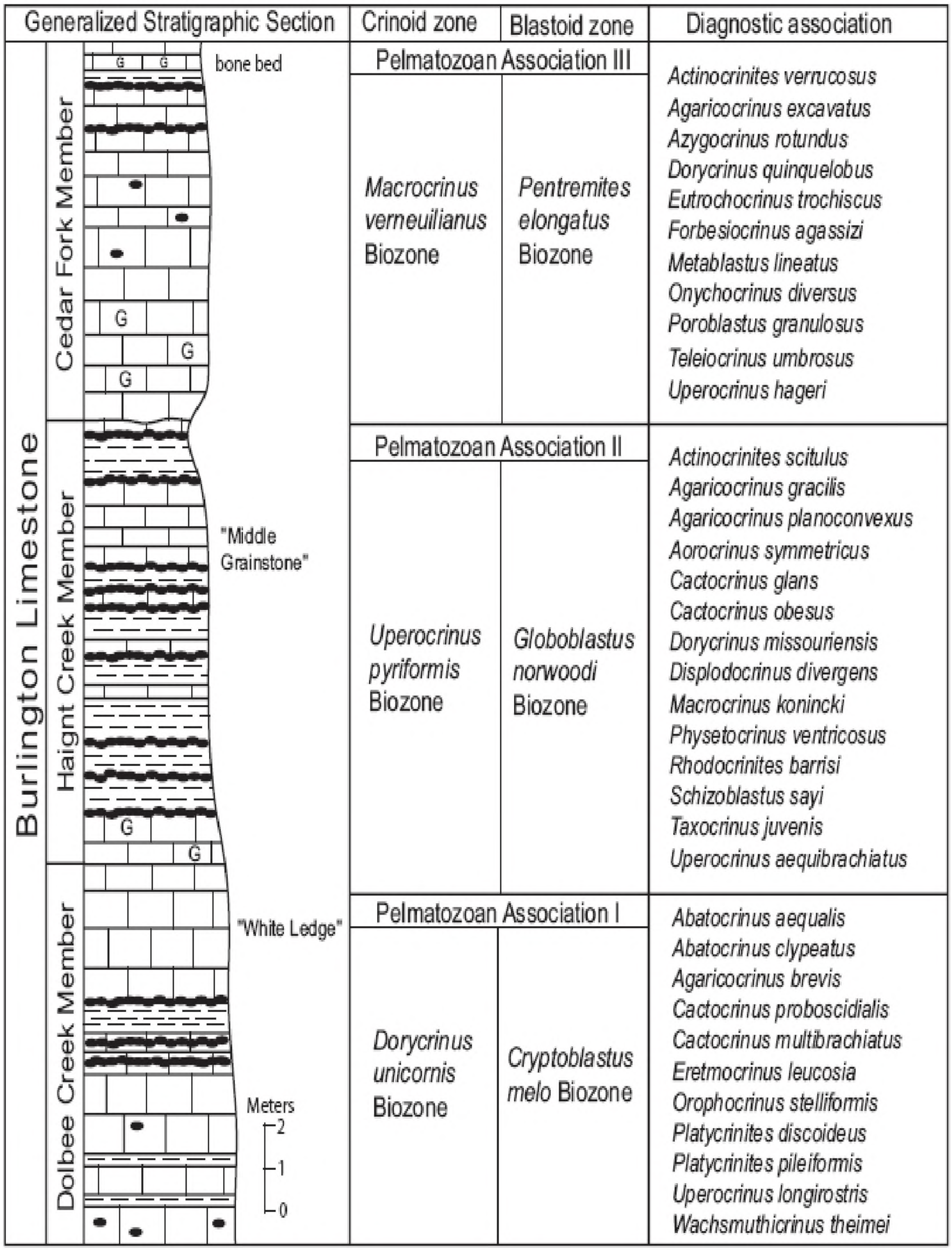
A REVISED BIOZONATION

The zonation schemes discussed above were based on lithological as well as paleontological characteristics. For example, Rowley's (1908) *Cactocrinus expansus* Horizon was originally named for the "White Ledge" of north central Missouri; a name given by local quarry men to an economically valuable, massive crinoidal grainstone (Laudon, 1937). In addition, Laudon originally named his *Dizygocrinus rotundus* Zone for glauconitic grainstones found at the base of the Cedar Fork Member as well as for the local abundance of *Azygocrinus rotundus* (Yandell and Shumard) in southeast Iowa. He also suggested that the fauna of this zone is not represented in Hannibal, Missouri, and Kaiser (1950) did not recognize this zone in southwestern Missouri. However, the fauna of the *Dizygocrinus rotundus* Zone is present throughout Missouri, but it cannot be characterized by the glauconitic grainstone or the unusually high abundance of *A. rotundus* that is present in southeast Iowa. The latter point illustrates another problem with the currently proposed biozonation schemes; several of the biozones are characterized by locally abundant or restricted species. Although *A. rotundus* occurs abundantly in southeast Iowa, it is relatively rare throughout Missouri. Additionally, Rowley's (1908) *Batocrinus calvini* Horizon is defined by the presence of *Abatocrinus calvini* (Rowley) an uncommon and locally restricted species.

Because many of the biozones were originally defined by lithologic differences and locally abundant or restricted species, it is difficult to use them outside of the limited geographic regions in which they were described. Thus, I propose a biozonation scheme that is applicable over the full geographic distribution of the Burlington Limestone, and one that is based entirely on paleontological data. The biozonation scheme presented below is based on a decade of personal field experience in the Burlington Limestone and the examination of museum collections housed in the Springer Room of the United States National Museum of Natural History, Harvard's Museum of Comparative Zoology, and the University of Iowa Paleontology Repository. Special attention was also given to stratigraphic collections from various Burlington Limestone localities made by Brad Macurda and Dave Meyer in the late 1960's and early 1970's that are housed at the University of Michigan. The biozonation scheme here proposed for the Burlington Limestone is divided into three parts that are generally equivalent to the positions of the Dolbee Creek, Haight Creek, and Cedar Fork Members. Although the proposed biozones roughly track the three Burlington members, it is important to note that the faunal assemblages described below are not defined by these members and can be traced even where lithological distinction of the members is not possible. Crinoid and blastoid biozones were established for each paleontological association. The names of these biozones were carefully chosen to represent species that: 1) are common representatives of the association over the entire geographic extent of the Burlington Limestone, 2) reach their acme, or maximum abundance within the confines of the biozone, 3) are easily recognizable, but not easily confused with other species by non-specialists and, 4) are reasonably stable taxonomically. If the taxa used in previous biozonation schemes met these criteria, then I honored the names used by prior authors; otherwise, I explain the designation of a new name. Figures and general descriptions of the species chosen to represent the biozones in this study are found in *Index Fossils of North America* by Shimer and Schrock (1944).

The naming of these biozones is secondary in importance to their faunal compositions; understanding the make-up of each pelmatozoan association is critical for addressing evolutionary and paleoecological questions pertinent to the crinoids and blastoids of the Burlington Limestone. I have listed a few of the diagnostic species from each pelmatozoan association (Figure 6), but it would be more valuable to know the approximate stratigraphic ranges of each pelmatozoan species in the formation. Thus, I attempted to create a complete table of the crinoids and blastoids present in the Burlington Limestone and their known distributions in relation to the associations recognized herein (Appendix). This table is discussed further under the subsequent section on crinoid and blastoid diversity.

Burlington Pelmatozoan Association I: The stratigraphically oldest association recognized in this study is referred to as the Burlington Pelmatozoan Association I (BPAI), and includes the *Dorycrinus unicornis* and *Cryptoblastus melo* Biozones. The biozones of the *D. unicornis*-*C. melo* Association generally encompass the zones discussed in this paper that are equivalent to the Dolbee Creek Member of the Burlington Limestone (Rowley 1908; Laudon 1937, 1973; Kaiser 1950). *Dorycrinus unicornis* (Owen and Shumard) was chosen as the key index crinoid for this zone rather than one of the previously used "zone species" because it possesses a diagnostic morphology that makes it difficult to confuse with any other species. Several species of *Abatocrinus* and *Cactocrinus* are also common in this zone, but they are currently in need of taxonomic revision, and the many species of these genera that are presently in the BPAI can be difficult to distinguish by non-specialists. *Cryptoblastus melo* (Owen and Shumard) was retained as the key index fossil of the blastoid biozone following Laudon (1937) and Kaiser (1950). *Cryptoblastus melo* is an excellent name for this blastoid biozone as the species is probably the most abundant echinoderm occurring



Crinoid zone	Blastoid zone	Diagnostic association
Pelmatozoan Association III		
Macrocrinus verneuilianus Biozone	*Pentremites elongatus* Biozone	*Actinocrinites verrucosus* *Agaricocrinus excavatus* *Azygocrinus rotundus* *Dorycrinus quinquelobus* *Eutrochocrinus trochiscus* *Forbesiocrinus agassizi* *Metablastus lineatus* *Onychocrinus diversus* *Poroblastus granulosus* *Teleiocrinus umbrosus* *Uperocrinus hageri*
Pelmatozoan Association II		
Uperocrinus pyriformis Biozone	*Globoblastus norwoodi* Biozone	*Actinocrinites scitulus* *Agaricocrinus gracilis* *Agaricocrinus planoconvexus* *Aorocrinus symmetricus* *Cactocrinus glans* *Cactocrinus obesus* *Dorycrinus missouriensis* *Displodocrinus divergens* *Macrocrinus konincki* *Physetocrinus ventricosus* *Rhodocrinites barrisi* *Schizoblastus sayi* *Taxocrinus juvenis* *Uperocrinus aequibrachiatus*
Pelmatozoan Association I		
Dorycrinus unicornis Biozone	*Cryptoblastus melo* Biozone	*Abatocrinus aequalis* *Abatocrinus clypeatus* *Agaricocrinus brevis* *Cactocrinus proboscidialis* *Cactocrinus multibrachiatus* *Eretmocrinus leucosia* *Orophocrinus stelliformis* *Platycrinites discoideus* *Platycrinites pileiformis* *Uperocrinus longirostris* *Wachsmuthicrinus theimei*

Figure 6. Pelmatozoan Associations of the Burlington Limestone. This figure summarizes the pelmatozoan associations described herein, including their relative stratigraphic positions, corresponding crinoid and blastoid biozones, and species characteristic of each association. Please refer the text for further discussion of these associations. The key for the stratigraphic section is presented in Figure 5.

therein. *Dorycrinus unicornis* and *C. melo* are also restricted to the BPAI, as well are the majority of crinoids and blastoids that occur in this association. The *D. unicornis-C. melo* Association also includes many rare genera that were carried over from underlying Kinderhookian strata, including species of *Belemnocrinus*, *Gilmocrinus*, *Holcocrinus*, *Nactocrinus*, *Megistocrinus* and *Paracosmetocrinus*.

Burlington Pelmatozoan Association II: The second association recognized in the study is referred to as the Burlington Pelmatozoan Association II (BPAII), and includes the *Uperocrinus pyriformis* and *Globoblastus norwoodi* Biozones. The biozones of the *U. pyriformis-G. norwoodi* Association include Rowley's (1908) Coral Horizon, the *Physetocrinus ventricosus* Zones of Laudon (1937) and Kaiser (1950), and the *Agaricocrinus planoconvexus* Zone of Laudon (1973). This association is roughly equivalent to the strata deposited in the Haight Creek Member of the Burlington Limestone. However, the transition from the BPAI to the BPAII may occur within the "White Ledge" or Laudon's (1937) *Cactocrinus proboscidialis* Zone of north central Missouri; strata considered to be equivalent to the Dolbee Creek Member of the Burlington Limestone. I observed a particularly fossil-rich exposure of the "White Ledge" in Hannibal, Missouri that contained the typical BPAI fauna throughout most of its thickness. However, the upper portion of this bed contained an abundance of BPAII forms such as *Agaricocrinus planoconvexus* (Hall) and *Physetocrinus ventricosus* (Hall) and a conspicuous absence of BPAI forms such as *D. unicornis*, *C. melo*, and diagnostic species of *Abatocrinus* and *Cusacrinus*. This may suggest that the transition from the *D. unicornis-C. melo* Association to the *U. pyriformis-G. norwoodi* Association began within a single facies. *Uperocrinus pyriformis* (Shumard) was chosen as the key index crinoid for this biozone even though *P. ventricosus* and *A. planoconvexus* can be equally abundant. *Physetocrinus ventricosus* was not retained as the namesake for this biozone because the stellate plates of this species may lead a non-specialist to confuse it with one of the many actinocrinitids that occur in the underlying BPAI. *Agaricocrinus planoconvexus* was not chosen because it is only abundant in the lower beds of the BPAII. Furthermore, there are several morphologically similar species of *Agaricocrinus* described from the Burlington Limestone and the taxonomy of this group is in need of revision before the Burlington *Agaricocrinus* species can be fully utilized as index fossils. *Globoblastus norwoodi* (Owen and Shumard) was chosen as the key index blastoid for this interval because it is the only abundantly occurring blastoid in this zone. Both *U. pyriformis* and *G. norwoodi* first occur in this zone and range into the uppermost strata of the Burlington Limestone; however, they reach their greatest abundance in the BPAII. Many other important crinoid and blastoid species reported as occurring in the upper Burlington first occur in this association including: *Actinocrinites scitulus* Miller and Gurley, *Cactocrinus glans* (Hall), *Macrocrinus konincki* (Shumard), *Strotocrinus glyptus* (Hall), and *Schizoblastus sayi* (Shumard). Interestingly, species that have been reported as occurring only in the lower Burlington Limestone also occur commonly in this association including *Cactocrinus obesus* (Keyes) and *Displodocrinus divergens* (Hall), again illustrating confusion surrounding the position of the lower-upper Burlington contact.

Burlington Pelmatozoan Association III: The stratigraphically youngest association recognized in this study is referred to as the Burlington Pelmatozoan Association III (BPAIII), and includes the *Macrocrinus verneuilianus* and *Pentremites elongatus* Biozones. The biozones of the *M. verneuilianus-P. elongatus* Association incorporate all of the zones discussed in this study that are referable to the Cedar Fork Member of the Burlington Limestone (Rowley, 1908; Laudon, 1937, 1973; Kaiser, 1952). *Macrocrinus verneuilianus* (Shumard) was chosen as the key index crinoid of this biozone rather than *Azygocrinus rotundus* (Yandell and Shumard) because (as discussed above) *A. rotundus* is only a dominant element of PBAIII in southeast Iowa and is relatively rare elsewhere. Nevertheless, *A. rotundus* is an extremely useful index crinoid for this zone in southeast Iowa, occurring in densities as high as 100 individuals per m^2. *Macrocrinus verneuilianus* occurs frequently with *A. rotundus*, but is a more useful index fossil, as it is a common member of this association throughout the entire geographic extent of the Burlington Limestone. Laudon (1937, 1973) referred to the upper portion of the Cedar Fork Member as the *Dorycrinus quinquelobus* and the *Pentremites elongatus* Zones. *Dorycrinus quinquelobus* (Hall) is a diagnostic crinoid of the BPAIII; however, it is relatively uncommon. *Pentremites elongatus* (Shumard) was retained as the index fossil for the blastoid biozone as it is one of the most abundant blastoids in this association. The only other blastoid that that reaches equally high abundance (and frequently more so) is *Poroblastus granulosus* (Meek and Worthen). However, it exhibits great disparity in abundance locally and is relatively inconspicuous because of its relatively small size. The crinoids *Teleiocrinus umbrosus* (Hall), *Uperocrinus nashvillae subtractus* (White), *Eutrochocrinus trochiscus* (Meek and Worthen), and the blastoid *Arcuoblastus shumardi* (Meek and Worthen) do not appear to occur in underlying biozones.

The fact that the biozones described above roughly mirror the Dolbee Creek, Haight Creek and Cedar Fork Members of the Burlington Limestone is likely a function of sea level fluctuations. Witzke et al. (1990) and Witzke and Bunker (1996) divided the Mississippian strata of Iowa into 10 third-order transgressive-regressive cycles of approximately one to three million years duration. The Dolbee Creek Member comprises Cycle 4 (the Dolbee Creek Cycle) and the Haight Creek and Cedar Fork Members are included in Cycles 5A and 5B, respectively (the Haight Creek Cycle). The grainstones of the Dolbee Creek Cycle contain crinoids of the *Dorycrinus unicornis-Cryptoblastus melo* Association. The crinoids of this association are very distinct from either of the overlying associations; very few species carry over into the BPAII or the BPAIII. Conversely, the grainstones of the Haight Creek Cycle contain many of the same species. Many commonly occurring crinoids and blastoids of the *Uperocrinus pyriformis-Globocrinus norwoodi* Association extend into the *Macrocrinus verneuilianus-Pentremites elongatus* Association, but the latter contains several species that are constrained therein.

CRINOID AND BLASTOID BIODIVERSITY

Anyone who has collected crinoids and blastoids from the Burlington Limestone should be able to relate to the sentiments expressed by Rowley (1891) who mentioned that "…the Burlington Limestone is, perhaps, the most interesting to the intelligent collector, not that its fossil treasures are more perfectly preserved or more abundant than individuals in the Keokuk or Chester divisions, but from the diversity of its Crinoidal remains and the great number of species of Echinoderms. The collector is always happening on something new, and his artistic eye is in constant rapture over the beautiful and ever changing sculpture of the calyx plates of the Actinocrinoids and the granular ornamentation of the Blastoids." Indeed, the Burlington Limestone contains the most speciose assemblage of crinoids and blastoids in the geologic record. Over 600 species of crinoids and blastoids have been described from the Burlington Limestone. Nevertheless, only about 400 species of crinoids and 30 species of blastoids are currently recognized as valid, and many of these are synonymous.

There are many reasons for redundant species descriptions in the Burlington Limestone. Early paleontologists did not work under a clear species concept and new species were introduced based on such minor morphological deviations as differences in arm number, ornamentation, or interray plating. Moreover, many species were considered formation- or locality-specific. This led several workers into the pitfall of circular reasoning, which is in part why Niles and Wachsmuth (1866) proclaimed that, "We have examined the species of Crinoids and noticed their stratigraphical distribution with care, and have found no evidence of any species occurring in both the Lower and Upper Burlington limestones." Taphonomic process also resulted in the naming of redundant species because compressed or otherwise distorted material appears different from perfect specimens. In addition, many species were described from incomplete material, such as the basal circlets of *Platycrinites*. Several of the earliest species descriptions of Burlington crinoids are incomplete or enigmatic. This, coupled with the fact that many of these species were never figured, resulted in the redundant description of several crinoids and blastoids. Wachsmuth and Springer (1897) certainly expressed the sentiments of many paleontologists when they wrote, "These descriptions, in many cases, were so indefinite that the identification of the species was almost impossible, and this created considerable annoyance and labor to later writers." Another matter of concern is that many "new species" were described from personal collections and are now lost. Similarly, several holotypes were destroyed. For example, Wachsmuth and Springer (1897) reported that "McChesney's types were all destroyed in the great Chicago fire." They also believed that all of Owen and Shumard's types were destroyed in a fire in Burlington or Keokuk, Iowa; however, Springer (1920, p. 7) discovered that these were "rescued from a rubbish barrel at the old David Dale Owen headquarters in New Harmony, Indiana," and are now reposited (at the Field Museum of Natural History) in Chicago. Unfortunately, ego also played a role in the current state of Burlington crinoid and blastoid taxonomy. Wachsmuth and Springer (1897) clearly addressed this issue when they said that, "The earlier authors…may readily be excused for describing their species from such material as they had. But at the present day the only excuse for this class of work that can be found is the desire of the authors to see their names appended to the greatest possible number of species… All we have in many cases is the assurance of the author that the species is so unlike any other that a comparison is unnecessary. We have found in practice that a declaration of this kind is a badge of suspicion, and is one of the most common indications of a synonym."

Many crinoid clades in the Burlington are in dire need of taxonomic "housekeeping". Wachsmuth and Springer (1897) presented an excellent summary of the camerate crinoids, and Springer (1920) treated most of the flexible crinoids. Nevertheless, the cladids of the Burlington Limestone are poorly understood. Kirk (1938, 1940, 1941, 1943b, 1945, 1947) described many new genera and species of cladids from the Burlington Limestone, but left many unresolved problems. Recently, Gahn and Kammer (2002) and Kammer and Gahn (2003) have revised the non-pinnulate cladids from the Burlington Limestone, and Kammer (in prep) is currently revising the pinnulate cladids.

Although several of the described Burlington species are synonymous, new species continue to be found and described from old museum holdings and new field collections. I have attempted to compile a table comprising the currently recognized crinoids and blastoids from the Burlington Limestone. This list was compiled from Webster's (1973, 1977, 1986, 1988, 1993) *Bibliography and Index of Paleozoic Crinoids* (now online at: http://crinoid.gsajournals.org/crinoidmod) and includes the originally reported (lower and upper Burlington) range and relative frequency of each species according to their distribution in the Burlington pelmatozoan assemblages. This table should be considered as a working draft, but aims to be a useful summary of Burlington pelmatozoan taxonomy and distribution. I have cursorily examined most of the original species descriptions and culled about 100 species from the original list of nearly 430. I eliminated species that are probable synonyms; however, it is very likely that additional synonyms remain in the list. Furthermore, I may have been overzealous in my efforts, and there may be species that may need to be reinstated. Many of the species that were culled include those (approximately 50) described by Miller and Gurley from 1893-1897. Kirk (1943a) explained that Miller and Gurley "described every specimen they could get their hands on—good bad or indifferent. As was well known to their contemporaries, the main purpose was to forestall the work of Wachsmuth and Springer." I have examined all of the species descriptions and figures published by Miller and Gurley from this period, and the great majority is assignable to previously described and common representatives of the Burlington fauna. In fact, it is unlikely that any of their Burlington crinoid species are valid. As such, I have even-handedly, but tentatively eliminated every species described by Miller and Gurley from the table presented herein.

Despite the problems associated with the taxonomy of Burlington pelmatozoans, the Burlington Limestone constitutes an incredibly diverse and evolutionarily important fauna. This is well illustrated by the fact that the majority of the underlying Kinderhookian faunas are represented by fewer than 50 species of crinoids and a handful of blastoids (Laudon 1933; Laudon and Beane,1937; Peck and Keyte 1938). The Burlington Limestone, with approximately 300 crinoids and 25 blastoids represents a six-fold increase in diversity over a few million years. Monobathrid camerate crinoid families such as the Actinocrinitidae, Batocrinidae, and Platycrinitidae underwent incredible morphological diversification on the Burlington Shelf (Lane, 1978). Moreover, flexibles, which are typically represented by only a few species in any given formation, were represented by 8 genera and nearly 20 species in the Burlington Limestone. The same can be said for the blastoids, which are represented by 15 genera and approximately 25 species. The Burlington cladid fauna is transitional between the Kinderhookian and Late Osagean faunas and shares genera with each. The evolutionary importance of the cladid faunas will be better understood following publication of Kammer's (in prep) current research on the group. The cladid genera *Barycrinus* and *Cyathocrinites* underwent considerable diversification on the Burlington Shelf, and phylogenetic studies of these genera by Gahn and Kammer (2002) and Kammer and Gahn (2003) suggest that many of these species originated from single, abundant, geographically widespread, and geologically long-ranging species such as *Barycrinus rhombiferus* (Owen and Shumard) and *Cyathocrinites iowensis* (Owen and Shumard).

The high species diversity of crinoids and blastoids in the Burlington Limestone is partially attributable to a fierce collecting effort from the 1850's to the present and extensive exposures throughout southeast Iowa, west-central Illinois, Missouri, and northwestern Arkansas. Nevertheless, the regional encrinites that define the Burlington Limestone promoted incredible pelmatozoan diversity (Ausich 1997, 1999). The carbonate grains deposited in the Burlington Limestone were generated almost entirely by the disarticulation of fossil crinoids and blastoids. These echinoderms were essentially living on a mobile substrate generated by their forbearers. Evidence that these sediments were unconsolidated is provided by the crinoids themselves; well-articulated crinoid crowns are often found buried by coarse crinoidal grainstone. Furthermore, the graded and low-angle cross-stratified crinoidal limestones are indicative of storm-generated sedimentary processes that transported the mobile disarticulated remains of these echinoderms. Many Burlington grainstones represent amalgamated storm beds, and as a result, only the most taphonomically resilient components of the pelmatozoan fauna are typically preserved. The calyxes of monobathrid camerate crinoids and blastoid thecae are among the most taphonomically robust skeletal constructions, and their abundance relative to other stalked echinoderm groups is likely inflated by taphonomic processes.

Crinoid and blastoid abundance and diversity was probably enhanced through the positive taphonomic feedback generated by the unconsolidated echinoderm bioclasts. Brachiopods, mollusks, bryozoans, corals, and other sessile marine invertebrates were present in the Burlington Limestone, but their diversity and abundance pale in comparison to the pelmatozoan echinoderms. The mobile sediments produced by the crinoids and blastoids likely inhibited the successful proliferation of many other fixed invertebrates, while at the same time producing a suitable substrate for their own attachment. Crinoids and blastoids used a variety of attachment strategies to adapt to the mobile substrates of the Burlington Limestone. Some species had extremely robust holdfasts with extensive radicular cirri, while others had a distally tapering holdfast that sat freely on the substrate. Many of the diplobathrid camerates had prehensile distal stalks that could be used to wrap around the stalks of other crinoids. Furthermore, small encrusting holdfasts have been observed on large distal columnals of *Platycrinites* and the taphonomically resistant calyx rim of *Strotocrinus glyptus* (Hall). Crinoids and blastoids also served as hosts to other invertebrates. For example, *Tremichnus* borings are commonly found on the plates of the calyx and stalk of these echinoderms (Brett, 1985). These are particularly abundant in genera with very large and/or stellate plates such as those found in the Actinocrinitidae, Dichocrinidae, and Platycrinitidae. Moreover, platyceratid gastropods, or diagnostic scars and boreholes from the same, have been found on several genera of Burlington pelmatozoans. Other echinoderms have even been observed using crinoids as hosts, such as ophiuroids on the genus *Actinocrinites* (examples include specimens in the personal collection of Karl Stuekerjuergen and numerous ophiuroid-infested genera in the Smithsonian collections).

Resource partitioning was another factor in the generation of pelmatozoan diversity on the Burlington Shelf, and may explain the much higher diversity attained by crinoids than blastoids. Fossil crinoids partitioned food resources through modifications of their feeding filtration fan and by differences in stalk length (Ausich, 1980). The food gathering morphology of crinoids is incredibly diverse, whereas that of the blastoids is more generalized. It is possible that the monomorphic feeding construction of the blastoids prevented them from diversifying to the same extent as the crinoids. Nevertheless, a greater proportion of blastoid species (than crinoid species) reached high levels of abundance. In fact, blastoids are numerically superior to crinoids at many localities in the Burlington Limestone, but their typically smaller size makes them less conspicuous.

Parasitism and predation were also likely factors in the morphological diversification of crinoids during the deposition of the Burlington Limestone through processes such as evolutionary escalation (Vermeij 1987). Platyceratid gastropods are often found positioned over the anal opening of fossil crinoids, and have typically been interpreted as commensals that fed on crinoid excrement (Bowsher

1955). However, a few studies have proffered evidence suggesting that at least some platyceratids were parasitic (Rollins and Brezinski 1988; Baumiller and Gahn 2002a; Gahn and Baumiller 2003; Gahn et al. 2003). If these gastropods were detrimental to their hosts, then natural selection would favor those crinoids with parasite-resistant morphological features. Gahn and Baumiller (2001, 2006) demonstrated that crinoids with long anal tubes were less frequently infested by platyceratid gastropods than crinoids that lacked them. They also demonstrated that anal tubes evolved several times within the *Compsocrinia* from parasitized, tubeless ancestors. These studies suggest that parasitism by platyceratid gastropods may have influenced the morphological diversification of fossil crinoids. Crinoids that are known to be infested by platyceratid gastropods in the Burlington Limestone include species of *Actinocrinites*, *Aryballocrinus*, *Cusacrinus*, *Dorycrinus*, *Eucladocrinus*, *Gilbertsocrinus*, *Physetocrinus*, *Platycrinites*, and *Strotocrinus*.

Predation may have provided another extrinsic evolutionary influence on crinoids and the teeth of durophagous or shell-crushing sharks are common in the Burlington Limestone, especially in the uppermost strata of the formation. Although predator-prey interactions are difficult to document in the fossil record, coprolites containing the remains of fossil crinoids have been reported (Volkmar 1970). More common are damaged and regenerated arms, spines, and calyxes of fossil crinoids. Damage and regeneration in Recent crinoids has often been attributed to predation; indeed, Meyer et al. (1984) observed crinoid arms dangling from the mouth of a saddled coralfish over the Great Barrier Reef, Australia. Similarly, regeneration patterns in fossil crinoids appear to be best explained by predation (Meyer and Ausich 1983). Laudon (1957) suggested that the abundance of crinoid stalk material and paucity of skeletal material representing the crowns of fossil crinoids in the Burlington Limestone indicated that shell-crushing sharks utilized crinoids as an important food source and essentially grazed over vast "crinoidal gardens." Signor and Brett (1984) demonstrated a coincident diversification in Paleozoic durophagous predators and an increase in the spinosity and plate thickness of fossil crinoids. They argued that predation on crinoids in the middle Paleozoic may have been sufficient to drive morphological change and evolutionary innovations in crinoids that would facilitate predator avoidance. Gahn and Baumiller (2005) have recently provided evidence suggesting that regeneration frequencies may have been higher in the Paleozoic than previously recognized; reporting regeneration frequencies as high as 27% for Mississippian crinoids. This provides further support to claims that predation was a significant factor in the evolutionary development of Paleozoic crinoids (Baumiller and Gahn 2004). Many genera and species of crinoids in the Burlington Limestone have robust spines on the tegmen (e.g. *Dorycrinus* and *Displodocrinus*), dorsal cup (e.g. *Goniasteroidocrinus* and *Wachsmuthicrinus*), anal tube (e.g. *Uperocrinus*), or anal sac (e.g. *Coeliocrinus* and *Pelecocrinus*) that may represent independently derived, anti-predatory characters. The development of broad medial calyx rims (e.g. *Eutrochocrinus* and *Strotocrinus*), dorso-ventrally flattened calyxes (e.g. *Agaricocrinus* and *Plemnocrinus*), defectively pinnulate and paddle-shaped distal arm brachials (e.g. *Cusacrinus* and *Eretmocrinus*), and either very large or very small body size may have also assisted in predator-avoidance or damage reduction. Broad medial calyx rims and paddle-shaped distal arms may have helped the crinoids with these traits avoid predation by making them appear larger than they actually were, similar to the predator-avoidance strategy of Australia's frilled lizard. Defectively pinnulate arms, or those that lack pinnules distally, evolved independently at least twice in camerate crinoids. The non-pinnulate arms of these crinoids may have permitted the loss of a substantial portion of the arm without a great loss in feeding efficacy. Dorso-ventral flattening and reduction of the visceral mass of the calyx may have reduced the probability of lethal predatory attacks by increasing the probability of the arms being damaged rather than vital areas. Although entertaining anti-predatory hypotheses for these structures is engaging, they prove difficult to test. However, many of the most spinose and seemingly best-defended crinoid genera are present in the *Macrocrinus verneuilianus-Pentremites elongatus* Association, which also contains the greatest concentration and diversity of shell-crushing shark remains. Many of these well-defended camerates abruptly declined at the end of the Osagean and became entirely extinct by the Meramecian. Waters and Maples (1991) suggested that the diminished dominance of this clade was caused by predator-mediated community reorganization.

CONCLUSIONS

The Burlington Limestone is renowned for incredible crinoid and blastoid diversity. However, not all of these species lived contemporaneously. At least three faunal associations can be distinguished in the Burlington Limestone and appear to coincide with significant fluctuations in sea level. The crinoids and blastoids of the *Dorycrinus unicornis-Cryptoblastus melo* Association are mostly restricted to the crinoidal grainstones of the Dolbee Creek Cycle, and the overlying pelmatozoan associations are restricted to the Haight Creek Cycle. The stark difference in faunal composition between the Dolbee Creek and Haight Creek Cycles and the similarity shared by the *Uperocrinus pyriformis-Globocrinus norwoodi* and *Macrocrinus verneuilianus-Pentremites elongatus* Associations is consistent with a sea-level fluctuation of greater magnitude occurring above the Dolbee Creek Member than in the "middle grainstone" of the Haight Creek Member. Whether the species of these associations were able to track the encrinites (and continue evolving in "greener pastures") during intervals of sea-level change, tolerate or adapt to the flooding of the carbonate shelf, or went extinct is unclear and requires further study. However, it is apparent that the associations recognized herein can be traced over the expanse of the Burlington shelf and perhaps beyond. The crinoid and blastoid faunas of the Lake Valley (New Mexico) and Redwall (Arizona) Formations are strikingly similar to those of the *Dorycrinus unicornis-Cryptoblastus melo* Association of the Burlington Shelf (Brower 1970; Macurda 1970), and similarities between the crinoid and blastoid fauna of the Nada Member of the Borden Formation (Kentucky) and the *Uperocrinus pyriformis-Globoblastus norwoodi* Association are incredible (Lane and DuBar 1983; Lee et al. 2005). The observation that many of the species that characterize these pelmatozoan associations extend well beyond the Burlington Shelf and occur in a myriad of facies suggests that the associations are not confined to a single environment. Therefore, it seems likely that many of the common and widely distributed species of Burlington crinoids should persist though facies changes in the Burlington Limestone, unless these changes represented rapid and drastic changes in sea level. The integrity of the echinoderm associations recognized herein over hundreds, if not thousands of miles suggests the presence of extensive epicontinental seas that were relatively free of physical and oceanographic barriers.

A more detailed analysis of species-level taxonomy and spatiotemporal distribution of Burlington crinoids and blastoids and those of coeval formations may yield insight into spatiotemporal morphological variation and endemism. Such information would be beneficial to the understanding of ancestor-descendant relationships and evolutionary processes acting upon the crinoids and blastoids during this pivotal interval of diversification. This is not an unrealistic task considering the abundance of exposures and echinoderms in the Burlington Limestone. However, if such a goal is to be met, then amateur and professional paleontologists alike must develop a clear understanding of the stratigraphic and taxonomic complexities (or simplicities, if you prefer) of the Burlington Limestone and keep this information with the specimens they collect. I certainly hope that this paper will be a helpful step in such an endeavor.

The three pelmatozoan assemblages defined in this study should be easy to recognize in the field over the entire extent of the geologic distribution of the Burlington Limestone, but they should not be used exclusively. The zones of Rowley (1908), Laudon (1937, 1973) and Kaiser (1950) can be recognized and be very useful at local scales. The best data of course, would be exact positional measurements of specimens from a diagnostic stratigraphic marker bed. However, I am aware that many Burlington fossils are collected as float and can only be traced back to a more generalized biozone. Regardless of what zonation scheme is chosen, I strongly encourage discontinuing the use of the "lower" and "upper" Burlington in reference to anything other than historical discussions of the Burlington Limestone and in reporting the stratigraphic occurrence of specimens from old collections.

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Appendix. Pelmatozoan echinoderms of the Burlington Limestone. A culled listing of currently recognized crinoids and blastoids of the Burlington Limestone, including the author of each species and reported lower vs. upper Burlington occurrences (lB = lower Burlington, uB = upper Burlington, Bu = Burlington undifferentiated). Refer to Webster (1973, 1977, 1986, 1988, 1993) for the citations listed in the table. The distribution and relative frequency of all species is also given for each Burlington pelmatozoan association (except for those that are unknown). Please refer to the text and Figure 2 for an explanation of these associations. This table should be used cautiously as it likely requires substantial revisions. However, it should be useful as a general guide to the crinoids and blastoids of the Burlington Limestone. The frequencies are indicated and defined as follows: (a) abundant–species that are extremely numerous at some localities, but only common at others; (c) common–species that are represented at almost every outcrop visited; (u) uncommon–species that are found only after considerable collecting effort; (r) rare–species that are only represented by very few specimens in all available collections.

#	**Crinoids**	**Author**	**Division**	**Association**		
	Monobathrids			**I**	**II**	**III**
1	*Aacocrinus arrosus*	(Miller, 1892)	Bu	r		
2	*Abatocrinus aequalis*	(Hall, 1858)	lB	c		
3	*A. calvini*	(Rowley, 1890)	lB	u		
4	*A. clypeatus*	(Hall, 1859)	lB	c		
5	*A. curiosus*	(Rowley, 1908)	lB	r		
6	*A. laura*	(Hall, 1861)	uB		r	u
7	*A. Lepidus*	(Hall, 1859)	lB	u		
8	*A. pistillus*	(Meek and Worthen, 1865)	uB		r	u
9	*A. rotadentatus*	(Rowley and Hare, 1891)	lB	r		
10	*A. tuberculatus*	(Wachsmuth and Springer, 1897)	lB	r		
11	*A. turbinatus*	(Hall, 1858)	lB	c		
12	*Actinocrinites eximius*	(Kirk, 1943)	uB			u
13	*A. multiradiatus*	(Shumard, 1857)	uB			c
14	*A. probolos*	Ausich and Kammer, 1991	uB			r
15	*A. scitulus*	(Meek and Worthen, 1860)	uB		c	r
16	*A. verrucosus*	(Hall, 1858)	uB			c
17	*Agaricocrinus bellatrema*	Hall, 1861	uB			r
18	*A. bellatrema major*	Wachsmuth and Springer, 1897	uB			r
19	*A. brevis*	(Hall, 1858)	lB	c		
20	*A. bullatus*	(Hall, 1858)	uB		c	c
21	*A. convexus*	(Hall, 1859)	uB		u	
22	*A. excavatus*	(Hall, 1861)	uB			u
23	*A. gracilis*	Meek and Worthen, 1861	uB		u	
24	*A. inflatus*	Hall, 1861	uB		u	r
25	*A. louisianensis*	Rowley, 1900	lB	r		
26	*A. nodosus*	Meek and Worthen, 1869	uB			c
27	*A. planoconvexus*	Hall, 1861	lB	r	c	
28	*A. pyramidatus*	(Hall, 1858)	lB	r		
29	*A. stellatus*	(Hall, 1858)	lB		u	c
30	*Ancalocrinus spinobrachiatus*	(Hall, 1859)	lB	u	u	

31	*Aorocrinus canaliculatus*	(Meek and Worthen, 1869)	lB	r		
32	*A. subaculeatus*	(Hall, 1858)	lB	r		
33	*A. symmetricus*	(Hall, 1858)	Bu		c	c
34	*A. wachsmuthi*	Rowley, 1901	lB	r		
35	*Aryballocrinus tenuidiscus*	(Hall, 1861)	lB	r		
36	*A. whitei*	(Hall, 1861)	lB-uB	u	u	u
37	*Auliskocrinus crassitestus*	(White, 1862)	uB			r
38	*Azygocrinus andrewsianus*	(McChesney, 1860)	uB			u
39	*A. dodecadactylus*	(Meek and Worthen, 1861)	uB			u
40	*A. rotundus*	(Yandell and Shumard, 1855)	uB			a
41	*Cactocrinus clarus*	(Hall, 1861)	lB	u		
42	*C. extensus*	Wachsmuth and Springer, 1897	lB	r		
43	*C. glans*	(Hall, 1859)	uB		c	u
44	*C. multibrachiatus*	(Hall, 1858)	lB	c		
45	*C. obesus*	(Keyes, 1894)	lB		c	
46	*C. opusculus*	(Hall, 1859)	lB	u		
47	*C. proboscidialis*	(Hall, 1858)	lB	c		
48	*C. reticulatus*	(Hall, 1861)	lB	u		
49	*C. sexarmatus*	(Hall, 1859)	lB	r		
50	*C. thalia*	(Hall, 1861)	lB	u		
51	*Camptocrinus praenuntius*	Springer, 1926	uB		u	r
52	*Coelocrinus concavus*	(Meek and Worthen, 1861)	uB			r
53	*Cusacrinus asperrimus*	(Meek and Worthen, 1869)	lB	r		
54	*C. chloris*	(Hall, 1861)	lB	r		
55	*C. coelatus*	(Hall, 1858)	lB	u		
56	*C. denticulatus*	(Hall, 1863)	lB	r		
57	*C. ectypus*	(Meek and Worthen, 1869)	lB	r		
58	*C. gracilis*	(Wachsmuth and Springer, 1897)	lB	r		
59	*C. limabrachiatus*	(Hall, 1861)	lB	r		
60	*C. longus*	(Meek and Worthen, 1869)	lB	r		
61	*C. penicillus*	(Meek and Worthen, 1869)	lB	r		
62	*C. spinotentaculus*	(Hall, 1859)	lB	r		
63	*C. tenuisculptus*	(McChesney, 1860)	lB	u		
64	*C. thetis*	(Hall, 1861)	lB	r		
65	*C. tuberculosus*	(Wachsmuth and Springer, 1897)	uB		r	
66	*Cytidocrinus sculptus*	(Hall, 1858)	lB	u	u	u
67	*Dichocrinus conus*	Meek and Worthen, 1860	lB-uB	u	u	u
68	*D. gracilis*	Broadhead, 1981	uB			r
69	*D. lachrymosus*	Hall, 1859	uB			r
70	*D. laevis*	Hall, 1859	lB	r		
71	*D. pocillum*	Hall, 1861	uB			u
72	*Displodocrinus divergens*	(Hall, 1859)	lB	u	u	
73	*Dorycrinus cornigerus*	(Hall, 1858)	uB		c	c
74	*D. missouriensis*	(Shumard, 1855)	uB		u	r
75	*D. pentagonus*	Rowley, 1900	uB		r	
76	*D. quinquelobus*	(Hall, 1859)	uB			u
77	*D. roemeri*	Meek and Worthen, 1860	uB			r

78	*D. subturbinatus*	(Meek and Worthen, 1860)	lB	r		
79	*D. unicornis*	(Owen and Shumard, 1850)	lB	a		
80	*D. unispinus*	(Hall, 1861)	lB	r		
81	*E. brevis*	Rowley, 1902	uB		r	
82	*E. calyculoides*	(Hall, 1860)	uB		u	u
83	*E. calyculoides nodosus*	Wachsmuth and Springer, 1897	uB			r
84	*E. clio*	(Hall, 1861)	lB	r		
85	*E. cloelia*	(Hall, 1861)	uB	r		
86	*E. corbulis*	(Hall, 1861)	lB	u		
87	*E. coronatus*	(Hall, 1859)	lB	r		
88	*E. depressus*	Keyes, 1894	uB			u
89	*E. expansus*	Keyes, 1894	lB	r		
90	*E. leucosia*	(Hall, 1861)	lB	u		
91	*E. matutus*	(Hall, 1861)	uB		u	
92	*E. minor*	Wachsmuth and Springer, 1897	uB		r	
93	*E. neglectus*	(Meek and Worthen, 1868)	lB	u		
94	*E. rugosus*	Wachsmuth and Springer, 1897	lB	r		
95	*Eucladocrinus pleurovimenus*	(White, 1862)	uB			u
96	*E. praenuntius*	(Wachsmuth and Springer, 1878)	uB			u
97	*Eutrochocrinus christyi*	(Shumard, 1855)	uB		u	c
98	*E. lovei*	(Wachsmuth and Springer, 1881	uB		r	r
99	*E. trochiscus*	(Meek and Worthen, 1868)	uB			u
100	*Macrocrinus gemmiformis*	(Hall, 1859)	lB	r		
101	*M. konincki*	(Shumard, 1855)	uB		c	u
102	*M. verneuilianus*	(Shumard, 1855)	uB		u	a
103	*Megistocrinus evansii*	(Owen and Shumard, 1850)	lB	u	r	r
104	*M. evansii crassus*	White, 1862	lB	r		
105	*Nunnacrinus locellus*	(Hall, 1861)	lB	u		
106	*N. puteatus*	(Rowley and Hare, 1891)	lB	r		
107	*Paradichocrinus liratus*	(Hall, 1861)	uB			u
108	*Physetocrinus asper*	(Meek and Worthen, 1869)	uB		r	r
109	*P. dilatatus*	(Meek and Worthen, 1869)	uB		r	r
110	*P. ornatus*	(Hall, 1858)	lB	u		
111	*P. ventricosus*	(Hall, 1858)	lB-uB	r	a	u
112	*Platycrinites americanus*	(Owen and Shumard, 1852)	lB	c	u	
113	*P. aqualis*	(Hall, 1861)	uB			u
114	*P. asper*	(Meek and Worthen, 1861)	uB			r
115	*P. burlingtonensis*	(Owen and Shumard, 1850)	lB	c		
116	*P. brevinodus*	(Hall, 1861)	lB-uB	u	u	r
117	*P. corbuliformis*	(Rowley and Hare, 1891)	lB	r		
118	*P. davisi*	(Wachsmuth and Springer, 1897)	lB	r		
119	*P. discoideus*	(Owen and Shumard, 1850)	lB	c		
120	*P. excavatus*	(Hall, 1861)	uB	u	u	
121	*P. geometricus*	(Wachsmuth and Springer, 1897)	uB		r	r
122	*P. glyptus*	(Hall, 1861)	uB		r	u
123	*P. nodostriatus*	(Wachsmuth and Springer, 1897)	lB-uB	r	u	
124	*P. ornogranulus*	(McChesney, 1860)	lB	c		

125	*P. pocilliformis*	Hall (1858)	lB	c	u	
126	*P. parvinodus*	(Hall, 1861)	lB	r		
127	*P. planus*	(Owen and Shumard, 1850)	lB	c	u	
128	*P. regalis*	(Hall, 1861)	lB	r		
129	*P. saffordi*	(Hall, 1858)	lB			u
130	*P. scobina*	(Meek and Worthen, 1861)	lB	u		
131	*P. sculptus*	(Hall, 1858)	lB	u	u	
132	*P. spinifer*	(Wachsmuth and Springer, 1897)	lB	r		
133	*P. spinifer elongatus*	(Wachsmuth and Springer, 1897)	lB	r		
134	*P. subspinulosus*	(Hall, 1859)	uB		u	
135	*P. trunculatus*	(Hall, 1858)	lB	u		
136	*P. verrucosus*	(White, 1865)	lB	u		
137	*P. wortheni*	(Hall, 1858)	lB	r		
138	*P. yandelli*	(Owen and Shumard, 1850)	lB	r		
139	*P. yandelli perasper*	(Meek and Worthen, 1865)	lB	r		
140	*Plemnocrinus beebei*	Kirk, 1946	uB		u	r
141	*P. homalus*	Kirk, 1946	lB			r
142	*P. occidentalis*	(Miller, 1891)	Bu			r
143	*P. subspinosus*	(Hall, 1858)	lB-uB	u	u	u
144	*P. tuberosus*	(Hall, 1858)	uB			r
145	*P. eminulus*	(Hall, 1861)	lB	r		
146	*Pleurocrinus halli*	(Shumard, 1866)	uB			r
147	*P. incomptus*	(White, 1863)	uB		u	r
148	*P. pileiformis*	(Hall, 1858)	lB	u		
149	*P. quinquenodus*	(White, 1862)	uB		r	r
150	*Springeracrocrinus praecursor*	(Springer, 1926)	uB		r	r
151	*Steganocrinus burlingtonensis*	Brower, 1965	uB			r
152	*S. concinnus*	(Shumard, 1855)	uB		r	r
153	*S. elongatus*	Kirk, 1943	uB		c	u
154	*S. multistriatus*	Brower, 1965	Bu			r
155	*S. pentagonus*	(Hall, 1858)	lB	c	u	r
156	*S. planus*	Brower, 1965	uB			r
157	*S. robustus*	Brower, 1965	uB		u	
158	*S. validus*	(Meek and Worthen, 1860)	uB			r
159	*Strimplecrinus ovatus*	(Owen and Shumard, 1850)	lB	r		
160	*S. pendens*	(Wachsmuth and Springer, 1897)	uB		r	r
161	*S. pisum*	(Meek and Worthen, 1869)	lB	u		
162	*S. plicatus*	(Hall, 1861)	uB			r
163	*S. striatus*	(Owen and Shumard, 1850)	lB-uB		u	c
164	*Strotocrinus glyptus*	(Hall, 1860)	uB		u	u
165	*Teleiocrinus adolescens*	Wachsmuth and Springer, 1897	lB-uB	r	r	r
166	*T. liratus*	(Hall, 1859)	uB			r
167	*T. umbrosus*	(Hall, 1858)	uB			c
168	*Uperocrinus aequibrachiatus*	(McChesney, 1860)	uB		c	u
169	*U. aequibrachiatus astericus*	(Meek and Worthen, 1860)	uB		c	u
170	*U. hageri*	(McChesney, 1860)	uB		r	c
171	*U. inflatus*	(Rowley and Hare, 1891)	lB	c		

172	*U. longirostris*	(Hall, 1858)	lB	c		
173	*U. nashvillae subtractus*	(White, 1862)	uB			u
174	*U. pyriformis*	(Shumard, 1855)	uB		a	c
	Diplobathrids					
1	*Cribanocrinus wachsmuthi*	(Hall, 1861)	lB	r		
2	*C. whitei*	(Hall, 1861)	lB	r		
3	*C. wortheni*	(Hall, 1858)	lB	r		
4	*"Gilbertsocrinus" fiscellus*	(Meek and Worthen, 1860)	lB	r		
5	*Goniasteroidocrinus obovatus*	Meek and Worthen, 1869	uB			r
6	*G. tuberculosus*	(Hall, 1859)	uB		r	r
7	*G. typus*	(Hall, 1859)	lB-uB	r	u	u
8	*Rhodocrinites barrisi*	(Hall, 1861)	uB		u	
9	*R. barrisi striatus*	Wachsmuth and Springer, 1897	ub		r	
10	*R. truncatus*	(Wachsmuth and Springer, 1897)	uB		r	
	Disparids					
1	*Catillocrinus wachsmuthi*	(Meek and Worthen, 1866)	uB			r
2	*Halysiocrinus dactylus*	(Hall, 1860)	lB-uB	u	u	u
3	*Synbathocrinus dentatus*	Owen and Shumard, 1852	uB		c	c
4	*S. papillatus*	Hall, 1861	Bu			
5	*S. wachsmuthi*	Meek and Worthen, 1869	uB		u	u
6	*S. wortheni*	Hall, 1858	uB			c
	Cladids					
1	*Abrotocrinus cf. A. unicus*	(Hall, 1861)	uB			r
2	*Acylocrinus striatus*	(Meek and Worthen, 1869)	lB	r		
3	*A. tortuosus*	(Hall, 1861)	Bu			
4	*A. tumidus*	Kirk, 1947	lB	r		
5	*Aphelecrinus delicatus*	(Meek and Worthen, 1869)	lB-uB	r	r	r
6	*A. meeki*	(Kirk, 1941)	lB	r		
7	*Ascetocrinus rusticellus*	(White, 1863)	uB			r
8	*A. scoparius*	(Hall, 1861)	lB	r		
9	*A. whitei*	(Hall, 1861)	lB	r		
10	*Atelestocrinus delicatus*	Wachsmuth and Springer, 1886	lB	r		
11	*A. robustus*	Wachsmuth and Springer, 1885	lB	r		
12	*Barycrinus crassibrachiatus*	(Hall, 1860)	uB		u	u
13	*B. magister*	(Hall, 1858)	uB			r
14	*B. rhombiferus*	(Owen and Shumard, 1852)	lB-uB	r	u	c
15	*B. sampsoni*	(Miller and Gurley, 1896)	lB	r		
16	*B. scitulus*	(Meek and Worthen, 1860)	lB	r		
17	*B. spurius*	(Hall, 1858)	lB-uB	r	u	u
18	*Belemnocrinus pourtalesi*	Wachsmuth and Springer, 1877	lB	r		
19	*B. typus*	White, 1862	lB	r	r	
20	*Blothrocrinus cultidactylus*	(Hall, 1859)	lB-uB	r	r	
21	*B. swallovi*	(Meek and Worthen, 1860)	uB			r

22	*Bursacrinus confirmatus*	White, 1862	lB	r		
23	*B. wachsmuthi*	Meek and Worthen, 1861	uB			r
24	*Cercidocrinus bursaeformis*	(White, 1862)	lB	r		
25	*Coeliocrinus dilatatus*	(Hall, 1861)	lB	r		
26	*C. subspinosus*	White, 1863	uB			r
27	*C. ventricosus*	(Hall, 1861)	lB-uB	r	u	u
28	*Corythocrinus tenuis*	Kirk, 1946	uB			r
29	*Costalocrinus cornutus*	(Owen and Shumard, 1850)	lB-uB	r	u	u
30	*Cyathocrinites barrisi*	(Hall, 1861)	lB	r		
31	*C. barydactylus*	(Wachsmuth and Springer, 1878)	uB			r
32	*C. deroseari*	Kammer and Gahn, 2003	lB	r		
33	*C. gilesi*	(Wachsmuth and Springer, 1878)	uB			r
34	*C. iowensis*	(Owen and Shumard, 1850)	lB-uB	c	c	c
35	*C. kelloggi*	(White, 1862)	lB-uB	r	r	r
36	*C. lamellosus*	(White, 1863)	uB			r
37	*C. rigidus*	(White, 1865)	lB	r		
38	*C. sampsoni*	(Miller, 1891)	lB	r		
39	*"Cyathocrinites" formosus*	(Rowley, 1905)	lB	r		
40	*Cydrocrinus robbi*	(Roy, 1929)	Bu			
41	*Decadocrinus scalaris*	(Meek and Worthen, 1869)	uB		r	r
42	*Eratocrinus elegans*	(Hall, 1858)	lB-uB	u	u	c
43	*E. ramosus*	(Hall, 1858)	uB			r
44	*Gilmocrinus cf. G. oneali*	Laudon and Beane, 1937	lB	r		
45	*Goniocrinus incipiens*	(Hall, 1861)	lB	r		
46	*Graphiocrinus simplex*	(Hall, 1858)	uB			r
47	*G. spinobrachiatus*	Hall, 1861	uB			r
48	*G. subimpressus*	(Meek and Worthen, 1861)	lB	r		
49	*G. whitei*	(Meek and Worthen, 1869)	uB			r
50	*Histocrinus juvenis*	(Meek and Worthen, 1869)	lB	r		
51	*Holcocrinus spinobrachiatus*	(Hall, 1861)	lB	r		r
52	*H. wachsmuthi*	(Meek and Worthen, 1861)	lB	r		
53	*Hypselocrinus calyculus*	(Hall, 1858)	Bu			
54	*H. fusiformis*	(Hall, 1861)	Bu			
55	*H. macrodactylus*	(Meek and Worthen, 1869)	lB-uB	c	c	c
56	*H. tethys*	(Meek and Worthen, 1869)	lB-uB	r	r	r
57	*Lanecrinus halli*	(Hall, 1861)	uB			u
58	*Linocrinus asper*	(Meek and Worthen, 1869)	lB	u		
59	*L. penicillus*	(Meek and Worthen, 1869)	lB-uB	u	c	c
60	*L. perangulatus*	(White, 1862)	uB			c
61	*L. scobina*	(Meek and Worthen, 1869)	uB		u	u
62	*Nactocrinus antiquus*	(Meek and Worthen, 1869)	lB	r		r
63	*N. nitidus*	Kirk, 1947	lB	r		
64	*Pachylocrinus carinatus*	(Hall, 1861)	uB			r
65	*P. clio*	(Meek and Worthen, 1869)	uB			r
66	*P. cuneatus*	(Quenstedt, 1876)	Bu			
67	*P. dichotomus*	(Hall, 1858)	uB			r
68	*P. liliiformis*	(Meek and Worthen, 1869)	uB			r

69	*P. ramulosus*	(Hall, 1861)	uB			r
70	*Paracosmetocrinus cf. P. strakai*	Strimple, 1967	lB	r		
71	*Parisocrinus labyrinthicus*	(Miller, 1891)	lB	r		
72	*P. tenuibrachiatus*	(Meek and Worthen, 1861)	lB-uB	u	u	u
73	*Pelecocrinus aqualis*	(Hall, 1859)	lB	u	r	
74	*P. insignis*	Kirk, 1941	uB			r
75	*Pellecrinus sp.*	Kammer and Gahn, 2003	lB	r		
76	*Poteriocrinites notabilis*	Meek and Worthen, 1869	lB	r		
77	*P. obuncus*	(White, 1862)	lB	r		
78	*P. waltersi*	(Rowley and Hare, 1891)	lB	r		
79	*Ramulocrinus rudis*	(Meek and Worthen, 1873)	uB		r	r
80	*Scytalocrinus cf. S. dodecadactylus*	(Meek and Worthen, 1860)	uB			r
81	*Springericrinus doris*	(Hall, 1861)	uB	r	u	u
82	*S. macropleurus*	(Hall, 1861)	lB	c		
83	*Tropiocrinus carinatus*	Kirk, 1947	uB		r	r
84	*Whiteocrinus florifer*	(Wachsmuth and Springer, 1877)	uB		r	
85	*Zygotocrinus enormis*	(Meek and Worthen, 1861)	lB	r		
	Flexibles					
1	*Forbesiocrinus agassizi*	Hall 1858	uB			r
2	*F. burlingtonensis*	Springer, 1920	uB			r
3	*Mespilocrinus chapmani*	Springer, 1920	uB		r	r
4	*M. konincki*	Hall, 1859	lB-uB	r	r	
5	*M. thiemei*	Springer, 1920	lB	r		
6	*Methichthyocrinus burlingtonensis*	(Hall, 1858)	lB	r		
7	*Nipterocrinus arboreus*	Worthen in Meek and Worthen, 1873	lB	r		
8	*N. wachsmuthi*	Meek and Worthen, 1868	uB		r	r
9	*Onychocrinus asteriaeformis*	(Hall, 1861)	uB			u
10	*O. diversus*	Worthen 1866	uB			u
11	*Parichthyocrinus nobilis*	(Wachsmuth and Springer, 1879)	uB			r
12	*Taxocrinus juvenis*	(Hall, 1861)	lB	u	u	
13	*T. ornatus*	Springer, 1920	lB	r		
14	*T. ramulosus*	(Hall, 1859)	uB			r
15	*Wachsmuthicrinus bernhardinae*	Springer, 1920	lB	r		
16	*W. iowensis*	Springer, 1920	uB		r	r
17	*W. spinifer*	(Hall, 1861)	lB	r		
18	*W. thiemei*	(Hall, 1861)	lB	u		
	Blastoids **Fissiculates**					
1	*Hadroblastus whitei*	(Hall, 1861)	uB			r
2	*Orophocrinus catactus*	(Rowley, 1908)	lB	r		
3	*O. gracilus*	(Meek and Worthen, 1870)	lB	r		
4	*O. stelliformis*	(Owen and Shumard, 1865)	lB	c		
5	*Phaenoschisma gracillimum*	(Rowley and Hare, 1891)	lB	r		
6	*P. laeviculum*	(Rowley, 1900)	lB-uB	r	r	r

	Granatocrinids					
1	*Arcuoblastus shumardi*	(Meek & Worthen, 1895)	uB			r
2	*Auloblastus clinei*	Beaver, 1961	uB			r
3	*Carpenteroblastus magnibasus*	(Rowley, 1895)	uB			r
4	*C. pentalobus*	(Rowley, 1901)	Bu			r
5	*Cryptoblastus melo*	(Owen & Shumard, 1850)	lB	a		
6	*C. pisum*	(Meek & Worthen, 1869)	lB-uB	r	r	
7	*Decemoblastus melonoides*	(Meek and Worthen, 1869)	uB			r
8	*Dentiblastus sirius*	(White, 1862)	uB		r	r
9	*Lophoblastus inopinatus*	(Rowley and Hare, 1891)	lB	u		
10	*L. tenuistriatus*	(Hambach, 1903)	Bu	r		
11	*Poroblastus granulosus*	(Meek & Worthen, 1865)	uB			a
12	*Schizoblastus aplatus*	(Rowley and Hare, 1891)	lB	r		
13	*S. marginulus*	(Rowley, 1901)	uB			r
14	*S. moorei*	(Cline, 1936)	uB			r
15	*S. sayi*	(Shumard, 1855)	uB		u	c
	Pentremitids					
1	*Globoblastus norwoodi*	(Owen and Shumard, 1850)	uB		a	c
2	*Pentremites elongatus*	(Shumard, 1858)	uB		r	a
3	*P. kirki*	(Hambach, 1903)	lB	r		
	Troosticrinids					
1	*Metablastus lineatus*	(Shumard, 1858)	lB-uB	r	r	u