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TRANSACTIONS OF THE WISCONSIN ACADEMY OF SCIENCES, ARTS AND LETTERS

Volume 71, Part I, 1983

Co-editors
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TRANSACTIONS OF THE WISCONSIN ACADEMY

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WISCONSIN ACADEMY OF SCIENCES, ARTS AND LETTERS

The Wisconsin Academy of Sciences, Arts and Letters was chartered by the State Legislature on March 16, 1870 as an incorporated society serving the people of the State of Wisconsin by encouraging investigation and dissemination of knowledge in the sciences, arts and letters.

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The TRANSACTIONS of the Wisconsin Academy of Sciences, Arts and Letters is an annual publication devoted to original papers, preference being given to the works of Academy members. Sound manuscripts dealing with features of the State of Wisconsin and its people are especially welcome; papers on more general topics are occasionally published. Subject matter experts review each manuscript submitted.

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Papers received after July 1 will be considered for the next annual volume. Manuscripts should be sent to:

PHILIP & KATHRYN WHITFORD
Co-Editors: TRANSACTIONS

2647 Booth St.
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DEDICATION

This memorial volume presents the results of a paleontological symposium sponsored by colleagues, alumni and students of The University of Wisconsin-Milwaukee, Department of Geological and Geophysical Sciences as a tribute to the productive life of Dr. Katherine Greacen Nelson. This symposium was held on the old Milwaukee Downer Campus in Milwaukee on January 1, 1983, and all participants were Katherine's students.

It is appropriate that this memorial volume, sponsored by contributions from former students and industries that employ her students, be published in the *Transactions* of the Wisconsin Academy of Sciences, Arts, and Letters. She worked for many years in a variety of capacities for the Academy, and was the first woman elected as President.

To Katherine Greacen Nelson, geologist, educator, and friend, we dedicate this volume with love for enriching the lives of so many people.

Katherine Greacen Nelson

KATHERINE GREACEN NELSON

Katherine Greacen was born in Sierra Madre, California on December 9, 1913. She was married to Attorney Frank H. Nelson of Milwaukee, Wisconsin. She died on December 29, 1982 in Milwaukee after a short but valiant fight against cancer.

After receiving the first Ph.D. in geology from Rutgers University in 1938, Katherine began her distinguished career of service at Milwaukee Downer College. After World War II duty in the oil fields of Texas, she returned to Milwaukee and made contributions at Milwaukee Downer Seminary, the Y.W.C.A., and Wisconsin State College before joining The University of Wisconsin-Milwaukee Faculty in 1956.

Although Katherine's professional accomplishments include numerous scholarly papers, she is best known for her devotion to teaching others about the earth. Most university professors restrict their teaching to college-level courses and the supervision of graduate students, but not Katherine. She was always generous in her educational endeavors, and was equally available to, and comfortable with, a bus load of school children visiting the Greene Museum or congressmen contemplating the potential for the Ice Age Scientific Reserve. She never undertook any assignment with thought of personal reward or recognition. All she ever cared about was helping an individual, a group, or an organization. Such selfless people are rare in our society.

In addition to being the first chairperson of the Department of Geological and Geophysical Sciences at UWM, Katherine found time to serve the University on dozens of committees, including two terms on the Faculty Senate. She was a Fellow of the Geological Society of America, and a member of the Paleontological Society and the American Association of Petroleum Geologists.

Katherine held offices in a score of service-oriented organizations. For special contributions toward the establishment of a Sigma Xi Club at UWM, she was elected President. In recognition of assistance to the Milwaukee Public Museum, she was appointed an Honorary Curator. For long-term service to the Wisconsin Geological Society, including a term as President, she was appointed an Honorary Member. She was President of Phi Kappa Phi, and was a nominee for President of the Earth Science Section of the American Association for the Advancement of Science at the time of her death. The Midwest Federation of Mineralogical and Geological Societies honored Katherine as Educator of the Year in 1982. She was an active contributor to programs of the National Association of Geology Teachers, and served as President of the Central Section. In 1978, this organization selected her as the first woman recipient of the prestigious Neil Miner Award for distinguished contributions to earth science education.

There is much more one could record about Katherine the doer, but what about Katherine the person? She was tranquil and energetic with a kind word and helping hand to all; and always with a beautiful smile. To her, the earth was a remarkable place—to be understood, appreciated and enjoyed. She labored tirelessly for this belief while imparting warmth, enthusiasm and joy to everyone with whom she came in contact.

ACKNOWLEDGMENTS

The Katherine G. Nelson Symposium and Memorial Program presented at The University of Wisconsin-Milwaukee on January 15, 1983 was coordinated by Richard A. Paull, and arrangements were facilitated by Frank J. Charnon, Gregory Mursky, Rachel K. Paull and Robert W. Taylor; all of the Department of Geological and Geophysical Sciences at The University of Wisconsin-Milwaukee. The other faculty, staff, and students in the department generously assisted in many aspects of the program. Dennis D. Bollmann, Marmik Oil Company, Denver, Colorado and Charles W. Gartmann, Placid Oil Company, New Orleans, Louisiana acted as session chairpersons.

The memorial program was conducted by L. Joseph Lukowicz, Ladd & Lukowicz, Denver, Colorado; Frank E. Horton, Chancellor, The University of Wisconsin-Milwaukee; Douglas S. Cherkauer, The University of Wisconsin-Milwaukee; Robert E. Behling, West Virginia University; and Rachel K. Paull, The University of Wisconsin-Milwaukee.

Rachel K. and Richard A. Paull directed the preparation and critical review of the manuscripts contained in this volume. However, the encouragement and assistance of LeRoy R. Lee, Executive Director of the Wisconsin Academy of Science, Arts and Letters; and Philip B. and Kathryn D. Whitford, Co-Editors of the *Transactions* were critical factors in making this publication possible.

The papers included in this volume were critically reviewed by: Dr. Timothy R. Carr, Arco Oil and Gas Company (Texas); Dr. James W. Collinson, The Ohio State University; Dr. Robert E. Gernant, The University of Wisconsin-Milwaukee; Dr. Markes E. Johnson, Williams College (Massachusetts); Dr. Bradford Macurda, Jr., The Energists (Texas); Dr. Rachel K. Paull, The University of Wisconsin-Milwaukee; Dr. Dietmar Schumacher, Pennzoil Exploration and Producing Company (Texas); Dr. Peter M. Sheehan, Milwaukee Public Museum and The University of Wisconsin-Milwaukee; and Dr. Dale R. Sparling, Southwest State University (Minnesota).

Financial support for publication of this memorial volume of the Transactions dedicated to Katherine Greacen Nelson was provided by The Amoco Foundation through the efforts of many geologists and geophysicists employed by Amoco Production Company; Richard W. and Julie S. Behling, Tulsa, Oklahoma; Conoco Incorporated through the efforts of William E. Laing; Cotton Petroleum Corporation through the efforts of Arthur L. Paquette and Donald E. Paull; Exploration Logging U.S.A. through the efforts of Robert J. Rose and Howard Greene; Exxon Company USA through the efforts of Robert L. Sunde; Jeffrey C. Gruetzmacher, Leaf River Group, Houston, Texas; The InterNorth Foundation through the efforts of Julie S. Behling; Dietmar Schumacher, Pennzoil Exploration and Production Company, Houston, Texas; Sohio Alaska Petroleum Company through the efforts of M. J. Marfleet and Edward A. Frankovic; Robert L. Sunde, Kingsville, Texas; Union Oil Company of California through the efforts of Charles W. King, Larry H. Smith and David E. Willis.

The generosity of the individuals and organizations listed above is gratefully acknowledged by all of Katherine's students, friends and colleagues.

In addition, thanks are offered to present and future contributors to the Katherine G. Nelson Scholarship fund established by the Department of Geological and Geophysical Sciences at The University of Wisconsin-Milwaukee.

MILWAUKEE'S GENTLEMEN PALEONTOLOGISTS

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Abstract

During the last half of the nineteenth century several large fossil collections were assembled from Silurian and Devonian rocks quarried in the vicinity of Milwaukee, Wisconsin. Conditions for collecting were favorable at that time because the quarries were small, low volume, hand-operated and more numerous compared to present-day operations. Low paid quarry workers were able to significantly supplement their incomes by selling fossils which insured a continual supply of specimens.

These collections were assembled by a few moderately wealthy, self-educated naturalists, who had the time, money and interest to secure large numbers of specimens. The most prominent of these gentlemen paleontologists were Increase A. Lapham (collection destroyed by fire in 1884), Fisk Holbrook Day (collection now at Harvard's Museum of Comparative Zoology), Thomas A. Greene (collection at The University of Wisconsin-Milwaukee), and Edgar E. Teller (collection at the National Museum of Natural History).

By assembling collections and publishing a few papers, these individuals stimulated paleontologic and stratigraphic research in the area by such notable geologists as James Hall, Robert Whitfield, Stuart Weller, and many others. Since most quarries in the area are abandoned, and because of the mechanized nature of large-scale quarrying at those remaining, it is impossible to assemble comparable collections of new material. These old collections, therefore, are of critical importance to future geologic work in the area, particularly in the fields of taxonomy, biogeography, biostratigraphy, taphonomy, paleoecology, and stratigraphy.

INTRODUCTION

During the last half of the nineteenth century, several important collections of Silurian and Devonian fossils were made in the vicinity of Milwaukee, Wisconsin by local naturalists, including I. A. Lapham, F. H. Day, T. A. Greene, E. E. Teller, and C. E. Monroe. These collections, which represented a great expenditure of time and money, stimulated the interest of many prominent scientists in the geology and paleontology of southeastern Wisconsin. The most important result of the subsequent research was the discovery and correct interpretation of Silurian reefs in the area—the first Paleozoic reefs to be identified in North America (Fig. 1).

Two primary factors influenced the assembly of these collections. Most important was the availability of fossil specimens, due to the methods and intensity of quarrying for lime and building stone. Also important, however, was the role of the naturalist in nineteenth century science and his motivation for an interest in natural history. Both of these factors have changed greatly, and the decline of the local stone industry has made it impossible to assemble comparable material. Because the older collections are irreplaceable, they remain a key element in geological research of the Milwaukee area and in Silurian and Devonian paleontology in general.

This paper discusses the conditions under

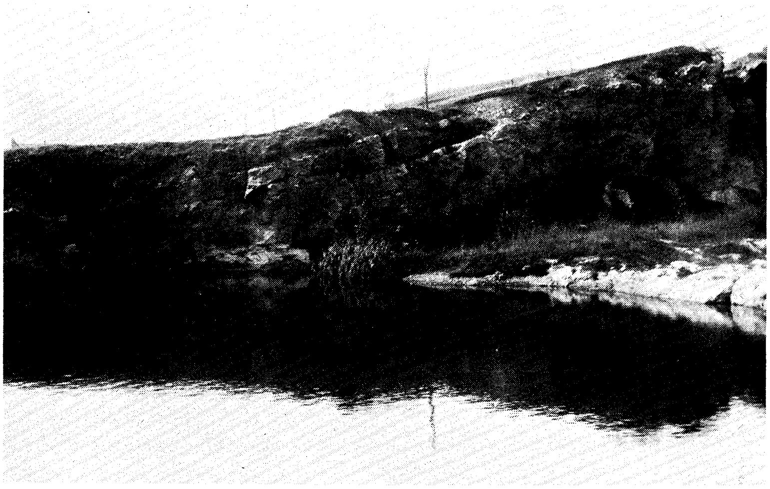

Fig. 1. Reef structure in the west wall of the Schoonmaker quarry, Wauwatosa, Wisconsin, 1899. This Silurian reef was the first Paleozoic reef described in North America (Hall, 1862). This quarry was also the locality from which Day, Greene, and Teller, as well as others, made extensive fossil collections. The area illustrated is near the present intersection of 68th and State Streets in Wauwatosa. Photo by W. C. Alden, Photo No. 115, U.S. Geological Survey Photo Library, Denver.

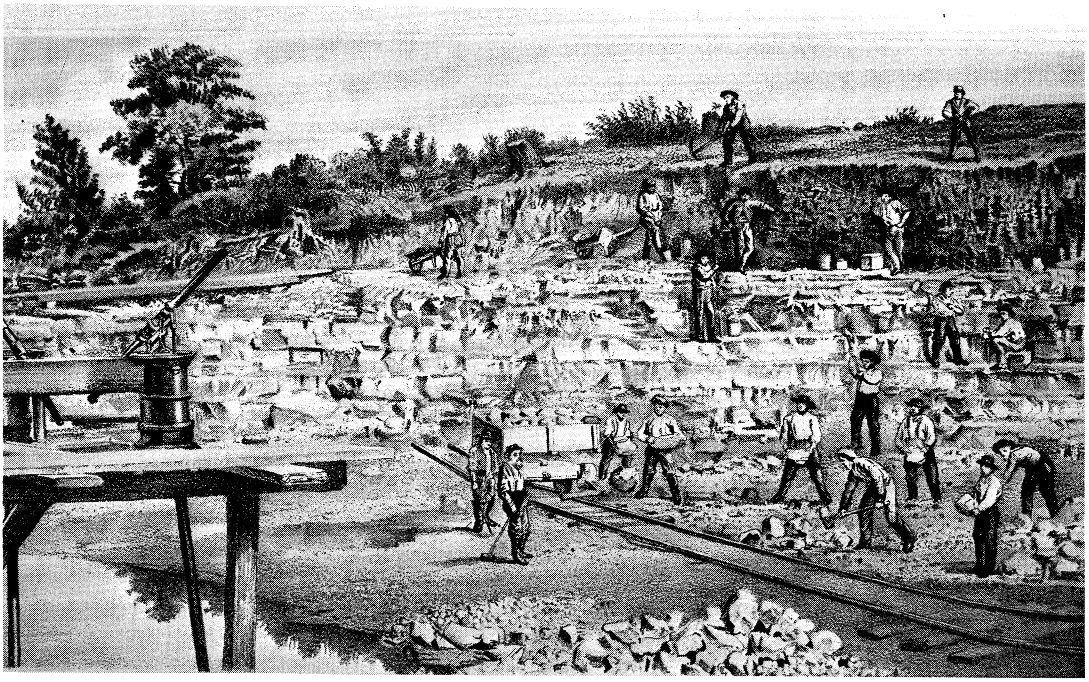

Fig. 2. Lithograph demonstrating typical nineteenth century quarrying methods. Quarry depicted was in Devonian rocks at Mill No. 1 of the Milwaukee Cement Company shortly after the company began operations, ca. 1876. The area shown in the lithograph is on the east bank of the Milwaukee River, near the old swimming beach in Estabrook Park, Milwaukee. From Chamberlin (1877); drawn from a photo taken by J. C. Miller.

which the collections were made, the prominent individuals who assembled them, and the way in which this collecting activity has contributed to geological research of southeastern Wisconsin.

MILWAUKEE'S STONE INDUSTRY

Silurian and Devonian dolomite underlies much of southeastern Wisconsin and was an important source of building materials throughout the 1800s. The development of the local stone industry and the methods of operation were important factors in the formation of the nineteenth century Milwaukee area fossil collections. Because a fairly thick cover of Pleistocene and Recent sediments limits natural bedrock exposures in southeastern Wisconsin, quarries were critical to extensive collecting and the rate of fossil discoveries was closely related to the growth of the stone industry. Local quarrying reached its peak in the late 1800s with the development of the natural cement industy, which utilized Devonian rock (Fig. 2).

Nineteenth century quarries were quite different from the large mechanized operations of today. Most were small, shallow, and the rate of rock extraction was slow. Due to the lack of mechanization, large numbers of low-paid laborers were employed. After blasting, blocks too big to be handled were broken with sledge hammers. All rock was picked up by hand and placed in carts or wagons, and building stone was trimmed with hammer and chisel (Fig. 2).

Probably most quarry workers had little desire to start personal fossil collections during their ten hour workdays. However, the opportunity to supplement their incomes was a compelling reason to develop an interest in paleontology. Milwaukee's gentlemen paleontologists supplied the financial incentive by regularly purchasing fossils from the workers. A single good specimen could fetch a dollar or two, a sum which doubled the daily wages of most quarry employees. Thus, the methods of quarrying and the active fossil market insured that few important fossils would escape the notice of the quarrymen.

Since the later 1800s, the number of quarries in the Milwaukee area has decreased from over thirty sites to only one. Most of the former sites are completely filled and covered, and the active quarries are unfavorable for collecting because of high vertical walls and large-scale operations. Also, quarry workers are no longer a dependable source of specimens since they have little direct contact with the rock and to double their daily wages through fossil purchases would be prohibitive. These changes have all contributed to a significant decrease in the availability of fossils, as well as rock exposures, which severely limits modern geological and paleontological research in southeastern Wisconsin.

GENTLEMEN PALEONTOLOGISTS

Fossil collecting was greatly influenced by the presence of several well motivated and competent naturalists who lived in the Milwaukee area during the time that quarrying activities were at their peak. These individuals were typical of the self-educated and self-supported researchers who were responsible for much of the advancement of science throughout the nineteenth century.

In the 1800s, scientific research and education took place sporadically and the quality was irregular. It was difficult to obtain advanced education in new specialized scientific areas such as geology, and it was even more difficult to find employment in these fields. However, these constraints did not prevent an increase in the popularity of all aspects of natural history throughout the nineteenth century.

Studying and collecting natural history specimens for one's "cabinet" became a socially acceptable and popular pastime. The quality of naturalist activities ranged from mindless collecting of everything and anything to some of the best research of the time. Milwaukee's gentlemen paleontologists fit into the middle of this range. While

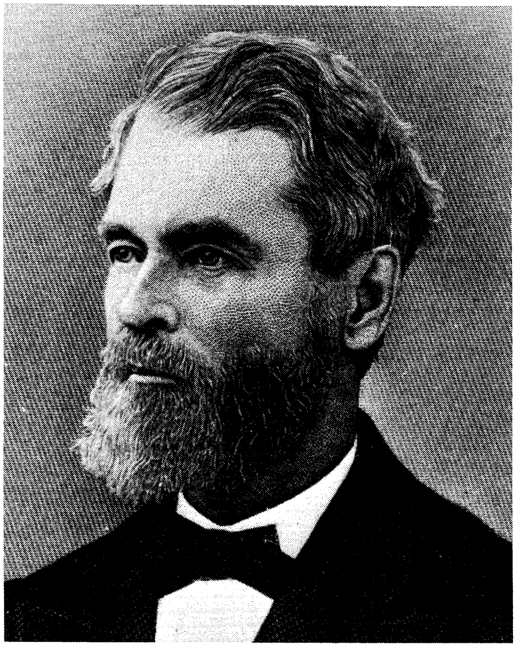

Fig. 3. Portrait of Increase A. Lapham (from Sherman, 1876).

men like I. A. Lapham did make substantial contributions to many fields of natural history, others were not as diversified in their interests nor did they publish as many scholarly papers. All were interested in several different branches of natural history, and these lifelong interests developed early. None of these individuals had advanced training in geology or other science, and were generally self-taught. They all enjoyed fairly high social standing and were successful enough in their chosen careers to have the time and money to devote to paleontological pursuits. The major contributions of these naturalists were the professional interest they stimulated in others and the comprehensive collections they diligently assembled. The following biographical sketches describe Milwaukee's best known gentlemen paleontologists and their activities.

Increase Allen Lapham

Increase Allen Lapham is well known as Wisconsin's first scientist and one of the state's most distinguished early citizens (Fig. 3). His numerous accomplishments in other fields of natural history may overshadow his paleontological contributions. However, he was the first to collect fossils in the Milwaukee area, and undoubtedly influenced the activities of his contemporaries.

Lapham was born at Palmyra, New York, on March 7, 1811. As a youth he worked as a stone cutter during construction of the Erie Canal at Lockport, New York (Sherman, 1876), and this work with fossiliferous Silurian rocks stimulated a lifelong interest in geology. He wrote his first scientific article at the age of 17, a short paper published in the American Journal of Science dealing with the geology around Louisville, Kentucky (Lapham, 1828). After spending several years as an engineer in Ohio, he moved to Milwaukee in 1836 at the request of Byron Kilbourn, and became chief engineer and secretary of the Milwaukee and Rock River Canal Company (Sherman, 1876). Soon after his arrival, he and Kilbourn began to seach the area for economically important rock and mineral deposits. Lapham also began to make observations on a variety of natural history subjects, which he continued to do throughout his life.

In 1846 Lapham sent a collection of Milwaukee area fossils to James Hall for identification. With the help of Hall's fossil identifications, Lapham determined the correct stratigraphic succession of rock units in Milwaukee. By the time his 1851 paper was published, he had defined the general Paleozoic stratigraphic section for eastern Wisconsin, established correlation with the New York section, and recognized the eastward dip of the rocks into the Michigan Basin.

In 1853 Lapham sent a manuscript entitled "American Paleontology" containing over 2000 fossil descriptions to Hall for completion and co-authorship (Winchell, 1894). Collaboration with Hall would have greatly elevated Lapham's stature as a geologist and paleontologist. Although Hall agreed to complete the project, he apparently did nothing with it and it was returned in 1860 at Lapham's request (Bean, 1936).

In 1873 Lapham was appointed head of the new state geological survey, and in this capacity he assembled a noteworthy group of young geological assistants, including T. C. Chamberlin (Beloit College) and Roland Irving (The University of Wisconsin). In 1875 he was replaced by a political crony of the new governor, but his early planning was in no small way responsible for the later success of the survey. He died on September 14, 1875, a few months after his removal from office.

Lapham's natural history collection, which included "10,000 fossils, minerals, shells, meteorites, and Indian relics" (*State Journal,* Dec. 16, 1884) was purchased by the state for The University of Wisconsin. Unfortunately, his entire collection was destroyed in the Science Hall fire of December 1, 1884 (*Milwaukee Sentinel,* Dec. 2, 1884). Only a partial list of Lapham's material exists in the published catalogue of the Wisconsin state mineral exhibit from the Centennial Exposition at Philadelphia in 1876, which consisted predominantly of specimens from his collection (Sweet, 1876). Lapham was generous with his specimens and many were given to, or exchanged with, other scientists. Some of James Hall's type specimens from Wisconsin, now in the American Museum of Natural History, are probably Lapham's specimens, although they are not so labelled. The Worthen Collection at the Illinois State Geological Survey contains at least one Lapham specimen and others are reported to be located at the Milwaukee Public Museum (Teller, 1912) and in the Greene Museum at The University of Wisconsin-Milwaukee.

Fisk Holbrook Day

Fisk Holbrook Day, the son of Reverend Warren Day and Lydia Holbrook Day, was born at Richmond, New York, on March 11, 1826 (Fig. 4). He attended Jefferson Medical College in Philadelphia, graduating in 1849 (*Lansing Journal,* 1903). Day moved to Wauwatosa, Wisconsin, in 1854, and was a prominent physician in Milwaukee County for almost 40 years. Besides having a private practice, Day was a physician for Milwaukee County hospital and poor farm for many years (Zimmermann, 1979).

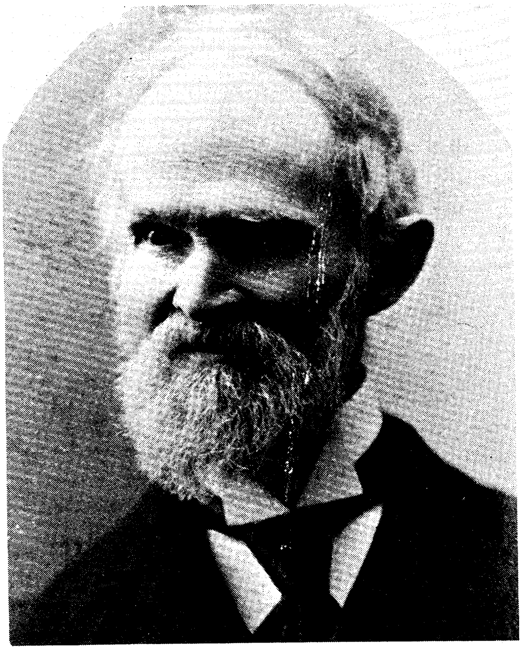

Fig. 4. Portrait of Fisk Holbrook Day (from Zimmermann, 1979).

Day was a naturalist with a wide variety of interests, including geology, botany, and archeology (Fig. 5). His paleontologic interests probably stemmed from his father's acquaintance with James Hall while in New York. Reverend Day had collected fossils and occasionally corresponded with Hall during the 1840s, and Hall visited the Day household to examine his collections. Hall later made several visits to Wauwatosa to study the fossils in F. H. Day's cabinet, and a few specimens figured by Hall in 1867 and 1870 were from the Day collection.

Day published one paper on Milwaukee area geology in 1877. This paper demonstrates that Day was very observant and an original thinker, confident enough in his

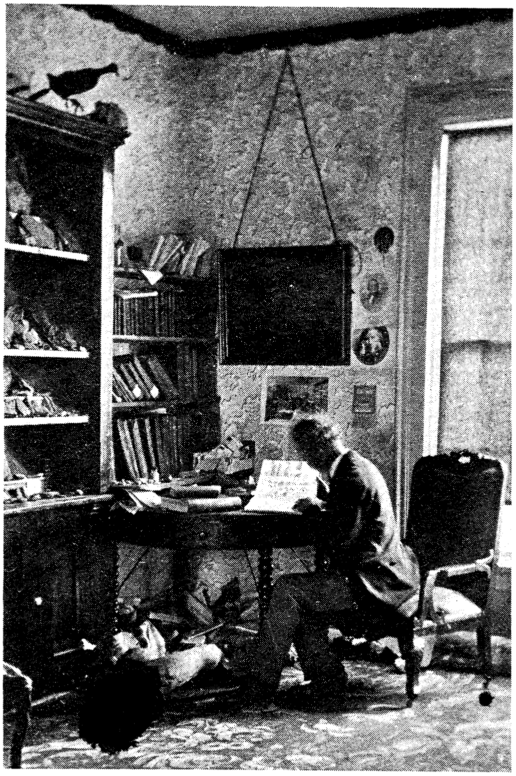

Fig. 5. F. H. Day in his study, ca. 1870s. Photo courtesy of Mary Dawson.

observations to dispute established geological authorities such as James Hall and Charles Doolittle Walcott. Day (1877) mentioned working on another paper about the general characteristics of trilobites that apparently was never published. However, he did supply a detailed faunal list from local quarries to T. C. Chamberlin, which was published in Volume 2 of *The Geology of Wisconsin.*

Day specialized in collecting local Silurian fossils, and by 1880 he had assembled a collection of the best quality ever made in southeastern Wisconsin. His cabinet contained may spectacular specimens, primarily from the Schoonmaker quarry. These included an orthoconic cephalopod over seven feet long, and a spectacular specimen of the trilobite *Bumastus dayi* (named in his honor) (Fig. 6).

In 1880 Day decided to sell his collection, and offered it to The University of Wisconsin (through T. C. Chamberlin) and to Harvard University. Most of the collection, including the best specimens, was purchased by Alexander Agassiz and donated to the Museum of Comparative Zoology at Harvard in 1881 (Raymond, 1916). While it may seem unfortunate that Day's collection was

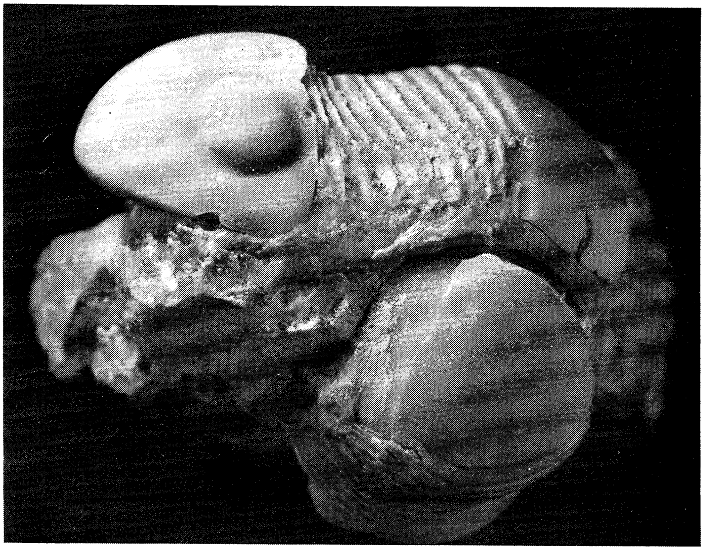

Fig. 6. Two specimens of the trilobite *Bumastus dayi* collected from the Silurian reef at the Schoonmaker quarry by Day, named in his honor by Raymond (1916). This was Day's most valued specimen, for which he was offered $100. This specimen is now No. 647 in the Museum of Comparative Zoology at Harvard.

sent out of the state, had it been sold to The University of Wisconsin probably it too would have been destroyed in the 1884 Science Hall fire. Even after Day shipped 8265 pounds of material to Harvard (*Milwaukee Sentinel,* Jan. 9, 1881), he still retained over 5000 fossils. In 1884 he sold a large number of the remaining specimens to Thomas Greene and much of his library to Edgar Teller. Day retired in 1893 and moved to Lansing, Michigan, where he died on May 31, 1904. At the time of his death he had several thousand specimens in his possession, which were later sold to The University of Michigan.

Day's material at Harvard was placed in the general collections and cannot be studied as a comprehensive unit. Much of it has not been catalogued, but it is in reasonably good shape. Besides containing most of Day's best specimens, the Harvard collection has material from Milwaukee area localities that is not represented elsewhere. Day's material in the Greene collection cannot be identified, but, based on the purchase price, it probably represents a large part of Greene's Wauwatosa material. The labels for many of Day's specimens at The University of Michigan have been lost, and little of his collection has been unpacked.

Thomas Arnold Greene

Thanks to the foresight of his family, T. A. Greene's correspondence, library, and, more importantly, his collections have been preserved in Milwaukee. This material, including several biographical studies (Buck, 1884; Conrad, 1895; Nehrling, 1895; Greacen and Ball, 1946a, b; Thomas, 1928) provides the most detailed information available for any of Milwaukee's gentlemen paleontologists.

Greene was born on November 2, 1827 in Providence, Rhode Island (Conrad, 1895) (Fig. 7). At the age of 16 he began training in a drug store, and five years later he moved to Milwaukee. Greene purchased a retail drug store, and shortly afterward went into partnership with Henry H. Button. Their firm became one of the largest wholesale drug businesses in the city, making Greene a wealthy man (Greacen and Ball, 1946a).

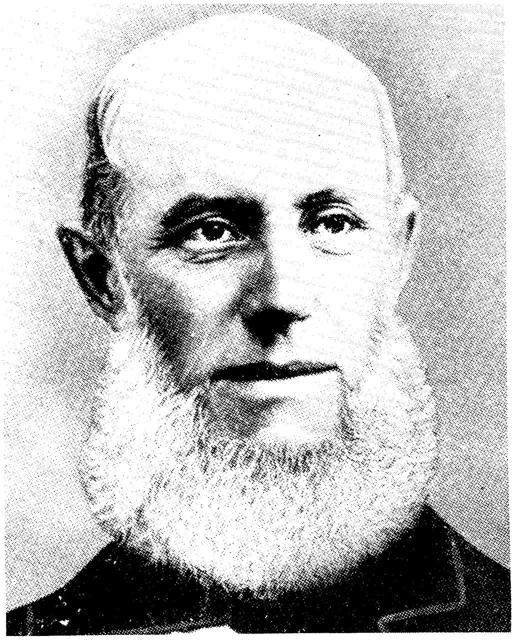
Fig. 7. Portrait of Thomas A. Greene (from Thomas, 1928).

Greene was very interested in botany and geology in his youth, and brought a collection of Rhode Island minerals with him to Milwaukee (Nehrling, 1895). During his first thirty years in Milwaukee, Greene devoted a little time to collecting and purchasing minerals, but there was no apparent interest in fossils. While he sustained an interest in botany and mineralogy, in subsequent years paleontology became his major concern. Because of poor health in 1878, he was advised by his physician to seek relief from the pressures of business. As a means of relaxing he began to collect and purchase fossils, and continued to do so until his death in the fall of 1893. Greene collected primarily at the cement quarries, the 26th Street quarry, and quarries at Racine and Wauwatosa. He corresponded with fossil collectors around the country to arrange exchanges or purchases. He also corresponded with many scientists and loaned specimens to them. James Hall, C. Wachsmuth, and J. Newberry all illustrated a number of Greene's specimens.

Although Greene acquired a thorough knowledge of Silurian and Devonian fossil identification, he apparently had no interest in writing scientific papers. His correspondence does reveal some geological data, and it also contains information on how he assembled his collection and gives insight into his personality.

Greene was quite serious and methodical in his efforts (Buck, 1884), and his goal was to obtain a comprehensive collection of both minerals and Silurian and Devonian fossils. Although he wanted the best possible specimens for his collection, he also purchased as many common specimens as possible. He was aggressive in his quest for specimens, and collecting soon became an obsession—certainly not the type of relaxation his doctor had prescribed. Greene's persistence in trying to convince other collectors to trade or sell specimens to him often resulted in their complete disinterest in further dealings with him. Greene seldom revealed information on the availability of fossils to other collectors, and in most letters he states that collecting had been better a few years before at all of his localities.

In addition to the large number of fossils purchased from quarry workers in Wisconsin, Greene also dealt with collectors and quarrymen in the Chicago area, and obtained Waldron (Indiana) fossils from J. Doty. His main supplier of Chicago area fossils from 1884 to 1893 was A. G. Warner. Warner appears to have earned a fair income by selling fossils to a small group of wealthy collectors, including Dr. J. Kennicott and W. Van Horne of Chicago. When Greene purchased Kennicott's collection in 1885 he also became Warner's main, and possibly only, customer. For the remainder of his life Greene purchased specimens from Warner on a regular basis, often receiving several boxes of fossils a month during the summer. It is interesting to note that Greene invariably paid Warner less than his asking price for the fossils. There was seldom any bargaining over the price, and it is difficult to determine whether Greene was always underpaying or Warner was always overcharging. As a result of these transactions

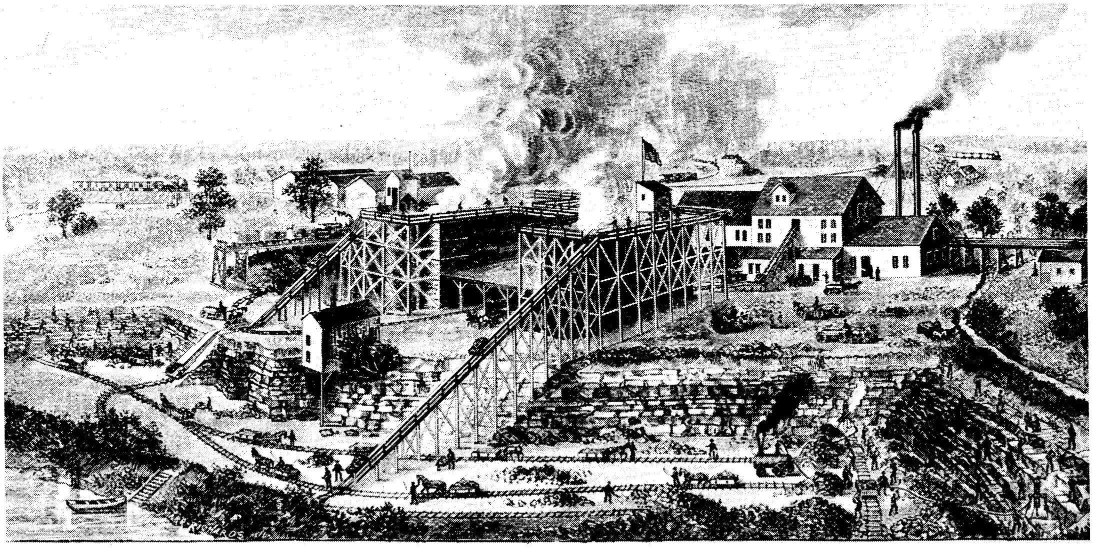

Fig. 8. Mill No. 1 of the Milwaukee Cement Company, ca. 1885 (from Barton, 1886).

Fig. 9. Thomas Greene's collection at his home, probably taken after his death in 1894 and before the dedication of the Greene Museum in 1913. Photos courtesy of the late Katherine G. Nelson.

Fig. 10. Another view of Thomas Greene's collection at his home. Photo courtesy of the late Katherine G. Nelson.

with Warner, Greene acquired the best collection of Chicago area Silurian reef fossils.

Greene's interest in Devonian fossils led him to purchase stock in the Milwaukee Cement Company (Fig. 8). Greene possibly made this investment more to .insure a constant supply of fossils than to realize financial gains, but he later became a member of the board of directors and vice president of the company (Greene and Berthelet, 1949).

He also had interesting and unusual dealings with the Horlick Lime and Stone Company in Racine. At most quarries he arranged to have workers and owners save fossils for him to purchase, but at this quarry he also paid to have workers break rocks for him while he was on the premises. He eventually arranged to have charges set in specific parts of the quarry ready to go off when he arrived. Anyone who has collected fossils in recent years knows this type of cooperation is unheard of in modern quarries, even if one could afford it.

Greene was a member of the Board of Trustees of the Milwaukee Public Museum from 1883 until his death in 1894. He arranged fossil purchases for the museum while on the board, but he also outbid the museum for specimens he wanted in his own collection (Greacen and Ball, 1946a).

Greene spent over $16,000 on his entire collection, including many of the wooden cases in which it is still housed. Of that amount, over $5000 was spent on fossils between 1878 and 1893. Greene's collection (Figs. 9 and 10) was kept by his family until 1911 when it was donated to Milwaukee-Downer College (Greacen and Ball, 1946a). The family also provided a fireproof building for the collection. In 1964 the collection was sold to The University of Wisconsin-Milwaukee for the bargain price of $20,000, and is now worth more than ten times that amount.

The Greene collection is the sole major nineteenth century Milwaukee area fossil collection to remain intact and in the area. Not only is it the largest collection of local Silurian and Devonian fossils, but it is also the largest single collection of Silurian reef fossils from the Chicago area. Although the Greene collection is undoubtedly the most important paleontologic research collection in the state, it has been only partially examined by specialists. However, it will remain a key element in any future geologic research in the area.

Edgar Eugene Teller

Edgar E. Teller was born on August 3, 1845 in Buffalo, New York (Fig. 11). In 1875 he moved to Milwaukee where he worked as a buyer for Plankinton and Armour (and its successor firms) until his retirement (Teller, 1924). He became interested in paleontology by stopping in at the Moody quarry (26th Street quarry) on his way to and from work in the early 1880s. Teller devoted most of his time to collecting Devonian fossils from the Milwaukee Cement Company quarries, but he also collected a large amount of Silurian

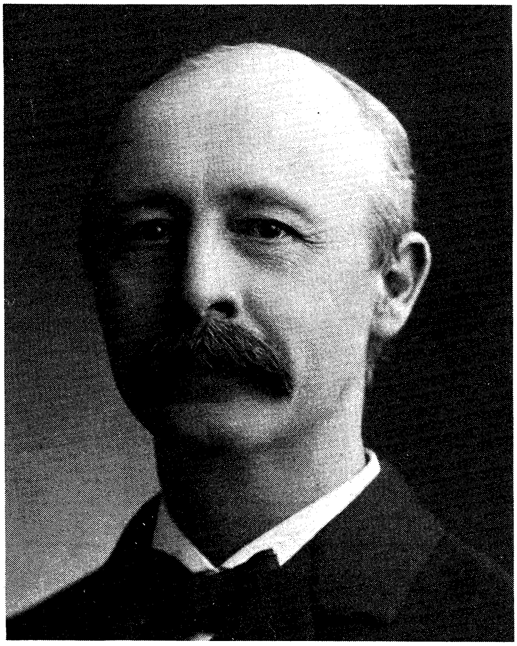

Fig. 11. Portrait of Edgar E. Teller, ca. 1895. Photo courtesy of Kathryn Teller.

material from the Moody quarry and lesser amounts from the Schoonmaker quarry and the Horlick quarry in Racine (Fig. 12), as well as some of the few complete trilobites known from the Cambrian Lodi Shale of Wisconsin.

Teller corresponded with, and loaned specimens to, a number of professional paleontologists, including James Hall, Robert Whitfield, Stuart Weller, Charles Eastman, Charles Walcott, and H. F. Cleland. Because of these associations, his collection contained, or supplied, more figured specimens than any other local naturalist's. He also wrote more scientific papers than other local collectors (Teller, 1900; 1906; 1910; 1912; Monroe and Teller, 1899), providing some of the most detailed descriptions of Wisconsin Devonian geology ever published (also see discussion about Monroe).

Teller was a major participant in the Wisconsin Natural History Society. He joined the society in 1885, serving as its president on several occasions, and as an editor and director until he returned to Buffalo in 1915. The demise of the society at this time was probably due in part to his departure. Teller was also interested in archaeology, and helped to establish the Wisconsin Archaeological Society as a separate organization from the Wisconsin Natural History Society in 1901 (Teller, 1924).

In 1908 Teller gave a large part of his collection to the Walker Museum at The University of Chicago (now part of the present-day Field Museum). Few of these specimens can now be identified as collected by Teller, but many of the Wisconsin Silurian and Devonian fossils in this collection undoubtedly were his.

Teller died in Buffalo on July 19, 1923. Both the National Museum of Natural History and Yale University were interested

Fig. 12. Main quarry of the Horlick Lime and Stone Company located along the Root River near Racine, Wisconsin, ca. 1888. The Silurian reef rock at this quarry supplied most of the fossils collected in the Racine area (from Art Publishing Co., 1888).

in his collection, and on April 3, 1924 his wife, Marie, gave the entire collection of 100,000 specimens and a library of several thousand volumes to the National Museum. This donation included nearly all of the type specimens described from his collection. Teller's material was assimilated into the National Museum's general collections and can no longer be examined intact. Several drawers of his Silurian specimens remain unsorted and uncatalogued. His books were incorporated into the museum library.

Charles Edwin Monroe

Charles Monroe was born in 1857, and later graduated from Oberlin College and The University of Michigan Law School (*Milwaukee Journal,* May 13, 1931) (Fig. 13). He moved to Milwaukee in 1884, and began a long career as a prominent attorney. He was apparently interested in several fields of natural history, of which botany was foremost.

Fig. 13. Portrait of Charles E. Monroe, ca. 1920s. Photo courtesy of the Milwaukee Public Museum, Neg. No. 417133.

In the 1890s and early 1900s, Monroe spent a considerable amount of time collecting and studying the Devonian fossils of Wisconsin. He was a close friend of Edgar Teller, and the two of them share credit for stimulating research on the Devonian rocks of the area. Together they made comprehensive collections of all the localities and stratigraphic units of the Wisconsin Devonian. They were the first to publish detailed descriptions of the stratigraphic occurrence of Devonian fossils and to subdivide Devonian strata. They published an important report on Devonian rocks and fossils encountered during excavation for water intake tunnels at North Point in Milwaukee. They also discovered the phyllocarid bed in the Silurian Waubakee Dolomite and supplied the phyllocarid specimens described by Whitfield (1896). In 1900 Monroe published a description of the Devonian rocks, which he discovered, at what is now Harrington Beach State Park near Lake Church, Ozaukee County, Wisconsin. He contacted several individuals, including Charles Schuchert and Stuart Weller, in an attempt to have this new fauna described, and it was probably a result of his efforts that one of Schuchert's students, H. F. Cleland, began his work on the Wisconsin Devonian.

Monroe was associated with the Milwaukee Public Museum for many years. He held the position of honorary curator of paleontology from 1897 until at least 1922, and was the only person to work on the museum's fossil collections until Ira Edwards was hired in 1916. A generous donor to the museum, he gave nearly all of his Wisconsin Devonian fossil collection to the museum between 1898 and 1900, including the spectacular jaw of *Eastmanosteus* figured by Eastman (1900) and Cleland (1911) (Fig. 14). Other fossils he collected became type and figured specimens in papers by Cleland, Pohl, Penhallow, and others.

After 1905 Monroe devoted almost all of his spare time to botany, and he made

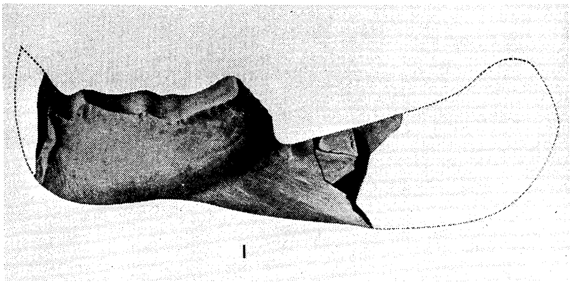

Fig. 14. Jaw of the Devonian fish *Eastmanosteus pustulosus* collected in 1899 by C. E. Monroe in the Milwaukee Cement Company quarries. The specimen is approximately 10 inches long and is now in the collection of the Milwaukee Public Museum (from Cleland, 1911).

several donations of botanical material to the Milwaukee Public Museum, including a collection of over 15,000 specimens in 1924. He moved to Oberlin, Ohio, in 1929, where he died in May, 1931, at the age of 74.

Other Local Collectors

Several other individuals are known to have made fossil collections in southeastern Wisconsin during the nineteenth century, but little specific information is known about their activities. For the most part, these collections have disappeared.

Professor Samuel S. Sherman, who taught at Milwaukee Female College in the 1860s and 1870s, collected and purchased fossils from quarrymen in the 1860s. Sherman moved to Chicago in 1879 where he worked for Sherman Brothers, a family business.

Walter Rankin of Carroll College collected fossils in the Waukesha area and some of his specimens are thought to be in the Day and Greene collections.

Philo Romayne Hoy was a general naturalist like Lapham, who confined his studies to the Racine area. Hoy was born in Mansfield, Ohio, in 1816, and was trained as a medical doctor. In 1846 Hoy moved to Racine (McMynn, 1893) and later that same year he and Lapham collected fossils together in the quarries north of Racine. Hoy also knew Day and Greene and accompanied them to Racine area quarries on many occasions. James Hall also received specimens from Hoy. Hoy's collection was divided between Day and the now defunct Racine College (Teller, 1912). Ornithology and botany are the fields of natural history for which Hoy is most often remembered.

F. L. Horneffer collected fossils from the cement quarries and the 26th Street quarry in Milwaukee during the 1890s (Teller, 1912). His fossils became part of Teller's collection, and included some of the type material in that collection. Horneffer continued collecting into the early 1900s, and accompanied Gilbert Raasch into the field on occasion (G. Raasch, 1973, pers. comm.).

After the turn of the century, quarrying activity in the area declined, and methods of operation changed. Social values, education, and employment opportunities also changed, and the gentlemen paleontologists faded from the scene. The only important local collections made since that time were assembled by Gilbert Raasch and Joseph Emielity. Both these men are Milwaukee natives who started collecting fossils as children, and went on to become professional geologists. Nearly all of their collections are now located in the Milwaukee Public Museum.

THE COLLECTIONS

Research Value

The four major surviving collections are of primary importance to paleontological research on the Paleozoic geology of southeastern Wisconsin. The Day, Greene, Teller, and Monroe collections are a source of unique and unstudied fossils and contain many type specimens. They cannot be duplicated in quantity, quality, or comprehensiveness, because most of the bedrock outcrops and quarries have disappeared and quarrying methods have changed. In addition, they are the only source of fossils and rock samples for many of the vanished localities. The later collections made by Raasch and Emielity supplement the older collections by covering more recent exposures, but do not replace them.

Although many of the fossils were collected more than one hundred years ago, they have not lost their usefulness for paleontologic research. Locality information accompanies most specimens, and by studying old geologic reports and the lithology of the specimens, it is possible to determine the exact geographic location and stratigraphic horizon in which the fossils were collected. It is also possible to determine reef or interreef origins for most of the Silurian material.

These collections are invaluable for taxonomic studies because they include many type specimens and numerous individuals of single taxa which are necessary for population studies. While the Day, Teller, and Monroe collections are no longer readily available for comprehensive faunal studies of specific localities, the Greene collection is ideal. It contains the most complete collection of North American Silurian reef fossils found in any museum. These historic collections are also important for research in biogeography, paleoecology, biostratigraphy, taphonomy, rates of evolution, and for general and local stratigraphic studies.

Preservation of the Collections

Many other nineteenth century fossil collections in the state, and throughout the country, have virtually disappeared through accident or neglect. Over 20,000 fossils were collected by the Wisconsin Geological Survey during the 1870s, and were equally divided among twelve different educational institutions in the state (Chamberlin, 1880). Approximately 1200 specimens were destroyed along with Lapham's collection in the Science Hall fire in 1884, but the fate of most of the others has not yet been determined. Only a few hundred of these specimens are known to exist.

Even in recent years, important collections have been seriously damaged by neglect. The W. C. Egan collection of Chicago area fossils in the Chicago Academy of Science is a good example. This collection was well organized as late as 1946 (Ball and Greacen, 1946), but by 1967 it was in disarray and many specimens, including types, cannot be located. The University of Wisconsin-Madison Geology Museum has also suffered long periods of neglect during which fossils disappeared and uncatalogued material was rendered useless because of missing locality information.

The Greene, Day, and Teller collections are all vulnerable in varying degrees to the same problems. Above all, a collection must be completely catalogued to prevent the loss of locality data. Once this is accomplished, the Day and Teller collections will be in little danger (although the Museum of Comparative Zoology is not exactly fireproof). Greene's collection is, and probably always will be, vulnerable to the type of neglect that small university collections often face. As long as a dedicated individual, like the late Dr. Katherine G. Nelson, took care of the collection there was a little danger of this happening. However, with her passing, the awareness of the importance of the Greene collection may fade. The University of Wisconsin-Milwaukee faces an important obligation in preserving the Greene collection and insuring its usefulness in the future.

SUMMARY

The collecting activity of Milwaukee's gentlemen paleontologists continues to be a major factor in geological research in the Milwaukee area. They made important observations, published papers, distributed specimens, and assembled comprehensive collections, all of which stimulated interest in the geology and paleontology of the area. They spent more time and money assembling their collections than would have been possible for any professional geologists of that time. Their fossils were studied by some of the most prominent paleontologists of the nineteenth century, including James Hall, F. B. Meek, J. S. Newberry, C. D. Walcott, C. Wachsmuth, R. P. Whitfield, P. E. Raymond, H. F. Cleland, C. R. Eastman, J. M. Clarke, Stuart Weller, A. F. Foerste, E. O. Ulrich, C. E. Resser, E. R. Pohl, and Frank Springer. Most of these collections focused attention on classic Silurian reefs in the area with their abundant and diverse faunas. On a local level, these collectors promoted and actively participated in natural history societies and museums.

It is no longer possible to assemble comparable collections on the Milwaukee area because of the change in quarrying methods, the general decline of that industry, and the lack of people willing to devote large amounts of both time and money to this pursuit. For these reasons the Day, Greene, Teller, and Monroe collections are more important than ever before.

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SILURIAN BENTHIC INVERTEBRATE ASSOCIATIONS OF EASTERN IOWA AND THEIR PALEOENVIRONMENTAL SIGNIFICANCE

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Abstract

The vertical and lateral distributions of benthic invertebrate associations in the Silurian carbonate sequence of eastern Iowa are interpreted in terms of widespread environmental changes created by relative changes in sea level and general water circulation patterns. Previous studies (especially Johnson, 1975, 1980) delineated three broadly-defined benthic invertebrate associations within the middle Llandoverian-lower Wenlockian sequence of eastern Iowa, and similar associations are recognized in younger Wenlockian strata in this study. The middle Llandoverian through middle Wenlockian interval in eastern Iowa includes three recurrent benthic associations characteristic of open-marine carbonate shelf environments: 1) coral-stromatoporoid, 2) pentamerid brachiopod, and 3) stricklandiid brachiopod. Petrographic, sedimentologic, and stratigraphic information evaluated for this study is consistent with the earlier suggestion that these associations respectively inhabited different depth-related benthic carbonate environments: 1) at or near fair-weather wave base, 2) generally below fair-weather wave base with episodic impingement of storm wave base on the bottom, and 3) below effective reach of fair-weather and storm wave base. However, the development of carbonate mounds (reefs) during Silurian deposition in eastern Iowa adds additional complexity to the paleotologic and sedimentologic framework. In addition, lateral biofacies variations suggest that basinal geometry influenced the geographic distribution of specific benthic associations.

The middle Wenlockian through Ludlovian interval in eastern Iowa is marked by a change from open-marine to restricted-marine carbonate deposition. A general offlap of the epeiric sea during that interval probably left eastern Iowa as a restricted embayment, in part hypersaline. When compared to the Llandoverian through middle Wenlockian interval, the younger Silurian benthic associations show a marked decline in diversity, and several major taxonomic groups are commonly absent. Abundant low-diversity brachiopod and coral-dominated faunas are well developed in the younger Silurian carbonate mound facies, but benthic invertebrate associations are characteristically sparsely developed to absent in the laminated inter-mound facies. However, Upper Silurian mound and inter-mound benthic associations generally increase in diversity eastward within the East-Central Iowa Basin. The stratigraphic distribution of these younger Silurian benthic associations is interpreted to be a joint response to relative changes in water depth and salinity stresses on the carbonate shelf.

INTRODUCTION AND COMMENTS

Silurian rocks of the central midcontinent region have been the subject of geologic and paleontologic investigations during the past 150 years. My personal interest in Silurian rocks was heightened during my teen and college years in Milwaukee, and Katherine Nelson played a significant role in cultivating that interest. Milwaukee is conveniently located in the Silurian outcrop belt, and Katherine took advantage of that fact by encouraging class field trips to nearby quarries. The Greene Museum collections (Univ. Wisc.-Milwaukee), tended by Katherine for many years, were the envy of local fossil collectors, like myself, and these collections certainly helped kindle student interest in Silurian paleontology.

While still living in Milwaukee, Don Mikulic and I first visited Silurian outcrops in eastern Iowa. These visits ultimately led to further study and graduate research on the Silurian rocks and fossils of Iowa (Witzke, 1976, 1981c; Mikulic, 1979). Although most of the Iowa Silurian rocks are extensively dolomitized, the contained fossils are commonly abundant and diverse. Paleontologic data obtained from the Iowa exposures and subsurface cores, when utilized with additional geologic information, form an essential basis for the interpretations of Silurian stratigraphy and depositional environments outlined in this report.

The general purpose of this report is to evaluate the vertical and lateral distributions of recurrent associations of benthic invertebrates within the Silurian sequence of eastern Iowa in terms of possible controlling paleoenvironmental parameters. Previously published paleocommunity models are reviewed and supplemented with new information, and models relating the various benthic associations to paleo-depth are independently tested utilizing petrographic and stratigraphic data. The study was approached through an analysis of paleontologic, sedimentologic, petrographic, stratigraphic, and structural information. Iowa Llandoverian stratigraphic data was geographically expanded over previous studies by utilizing subsurface cores (2 inch diameter). A first attempt at synthesizing Iowa Wenlockian-Ludlovian data in terms of regional sedimentation and benthic associations is presented in this report.

This report is intended to summarize some of the major conclusions of my dissertation research and to compare these results with some previous ideas. Because of the summary-and-review character of this paper, complete details of stratigraphic, petrographic, and paleontologic documentation cannot be presented in this volume. Further documentation is presented in Witzke (1981c).

STRATIGRAPHY

The sequence of Silurian carbonate rocks is exceptionally well exposed in the outcrop belt of eastern Iowa, and supplementary exposures were examined in adjacent Illinois and Wisconsin. Integration of surface and subsurface (core) sections in Iowa has necessitated revision of previous stratigraphic interpretations. Following the lead of Wilson (1895) and Calvin and Bain (1900), Iowa Silurian lithostratigraphic relationships have recently been delineated (Johnson, 1975, 1977a; Witzke, 1981a, 1981c; Bunker *et al.*, 1983). A generalized interpretation of the composite eastern Iowa Silurian stratigraphic sequence is schematically illustrated in Figure 1. Units within the Hopkinton Formation are informally labelled Hopkinton A, B, and C which correspond, respectively, to the "*Syringopora*" and "*Pentamerus* beds," "*Cyclocrinites* beds," and "*Favosites* beds" of Johnson (1975). Member names within the Hopkinton Formation were recently proposed by Johnson (1983), which in ascending order include the Sweeney, Marcus, Farmers Creek, and Picture Rock Members.

The Scotch Grove Formation has been recently proposed as a stratigraphic unit by Bunker *et al.* (1983) to include the interval above the originally defined top of the Hopkinton and below the laminated and mounded carbonates of the Gower Formation. The Scotch Grove is characterized by a complex series of mounded (reef) and flat-lying carbonate facies that have been given informal facies names (see Fig. 1). The lower Scotch Grove interval of this report was included within the upper Hopkinton Formation by Johnson (1975, 1983). Johnson (1983) recognized members within this interval which he assigned, in ascending order, to the Johns Creek Quarry, Welton ("Emeline facies" of this report), and Buck Creek Quarry Members. Because of the recent status of Johnson's (1983) stratigraphic classification, time did not permit complete incorporation of the new terminology into

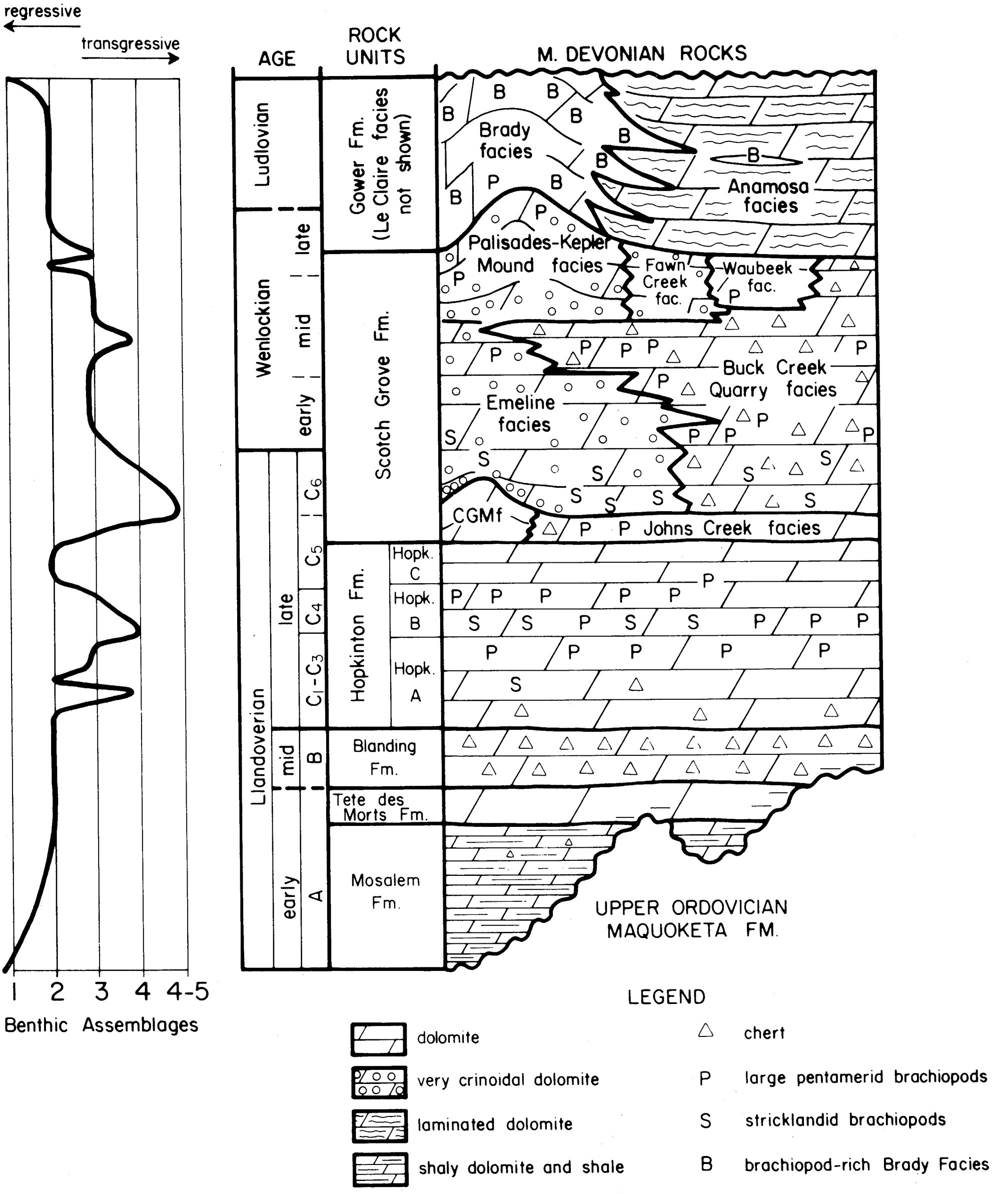

Fig. 1. Generalized Silurian stratigraphic sequence in east-central Iowa. Formal and informal stratigraphic terminology largely adapted from Johnson (1980), Witzke (1981c), and Bunker *et al.* (1983). Facies illustrated within the Scotch Grove and Gower Formations are highly schematic; the distribution of very crinoidal dolomites is shown for the Scotch Grove Fm. only. The sequence of Benthic Assemblages shown at left is generalized and adapted from Johnson (1980) and Witzke (1981c). Vertical scale is time. CGMf-Castle Grove Mound facies.

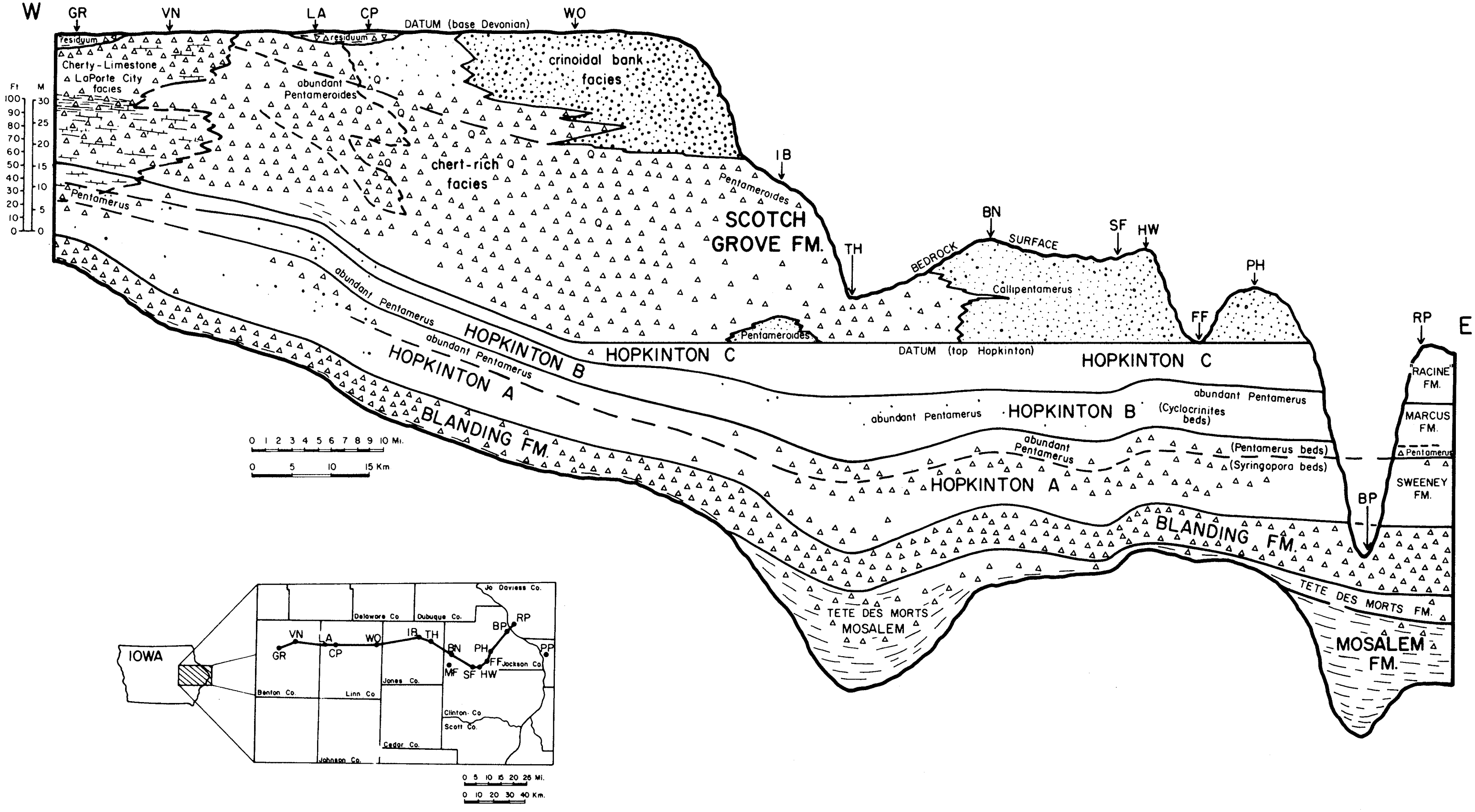

Fig. 2. East-west stratigraphic cross-section of Silurian strata in east-central Iowa. Datum is base of Devonian carbonates in west; datum is lowered to top of Hopkinton Fm. in east where Devonian rocks are absent. Symbols: triangles (chert), small circles (very crinoidal wackestone and packstone textures), Q (quartz-lined vugs), discontinuous thin lines (argillaceous carbonates), hachured lines (LaPorte City Fm. limestones), solid or discontinuous heavy lines (stratigraphic or biofacies boundaries). Subsurface Hopkinton B pentamerid occurrences generalized as *Pentamerus,* although *Harpidium maquoketa* is apparently represented in the eastern sections. Two-letter locality designations referenced in Witzke (1981c). Illinois stratigrapic terminology shown at locality RP.

this report, although union of informal terminology with the formal stratigraphic schemes is recommended for future publications. The Gower Formation includes three general facies: 1) flat-lying laminated dolomites of the Anamosa facies, 2) mounded (reef) brachiopod- and coral-rich rocks of the Brady facies (Philcox, 1970a), and 3) mounded to flat-lying crinoidal and brachiopod-rich rocks of the LeClaire facies. Many mounded (reef) carbonate exposures previously assigned to the LeClaire facies are now assigned to the Palisades-Kepler Mound facies of the Scotch Grove Formation.

The eastern Iowa Silurian sequence is composed primarily of dolomite and cherty dolomite. However, the dolomite sequences are replaced, in part, to the west and north by limestones and cherty limestones assigned to the LaPorte City and Waucoma formations (Witzke, 1981c). The fortuitous preservation of Silurian limestone facies in Iowa allows direct comparison of limestone petrographic fabrics with their dolomitized equivalents.

The thickest known sequence of Iowa Silurian rocks (146 m) occurs within the Silurian outcrop belt of east-central Iowa, and the Silurian sequence thins beneath the Devonian cover to the north, west, and south. Recent investigations in Iowa identified a Silurian structural and stratigraphic basin centered in eastern Iowa (Bunker, 1981; Bunker *et al.*, 1983; Witzke, 1981c). This paleobasin is termed the East-Central Iowa Basin. Although the central basin area was uplifted prior to Pennsylvanian deposition (ibid.), and the area has been subjected to extensive erosional truncation, thickening of individual Silurian stratigraphic units towards the center of the East-Central Iowa Basin is clearly evident in cross-section (Fig. 2). Erosional remnants of Silurian strata preserved in southwestern Wisconsin outliers compare closely with Lower Silurian sequences in the central basin area of eastern Iowa (Bunker *et al.*, 1983).

Brachiopod and conodont biostratigraphic studies in the eastern Iowa Silurian sequence provided a basis for inter-regional chronostratigraphic correlation (Johnson, 1975, 1979; Witzke, 1978, 1981c). The age relationships of the Iowa Silurian sequence are shown on Figure 1.

BENTHIC FOSSIL ASSOCIATIONS AND PALEOENVIRONMENTAL INTERPRETATIONS

Benthic Associations

Recurring associations of fossils (commonly termed communities) in the eastern Iowa Silurian sequence, when supplemented with stratigraphic, sedimentologic, and petrographic information, provide a basis for interpreting environmental changes through time. Ziegler (1965) and Ziegler *et al.* (1968) pioneered studies in Silurian community paleoecology and documented recurrent associations of brachiopods and other fossils in the Llandovery Series of the Welsh Borderland. They interpreted the distribution of these fossil associations to be environmentally controlled, and they correlated the controlling environmental parameters with water depth. Later studies, most of which are not enumerated here, identified other supposed depth-related Silurian fossil associations at other localities in Europe and North America. Johnson (1975, 1977a, 1980) identified five basic and recurrent fossil associations (or communities) in the Iowa Llandoverian sequence that, in part, paralleled Ziegler's in the Welsh Borderland. Johnson listed these in order of increasing water depth: 1) *Lingula,* 2) coral-algal, 3) pentamerid, 4) stricklandiid, and 5) "*Clorinda*-equivalent." Although some brachiopod taxa are shared between the Iowa and Welsh Borderland Llandoverian, many important differences in taxonomic composition between the two areas are noted, in part because of contrasting substrates (carbonate vs. terrigenous clastic). Most marine ecologists recognize modern marine communities as unique congregations of organisms, recognizable at the species level ("Peterson Animal Community" concept of Watkins *et al.,* 1973). In this context, the recurrent associations of fossils in the Iowa Silurian are not members of the same communities present in the Welsh Borderland. A broader community concept, the "parallel community," has also been defined which includes "a grouping of separate, related Peterson animal communities, describing an ecologic unit of great areal and temporal" extent recognized by similar associations of "characteristic genera" or "families" (ibid., p. 56).

In this study, the term "community" is not utilized, primarily to avoid confusion between the various community definitions, and the general term, "association," is preferred. As utilized here, a benthic association is defined to include a combination of taxa (usually at the generic or family level) that occur together in a specific stratigraphic interval and collectively form a discrete grouping unique from other associations. Although benthic associations could be defined and analyzed at any taxonomic level, including species level, the stratigraphic representation of the various associations is dependent on the hierarchic level employed by the observer (Anderson, 1973a). In a general sense, the benthic association definition utilized in this report roughly coincides with the "parallel community" concept.

The recognition and establishment of discrete benthic association types is, in part, an artificial procedure, and a certain degree of overlap in taxonomic composition between some associations is noted. There may be a degree of variation in the relative abundance of individual taxa within single benthic association types at different localities and in different collections. Nevertheless, the benthic association approach affords a reasonably consistent way of categorizing a mass of paleontologic information into environmentally and paleoecologically significant entities. In this study, most benthic associations are recognized and defined by the co-occurrence of two or three prominent key taxa in a single collection, and, although additional taxa are usually noted within a particular association, the full complement of additional taxa may not be recovered in all collections. The key taxa that define a particular association must be relatively abundant, although the name-bearing members of each association are not necessarily the most abundant fossil types present. For example, the skeletal volume of echinoderm grains in many of the Iowa Silurian benthic associations far exceeds that of the name-bearing members of the association. The benthic association concept utilized in this study is a broadly defined one that is suited for field observations as well as numerical assessment of dolomite block collections in the laboratory. In addition, rock core from Iowa subsurface Silurian intervals has yielded macrofossil collections that provide important data on the stratigraphic and geographic extent of various benthic associations, even though collection sample sizes are comparatively small and the sampling interval is generally thicker than in block collections derived from surface exposures. Rock core descriptions and fossil lists are recorded in Witzke (1981c).

An abbreviated review of the various benthic associations represented in the Iowa Silurian sequence and their environmental significance is presented later in this report. To a large extent, the Iowa Llandoverian associations used here closely parallel the community definitions of Johnson (1975, 1980). The reader is referred to the studies of Johnson (ibid.), Witzke (1976, 1981c), Witzke and Strimple (1981), and Mikulic (1979) for a more complete listing of the taxonomic composition and diversity of the various Iowa Llandoverian and early Wenlockian associations. In addition, valuable information on community evenness, diversity, and lateral homogeneity (as determined from block collection counts and "stretch-line" fossil censuses taken from Lower Silurian strata in the Iowa outcrop belt) is given by Johnson (1977a, 1980). A partial taxonomic listing of the various mid Wenlockian through Ludlovian benthic associations is given by Witzke (1981a, 1981c).

Benthic Assemblages

Boucot (1975, p. 11) introduced the term "Benthic Assemblage" for "a group of communities that occur repeatedly in different parts of a region (during some times even worldwide) in the same position relative to shoreline," and further suggested that "Benthic Assemblages are probably temperature-controlled as well as highly correlated with depth." Because community structures changed through time and individual taxa evolved, the Benthic Assemblage approach affords a method to compare the taxonomic and environmental similarities of various benthic associations on a broad temporal and geographic scale. Boucot (1975) proposed a simple numerical listing of Benthic Assemblages (B.A.), which increase in number moving away from the shoreline into progressively deepening water (e.g., B.A. 1—near shore, B.A. 6—farthest offshore). Boucot and others have categorized a great variety of Silurian fossil associations from around the world according to their general Benthic Assemblage position, and I have utilized Boucot's B.A. categories for the various Iowa Silurian associations. However, I have not uncritically utilized the B.A. categories, but have attempted to define the environmental parameters affecting each benthic association from sedimentologic, stratigraphic, petrographic, and other criteria. "Meaningful paleoecologic analysis of fossil assemblages is impossible without using environmental data which are independent of the paleontologic record," as stressed by Makurath (1977, p. 251). As such, the assertion that Benthic Assemblages are depth-related can be independently evaluated for specific Iowa Silurian benthic associations.

In general, the Iowa Silurian sequence was deposited in carbonate shelf environments within a "clear-water" epeiric sea, and terrigenous clastic influx was extremely low. The temporal and geographic distribution of the various benthic associations was related to environmental and biotic influences operating within the epeiric sea. Environmental factors that may have influenced the distribution of the various Iowa associations include water circulation patterns, salinity, relation to wave base, water turbulence, turbidity, light penetration, temperature, substratum, and nutrient availability. Most of these factors are strongly related to water depth and shelf physiography in areas of "clear water" carbonate shelf deposition (Irwin, 1965). Irwin (1965) stressed the importance of relative sea level change as a major controlling factor on the temporal sequence of environments on "clear water" carbonate shelves, and Anderson (1971, p. 301) suggested that recurrent benthic invertebrate associations are directly correlated with depth-related environmental zones in the epeiric seas.

If the distribution of Benthic Assemblages is depth-related, then the sequence of assemblages can be locally used to characterize relative changes in sea level, as previous workers have done for the Silurian of North America and Europe. Although some workers have criticized this approach (e.g., Makurath, 1977; Watkins, 1979), as will be shown, the stratigraphic and petrographic evidence from the Iowa Silurian generally supports *relative* differences in water depth for the various benthic assemblage types. However, the sequence of benthic assemblages in the Iowa Silurian is not necessarily a reflection of *absolute* changes in water depth since there is no assurance that each benthic assemblage maintained the same absolute depth range through time in a specific region. Sheehan (1980, p. 21) further suggested: "Benthic Assemblages are depth related in that, from shallow to deep, a consistent pattern of communities is maintained. But B.A.'s are not depth specific since the actual depth a given community inhabited probably varied significantly."

TABLE 1. Thin section point-count data averages from LaPorte City Formation limestones. General stratigraphic positions listed according to dolomite facies equivalents in the Hopkinton and Scotch Grove formations. (n = number of thin sections point-counted).

Stratigraphic equivalent	*n*	*Percentage of total rock volume*				*Percentage of skeletal grains*						
		matrix micrite & spar	*chert, chalcedony*	*skeletal grains*	*quartz silt & sylolites*	*echino-derm*	*bryo-zoan*	*brachi-opod*	*trilo-bite*	*ostra-code*	*sponge*	*indeter-minate*
Lower Scotch Grove	9	83	3	14	<1	60	16	14	1	1	2	6
Hopkinton C	5	69	<1	30	<1	77	1	1	<1	2		19
Hopkinton B	3	69	<1	30	<1	66	2	13				19

TABLE 2. Macroskeletal grid-count data averages from Waucoma and LaPorte City Formation limestones. Data for skeletal material >3mm only. General stratigraphic positions listed according to dolomite facies equivalents. (n = number of M^2 grid counts; * = present on outcrop but not on grids).

Stratigraphic equivalent	*n*	*Percentage macroskeletal volume*		*Average percentage of total macroskeletal volume*						
		average	*variation*	*stromatop-oroid*	*Favosites*	*Halysites*	*solitary rugosans*	*indet. coralline*	*brachi-opod*	*nautil-oid*
Hopkinton C	4	1.8	0.7-4.2	59.0	29.6	2.7	7.9	0.3	0.4	
Tete des Morts	2	1.6	1.2-2.0	95.4	*		1.2		0.3	3.1

Depth-related environmental factors that influenced carbonate depositional patterns, in particular those related to wave current activity, can be interpreted from petrographic and sedimentologic evidence. Such independent lines of evidence provide information critical for evaluating the *relative* depth positions of the various Iowa Silurian benthic associations.

Although the distribution of many Iowa Silurian benthic associations was apparently depth related, evaluation of additional non-depth-related environmental factors is also needed for adequate classification. In this report, all Iowa Silurian carbonate environments and their contained benthic associations are categorized into two general groupings: 1) open-marine, and 2) restricted-marine (varying degrees of elevated salinity).

OPEN-MARINE BENTHIC ASSOCIATIONS

General Characteristics

Iowa middle Llandoverian through middle Wenlockian rocks contain paleontologic and sedimentologic features suggestive of open-marine (stable marine salinity) carbonate depositional environments. 1) The contained faunas are characteristically diverse and include a number of biotic groups commonly regarded as stenohaline (see Heckel, 1972). In particular, echinoderm debris, commonly in great abundance, is present in all benthic associations here assigned to open-marine environments. 2) Iowa Silurian open-marine environments were generally characterized by the deposition of skeletal wackestone and packstone textures. All sedimentologic evidence suggestive of elevated salinites during deposition is absent. Unlike the restricted-marine environments discussed later, evaporite crystal molds, laminated carbonates, and oolites are conspicuously lacking.

Coral-Stromatoporoid Associations

Coral-stromatoporoid associations are noted in the Tete des Morts and Blanding formations, the Hopkinton A, B, and C intervals, and the lower La Porte City Formation. These associations are characterized by conspicuous tabulate corals (*Halysites, Favosites, Syringopora*) and disc-shaped stromatoporoids on outcrop. Other macrofossils commonly encountered include rugose corals (*Heliolites, Arachnophyllum,* solitary rugosans), brachiopods (*Hesperorthis, Leptaena*), nautiloids, and trilobites (*Stenopareia*). The brachiopod *Cryptothyrella* has also been recovered from the Blanding Formation (Johnson, 1977a). This recurrent coral-stromatoporoid association is assigned a B.A. 2 position following Boucot (1975). Although corals and stromatoporoids are conspicuous on outcrop, petrographic analysis reveals that the dominant skeletal constituent of these associations is disarticulated echinoderm debris (primarily crinoid with minor cystoid) less than 2 mm in diameter (Witzke, 1981c). Dolomitization has hampered recognition of the crinoidal component, although petrographic study reveals that moldic or dolomite-replaced crinoidal wackestone and packstone fabrics predominate in these associations (ibid.). Strata equivalent to Hopkinton C in the LaPorte City limestone contain a conspicuous coral-stromatoporoid fauna. However, petrographic study of these limestones reveals skeletal wackestone and packstone textures containing a great abundance of small echinoderm debris (see Table 1). Data in Table 1, due to thin section size limitations, is only for the rock matrix between the conspicuous coral and stromatoporoid colonies. Grid measurements (m^2) on vertical exposure faces indicate that corals and stromatoporoids, on the average, comprise less than 2% of the total rock volume in limestone strata containing coral-stromatoporoid associations (Table 2). Cross-sectional dimensions of all macroskeletal constituents within the m^2 grid whose long dimension exceeded 3 mm were recorded. However, this data tended to overestimate coralline skeletal volume since corallite spar fillings were included in the volumetric measurements.

Johnson (1975, 1977a, 1980) interpreted the flat disc-shaped fossils in these associations as blue green algal stromatolites, and labelled this benthic association the "coral-algal community" accordingly. However, Johnson (1980, p. 200) acknowledged that some stromatoporoids "were undoubtedly included under this classification." All these disc-shaped fossils are herein interpreted as stromatoporoids and not algal stromatolites for two reasons. First, although the dolomitized or silicified specimens are typically poorly preserved, better preserved specimens bearing monticules and pillars are clearly stromatoporoids. Where identical benthic associations were examined in the LaPorte City and Waucoma limestones, no stromatolites were observed, and all laminar disc-shaped fossils were consistently recognizable as stromatoporoids. Second, there are no modern or ancient examples of isolated stromatolitic discs occurring within a groundmass of skeletal wackestone and packstone. Although normal-marine subtidal stromatolites have been identified in modern oolitic sand environments in the Bahamas (Dravis, 1983), the crudely laminated columnar heads and the surrounding sediment differ significantly from the Iowa Silurian examples. In general, most post-Lower Ordovician stromatolites are typically associated with environments of increased salinity or restricted circulation, whereas the Iowa examples occur in normal-marine associations.

Additional petrographic observations provide useful information for evaluating environmental parameters during deposition. Limestone fabrics include abraded skeletal grains, and the grains are, in part, moderately well sorted, suggesting relatively high-energy conditions in the B.A. 2 environments. However, skeletal wackestone and packstone textures indicate that carbonate mud was not completely winnowed out during deposition. Micrite envelopes occur around some skeletal grains in these associations. Moderate to strongly agitated open-marine conditions apparently prevailed in the B.A. 2 environments, and bottom conditions were apparently within the photic zone. Johnson (1980, p. 208) interpreted the flat, disc-shaped morphology of the corals and stromatoporoids as a probable response to the hydrographic factors, and further suggested that "effective wave base" may have reached the bottom during deposition of these intervals bearing such associations.

Pentamerid Brachiopod and Related Associations

Associations of large-shelled pentamerid brachiopods have been assigned a B.A. 3 position by Boucot (1975) and others. A variety of large pentamerid taxa are represented within the eastern Iowa sequence in the following stratigraphic positions: 1) *Pentamerus oblongus,* upper Hopkinton A, basal Hopkinton C; 2) *Harpidium (Isovella) maquoketa* (see Boucot and Johnson, 1979), Hopkinton B; 3) *Pentameroides subrectus,* basal and middle Scotch Grove (Johns Creek and Buck Creek Quarry facies); 4) *Pentameroides (Callipentamerus) corrugatus,* middle Scotch Grove (Emeline and Buck Creek Quarry facies); 5) *Rhipidium* sp., upper Scotch Grove (Waubeek facies). Due to incomplete recovery or poor preservation, *H. maquoketa* was not consistently distinguishable from *P. oblongus* in subsurface rock cores. Although all Hopkinton B pentamerids are tentatively listed as *Pentamerus* on the Figure 2 subsurface cross-section, many of the Hopkinton B specimens probably belong to *H. maquoketa* (which was assigned to *Pentamerus maquoketa* in earlier reports). In general, *Pentamerus* and *Harpidium* associations are spatially homogeneous and geographically widespread within specific stratigraphic intervals (Johnson, 1980). However, *Pentameroides, Callipentamerus,* and *Rhipidium* associations are not ubiquitous in specific stratigraphic intervals, but occur in spatially disjunct facies accumulations or "banks" (Witzke, 1981c). Although lacking large pentamerids, additional benthic associations laterally equivalent to the *Rhipidium* association in the upper Scotch Grove Formation (Buck Creek Quarry and Waubeek facies) are recognized and tentatively assigned a B.A. 3 position (Witzke, 1981a,b,c).

In general, the Iowa B.A. 3 associations are taxonomically more diverse than the B.A. 2 associations, although the brachiopod component is typically dominated by a single species. Additional biotic elements, not necessarily present in all pentamerid associations, include corals (primarily tabulates and solitary rugosans, some colonial rugosans), bryozoans, brachiopods (orthids, strophomenids, spiriferids), gastropods, nautiloids, trilobites, ostracodes, crinoids (rare articulated cups), and calcareous algae. Ecologic succession in the Hopkinton pentamerid associations is discussed by Johnson (1977b). Coralline developments or biostromes (highest diversity coral faunas noted in the Iowa Silurian) are evident in portions of the middle Scotch Grove Formation associated with abundant *Pentameroides* (Witzke, 1981c). Coralline biostromes associated with *Pentameroides* also occur within the basal Scotch Grove (Johnson, 1977a). Upper Scotch Grove B.A. 3 associations that lack large pentamerids are faunally varied and, although not enumerated here, include scattered small pentamerid (gypidulinid) brachiopods (ibid.).

Pentamerus, Harpidium, and *Pentameroides* associations in portions of the Hopkinton and Scotch Grove formations include small numbers of stricklandiid brachiopods, forms generally characteristic of B.A. 4 stricklandiid associations. The intermixing of pentamerid and stricklandiid faunas may suggest a degree of gradational overlap between B.A. 3 and B.A. 4 associations at times during deposition of the Iowa Silurian carbonates.

Pentamerid accumulations in the Iowa Silurian are preserved in two general ways with "a complete preservational spectrum" between the two extremes: 1) articulated brachiopod shells in life position with scattered truncated "submarine erosion" surfaces, and 2) "disarticulated shells accumulated as coquinas" (Johnson, 1977b, p. 86, 92). Johnson (ibid.) suggested periodic "scouring of the sea bottom" as a mechanism for the origin of the truncation surfaces. Many disarticulated pentamerid accumulations sampled by Johnson (1977a) showed a preservational bias of pedicle valves over brachial valves, suggesting a degree of current sorting. Bridges (1975, p. 89) described "storm-generated coquinas of *Pentamerus*" from the Welsh Borderland, and Anderson (1973b) suggested that pentamerid associations in the Appalachian Basin area inhabited skeletal sand substrates that were "occasionally wave reworked." Some pentamerid accumulations in the Iowa Silurian may represent storm lags. Iowa pentamerid associations occur within rocks displaying skeletal wackestone to packstone textures, both in dolomite and limestone facies. Echinoderm debris (most less than 2 mm diameter) is considerably more important volumetrically than macrofossil block counts would suggest, and the echinoderm component of the pentamerid associations can only be adequately evaluated petrographically (see Table 1; *Pentamerus*-bearing limestones, Hopkinton B equivalents). Moldic and dolomite-replaced echinoderm grains are also abundantly evident petrographically in the dolomite facies (Witzke, 1981c). *Pentamerus*-bearing limestones in the LaPorte City Formation contain some abraded grains, and agitated conditions were apparently present at times during the deposition of the B.A. 3 associations. However, abraded grains and current sorting are not pervasive throughout the pentamerid-bearing sequences, and agitated high-energy conditions were probably present in the B.A. 3 environments only at irregular intervals. Overall, the sedimentary evidence in the B.A. 3 pentamerid associations is consistent with a depositional environment generally below wave base. Johnson (1980, p. 208) also suggested that the pentamerid associations generally occupied a position "at or below effective wave base." The abundance of micrite and articulated fossils generally supports this interpretation. However, periodic turbulent conditions produced truncation surfaces, shell transport and sorting, and abraded grains, perhaps as a result of periodic storms in which storm wave base impinged on the bottom.

Carbonate Mound (Reef) and Related Associations

Open-marine carbonate mound (reef) facies are noted at two positions in the Scotch Grove Formation: 1) small-scale mounds (about 5-10 m high, 30-70 m across) informally included in the Castle Grove Mound facies, and 2) large-scale mounds (forming coalesced mounded complexes to 2.5 km across; single mounds up to 1 km across, 45 m thick) informally included in the Palisades-Kepler Mound facies (Witzke, 1981a,c). Both mound facies are laterally replaced, in part, by flat-lying intermound strata containing probable B.A. 3 associations. Stratigraphic relations indicate that, during deposition, the mound facies were elevated on the sea floor relative to the intermound facies. Since the B.A. 3 associations in the Palisades-Kepler mounds lived in shallower water than equivalent B.A. 3 associations in the intermound areas, the contention that each benthic assemblage occupied a distinct bathymetric zone characterized by a specific absolute depth range is probably incorrect. Mounds within the Castle Grove Mound facies contain central "cores" of dense dolomite with mudstone and wackestone textures containing scattered large colonies (to 3 m) of rugose and tabulate corals and crinoid debris. "Flank" beds (crinoid and fenestellid bryozoan packstone textures) bury the central mounds and contain a diverse assemblage of fossils. Philcox (1970b), Johnson (1980), and Witzke (1981c) noted a variety of brachiopods, crinoids, and other fossils in the "flank" beds that are characteristic of B.A. 4-5 associations. The "flank" beds post-date the development of the mounds that they enclose, and probably correlate with similar faunas in the lower Emeline facies. Development of the Castle Grove mounds was coincident with deposition of the flat-lying Johns Creek facies containing a B.A. 3 pentamerid association. However, active mound development apparently ceased during C_6 late Llandoverian as environments changed and B.A. 4-5 associations became established in eastern Iowa.

The benthic associations in the carbonate mounds of the Palisades-Kepler Mound facies are varied and diverse, although crinoids are volumetrically the dominant benthic invertebrate present in most of the mounds. Echinoderm debris is characteristically large (more than 3 mm diameter), and where identifiable echinoderms are present, the fauna is dominated by a variety of camerate crinoids (especially *Eucalyptocrinites, Siphonocrinus*) with lesser numbers of flexible and inadunate crinoids (especially *Crotalocrinites*) and cystoids (*Caryocrinites*). The carbonate mounds are primarily constructed of carbonate mud and crinoid debris with lesser quantities of other fossils, most notably corals and stromatoporoids. "The distribution and orientation of colonial coelenterates shows that in Iowa they did not construct rigid, wave-resistant frames, but were subordinate to crinoids in the reef-building role" (Philcox, 1971, p. 338). Relict isopachous fibrous submarine cements are observed petrographically, and the mounds apparently became rigid features on the sea floor primarily through submarine cementation processes (Witzke, 1981c). *Favosites* is the commonest coral in the facies, and a variety of other tabulates and solitary and colonial rugosans are also present. Branching and fenestellid bryozoans are locally significant within the mounds, especially in possible grain flow deposits in the flanking beds. Nautiloid and trilobite predators and scavengers in the mound environments were commonly concentrated by currents into fractures and depressions ("pockets") within the mound. A variety of brachiopods are present in the Palisades-Kepler mounds, but usually none is abundant. Within crinoidal and bryozoan-rich beds, the brachiopod fauna is primarily characterized by *Atrypa,* rhynchonellids, and strophomenids. Large pentamerid (*Conchidium, Lissocoelina*) and trimerellid brachiopods are locally present in the mounds; these brachiopods are included in a B.A. 3 position by Boucot (1975). In addition, sponge spicules, gastropods, bivalves, and calcareous green algae (*Ischadites*) are noted in the mounds.

Faunas within the Palisades-Kepler mounds are generally characterized by a greater abundance of large and more robust benthic invertebrates than contemporaneous faunas in the intermound position. The mound facies include an abundance of large camerate crinoids, rugose and tabulate corals (to 65 cm), and stromatoporoids, whereas the intermound Waubeek and Buck Creek Quarry facies associations are characterized by smaller crinoids and corals (rarely exceeding 8 cm). Colonial tabulates are the most abundant corals in the mound facies, whereas small solitary rugosans dominate the coral faunas in the intermound facies. Large, relatively smooth-shelled trilobites (e.g., *Bumastus*) were most successful in the mound facies, whereas smaller, more ornate trilobites (e.g., *Encrinurus*) achieved greater success in the intermound facies. Rhynchonellid, large pentamerid, and trimerellid brachiopods fared best in the mound facies, whereas generally small and thinner-shelled brachiopods (e.g., orthids, meristellids) achieved a higher level of success in the intermound facies. The general abundance of benthic invertebrates was considerably greater in the mound facies than in equivalent intermound facies, possibly reflecting the greater availability of nutrient-rich currents in the shallower water mound environments and greater habitat complexity.

The upper Scotch Grove Fawn Creek facies faunas and lithologies are similar to those in the mound facies, although the volume of skeletal grains in the non-mounded Fawn Creek facies is proportionately slightly less than in the mound facies, and the coralline fauna is of generally smaller size than in the mounds. The Fawn Creek facies probably represents a skeletal bank facies that occupied an intermound environmental position intermediate between the mound facies and the more distal intermound Buck Creek Quarry and Waubeek facies.

Stratigraphic relations clearly indicate that the carbonate mound environments occupied a shallower water position than the adjacent flat-lying intermound facies. Correspondingly, evidence of wave and current activity is more pronounced in the mound facies. The abundance of skeletal packstone and grainstone textures in the Palisades-Kepler mounds suggests that carbonate muds were partially to completely winnowed during deposition of some beds. Some beds with packstone-grainstone textures consist of crinoidal debris of relatively uniform size, which implies possible current sorting. In addition, some packstones contain possible current-oriented crinoid stems. Wedge-shaped grain flow deposits, some of which exhibit graded bedding, flank some of the mounds, suggesting periodic downslope mass movements. Overturned and transported corals are commonly observed, which were probably moved during periodic influxes of turbulent conditions across the mounds.

Philcox (1971, p. 345) studied coral growth forms and their relationship to the surrounding sediment in the Palisades-Kepler Mound facies, and suggested that "reef sedimentation was an irregular process" with "marked fluctuations in sediment rates" across the mounds. He also found "evidence for periodic local removal of sediment." These observations indicate that periodic water turbulence, possibly generated during storm events, played an important role in mound sedimentation. Less turbulent water currents were probably present across the mounds on a more regular basis. The abundant and diverse biota that inhabited the mounds required a continual influx of nutrients. The pervasive submarine cementation that occurred in the mounds probably required movement of large quantities of water through the mounds. Accumulations of nautiloids and trilobites within the mounds are also indicative of current activity (Mikulic, 1979). However, the lack of a rigid skeletal framework suggests that the mounds were not continuously exposed to high-energy environments. Philcox (ibid.) also concluded that "turbulence was normally limited" during the growth of the Palisades-Kepler mounds, although the mounds apparently grew upward into more agitated environments through time. The vertical limits to mound growth may have been controlled by normal fair-weather wave base, since the lack of a skeletal framework may have precluded further mound growth into the highly agitated wave-washed environments. Corals are most abundant in the upper portions of the mounds (Philcox, 1971), where presumably the greatest degree of current activity would have been operating during mound deposition. In summary, all evidence indicates that current activity and storm events exerted considerably more influence on sedimentation in the mound environments than in the laterally equivalent and deeper-water B.A. 3 environments in the intermound position.

Stricklandiid Brachiopod and Related Associations

Stricklandiid brachiopod and related associations occur at several positions in the eastern Iowa Silurian sequence (stricklandiid taxonomy after Johnson, 1979, 1983: 1) middle portion of Hopkinton A (*Stricklandia lens progressa*), 2) lower to middle Hopkinton B (*S. laevis*), 3) lower Scotch Grove Formation, Emeline and Buck Creek Quarry facies (*Costistricklandia castellana*), and 4) mid Scotch Grove Formation, Emeline, Buck Creek Quarry, and basal Fawn Creek facies (*C. castellana, C. multilirata*). Overall, the stricklandiid associations contain the most diverse benthic faunas recovered in the entire Iowa Silurian sequence. However, *Stricklandia* associations are interbedded with coral-stromatoporoid associations in one to several thin bands in the middle portion of the Hopkinton A in the eastern and northeastern Iowa outcrop belt, and these stricklandiid associations, typically characterized by corals and one to two species of brachiopods (Johnson, 1977a), are of generally lower diversity than younger Iowa stricklandiid associations. Although stricklandiid associations are usually assigned a B.A. 4 position (Boucot, 1975), interbedding of Hopkinton A stricklandiid associations with B.A. 2 coral-stromatoporoid associations suggests that the Hopkinton A stricklandiids may have occupied a position more closely analogous to B.A. 3 pentamerid associations. Johnson (1980, p. 206) further suggested that "there is very little difference" in general paleocommunity structure between the Hopkinton A "*Stricklandia* community" and typical Hopkinton "pentamerid communities," perhaps due to similarities in shell packing (Johnson, 1979). Stricklandiids occur as a minor component of pentamerid-dominated brachiopod associations in younger intervals of the Hopkinton and Scotch Grove formations, suggesting that stricklandiids were apparently adapted for life in some B.A. 3 environments.

On the other hand, stricklandiid and related associations in the Hopkinton B and lower Scotch Grove (Emeline and Buck Creek Quarry facies) are very diverse and include faunal elements, excluding the stricklandiids, that are generally characteristic of B.A. 4 to B.A. 5 positions (Boucot, 1975). These associations commonly include: 1) sponge spicules, 2) stromatoporoids, 3) tabulate and rugose corals (most less than 10 cm diameter), 4) inarticulate, orthid, strophomenid, rhynchonellid, pentamerid, and spiriferid brachiopods, 5) bryozoans (abundant branching and fenestellid forms), 6) gastropods, bivalves, and nautiloids, 7) trilobites, and 8) echinoderms. The echinoderm faunas are dominated by a highly diverse assemblage of camerate crinoids (Witzke and Strimple, 1981), although inadunate and flexible crinoids, blastoids, paracrinoids, and rhombiferan cystoids also occur (Witzke, 1976). Johnson (1977a, p. 38-91) recognized additional stricklandiid-related associations in the lower Emeline facies: 1) "a unique bryozoan and trilobite fauna" and 2) "a high diversity fauna comparable to a cloridan community" (cloridan brachiopod communities assigned B.A. 5 position by Boucot, 1975). A similar bryozoan-rich association containing brachiopods (*Atrypa, Protomegastrophia, Dicoelosia*), solitary rugosans (including *Palaeocyclus*), crinoid debris (including abundant *Petalocrinus*), and trilobites occurs above *Pentameroides*-bearing beds in the middle Scotch Grove Formation (Buck Creek Quarry facies).

Closely similar stricklandiid associations occur within both the Buck Creek Quarry and Emeline facies in the lower Scotch Grove Formation, although the highly crinoidal Emeline facies contains proportionately more skeletal material. Wackestone and packstone textures are characteristic, and crinoidal debris is the dominant skeletal constituent in both facies (see Table 1 point-count data for a limestone interval equivalent to the lower Buck Creek Quarry facies). Petrographic and sedimentologic observations pertinent to environmental interpretations include: 1) skeletal grain abrasion/breakage not observed, 2) absence of current sorting or graded bedding, and 3) micrite envelopes around grains not observed. These features suggest relatively quiet depositional conditions in deeper-water environments than the B.A. 2 and 3 associations. In addition, the benthic faunas that thrived in the stricklandiid associations include forms whose delicate or thin-shelled morphology seems poorly suited for survival in agitated environments (Johnson, 1980). The presence of articulated echinoderms is consistent with a quiet depositional environment. Johnson (1980) proposed a relatively calm water depositional environment for the stricklandiid associations, "well below effective wave base." Although effective wave base can be substantially lowered during periodic storm events, the B.A. 4-5 associations in the Iowa Silurian lack sedimentologic evidence of episodic turbulence and thus are reasonably inferred to have occupied environments generally below maximum storm wave base. However, B.A. 4-5 environments in Iowa occupied a position partially or wholly within the photic zone (contrary to Boucot, 1981, p. 247), inasmuch as calcareous green algae have been recovered in stricklandiid associations in the Hopkinton and lower Scotch Grove formations.

Conclusions and Geologic Implications

The distribution of open-marine benthic associations in the Iowa Silurian was strongly controlled by depth-related environmental factors, primarily general position with respect to effective fair-weather and storm wave bases. As such, the temporal changes from one benthic association type to another can be reasonably correlated with depth-related environmental changes. The spatial distribution of various associations within specific stratigraphic intervals can also be evaluated in terms of depth-related facies changes over a geographic expanse. Johnson's studies within the eastern Iowa Lower Silurian outcrop belt led him to conclude several things about that region: 1) "the generally flat, Iowa sea bottom supported only a single spatially monotonous community at a time" (1977a, p. 118); 2) "their lateral uniformity in composition and structure was pervasive'' (1980, p. 213); and 3) ''contemporaneous facies, if present, existed in such widely spaced belts as not to be obvious in this particular region'' (1975, p. 130). However, comparisons of the Hopkinton benthic associations in the subsurface west of the outcrop belt (Linn-Benton counties; see map Fig. 2) with those in the outcrop belt suggest lateral variations in the distribution of benthic associations and facies on a slightly broader geographic scale.

The Hopkinton Formation doubles in thickness as one proceeds from the Benton County subsurface to the central area of the East-Central Iowa Basin (see Fig. 1), and the interpreted distribution of the contained benthic associations displays a pattern that is consistent with the basinal geometry (Fig. 3). Figure 3 is presented as a generalized and interpretive model that attempts to rectify the fossil distributions recognized in the western subsurface cores with those known in the Iowa Silurian outcrop belt. Subsurface data cannot be elaborated here, although core data recorded by Witzke (1981c, p. 486-544) forms the primary basis for the illustrated interpretations. Although *Stricklandia* associations occur in the middle Hopkinton A in the outcrop belt, the thinned Hopkinton A in the western subsurface has yielded no elements of this association (Fig. 3). The most dramatic lateral change in benthic associations apparently occurs in

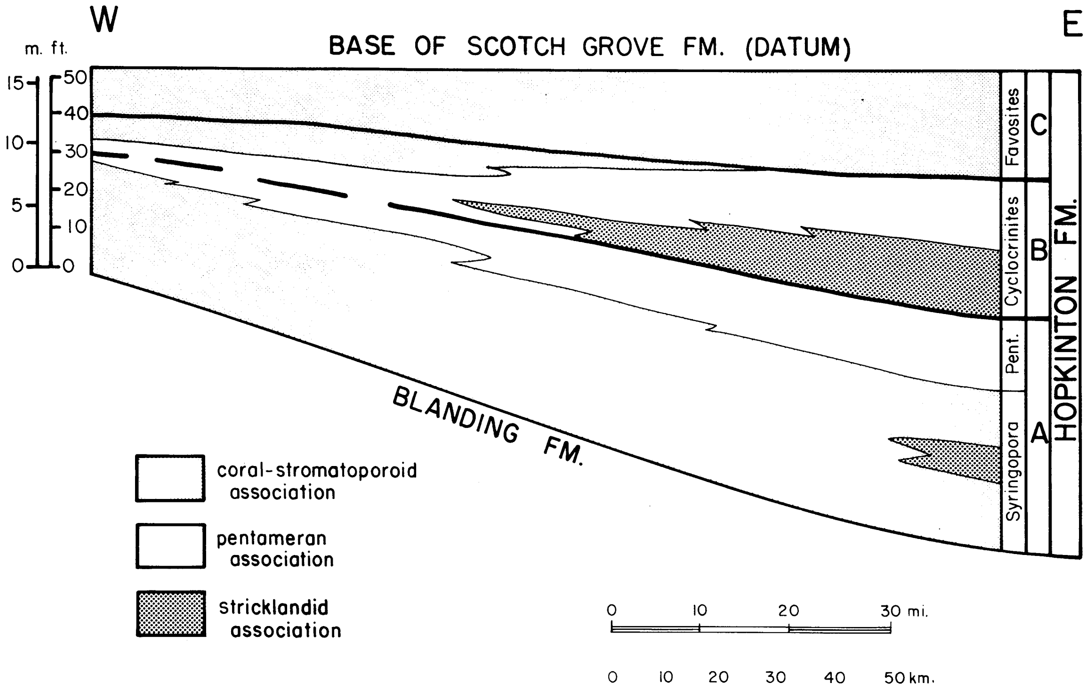

Fig. 3. Generalized interpretation of the vertical and lateral variation in the distribution of benthic associations in the Hopkinton Formation of east-central Iowa. Cross-section line is essentially the same as that used in Figure 2. The sequence of associations in the eastern outcrop belt is derived, in part, from Johnson (1975, 1977a). Subsurface paleotologic data in western subsurface sections generalized from Witzke (1981c). Distribution of Hopkinton A stricklandiid association is schematic, and is represented by several thin zones in the middle to upper ''*Syringopora* beds.'' The interpreted distribution illustrates an ''Israelsky Wedge,'' suggesting that Iowa Hopkinton deposition occurred during a major transgressive-regressive bathymetric cycle.

Hopkinton B. In the outcrop belt the Hopkinton B is characterized by a lower interval with a *Stricklandia* association and an upper interval with a pentamerid association (Johnson, 1980). However, the western subsurface Hopkinton B interval characteristically contains pentamerid associations in the lower portion, and the upper portion contains an abundant tabulate coral fauna with additional fossils (cup corals, stromatoporoids, crinoids, bryozoans, orthids, gastropods). The fauna in the upper interval is tentatively assigned to the coral-stromatoporoid association, although it contains a slightly more diverse fauna than that noted in similar associations in Hopkinton A and C. This association lacks the pentamerid and stricklandiid brachiopods present in the deeper water Hopkinton associations toward the east (Fig. 3). These observations suggest the following interpretations: 1) the lower Hopkinton B *Stricklandia* association in the central portion of the East-Central Iowa Basin is replaced westward by pentamerid associations, and 2) upper Hopkinton B pentamerid associations in the central area of this basin are replaced westward by a coral-stromatoporoid association.

As illustrated in Figure 3, the interpreted spatial distribution of the various Hopkinton benthic associations forms an "Israelsky Wedge" (Israelsky, 1949) in which, at any given time, deeper-water associations occupied the central basin area with stratigraphically equivalent shallower-water associations developed toward the basin margin. These observations offer independent evidence of the depth significance of each association type, since an "Israelsky Wedge" records the "deepening and shallowing phases of a bathymetric cycle" as determined by the relative positions of "bathymetrically controlled" benthic associations (Krumbein and Sloss, 1963, p. 386).

A sequence of probable depth-related open-marine benthic assemblages is identified in the Iowa Silurian, and these assemblages can be correlated with general depth-related environmental zones of Irwin (1965) and Anderson (1971). However, at any given time during the Silurian, only one or two benthic assemblage positions were represented in eastern Iowa. The full complement of onshore to offshore environments (B.A. 1-B.A. 6) at any one time, if developed, probably spread over a much broader geographic area in the epeiric sea. A hypothetical onshore-offshore transect depicts the position of B.A. 1 to 5 environments over a broad geographic area in the central midcontinent (Fig. 4), presumably many hundreds of kilometers across. The farthest offshore environments (B.A. 4-5) are shown in a position well below wave base. However, in Iowa, these environments were characterized by a diverse benthic biota that would have required a degree of current activity to replenish nutrients and maintain stable salinities. B.A. 3 associations inhabited two general carbonate environments in

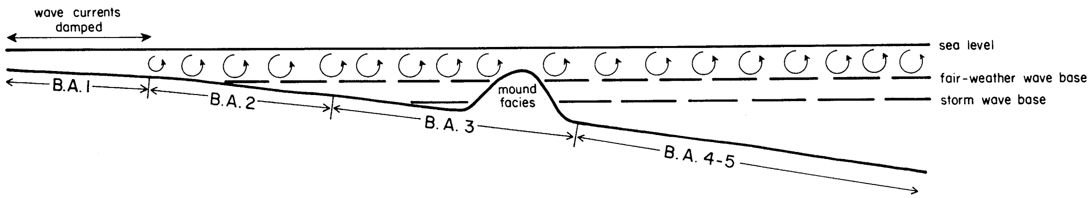

Fig. 4. Hypothetical onshore to offshore transect depicting environmental zones in the Early Silurian epeiric sea in the central midcontinent. Transect is presumably many hundreds of kilometers across. Relative positions of Benthic Assemblages 1 to 5 are shown in relation to fair-weather and storm wave bases. Stable open-marine salinities are maintained across the area occupied by B.A. 2-5, but wind-generated currents are damped in the B.A. 1 position where elevated salinities may be developed. The various environmental zones would migrate across the bottom during relative changes in sea level.

the Iowa Silurian: 1) flat-lying substrate (commonly pentamerid-bearing), and 2) carbonate mound (reef) environments. The flat-lying associations are positioned generally below fair-weather wave base, although periodic turbulent conditions suggest that storm wave base occasionally reached the bottom. On the other hand, carbonate mound environments were subjected to a greater degree of wave and current activity than the flat-lying environments and are placed in a position on Figure 4 where they would have been recurrently subjected to storm events but, in general, immediately below normal fair-weather wave base. B.A. 2 environments are positioned near wave base in the clear water epeiric sea, in part above and in part immediately below wave base (Fig. 4). B.A. 1 associations in Iowa display evidence of restricted circulation and elevated salinities and are discussed in the next section.

RESTRICTED-MARINE BENTHIC ASSOCIATIONS

General Characteristics

Restricted-marine benthic associations inhabited environments of elevated or fluctuating salinity. During portions of the Iowa Silurian (early Llandoverian, late Wenlockian-Ludlovian) these environments encompassed a broad range of salinity variations constrained between two general extremes: 1) salinities close to normal-marine, and 2) hypersaline environments in which solutions were occasionally concentrated high enough to precipitate gypsum or halite. This spectrum of environmental conditions influenced sedimentation in a variety of ways, and a variety of distinctive rock types occur in intervals bearing restricted-marine associations. General rock types include: 1) dolomites with skeletal wackstone, packstone, or grainstone textures, 2) unfossiliferous or sparsely fossiliferous dolomites with mudstone textures, 3) domal and sheet-like stromatolitic carbonates, 4) thinly-bedded dolomites and shaly dolomites, 5) laminated dolomites, and 6) dolomites containing evaporite crystal molds. In addition, the contained faunas are characteristically of lower diversity than the open-marine faunas, and several invertebrate groups commonly regarded as stenohaline (see Heckel, 1972) are absent in many of the associations.

Lingulid Brachiopod and Related Associations

Deposition of the Mosalem Formation in eastern Iowa occurred above an irregular Ordovician shale surface along the margin of the transgressing Early Silurian epeiric sea. The surrounding shale hills supplied clays to the Mosalem environments, where argillaceous carbonate deposition prevailed. Mosalem deposition in Iowa was restricted to the eastern part of the state, apparently within isolated cul-de-sacs and embayments in a nearshore position. The Ordovician shale hills were progressively buried by Silurian sediments as the Silurian transgression progressed, and authochthonous open-marine carbonate depositional patterns became established across much of Iowa by the middle Llandoverian (Blanding Formation).

The benthic associations contained in the Mosalem Formation are assigned a nearshore B.A. 1 position. Unlike the younger Iowa Llandoverian environments where normal-marine faunas are well represented, the Mosalem biota is a low-diversity assemblage locally dominated by lingulid brachiopods. Rhynchonellid and strophomenid brachiopods and gastropods are also locally noted (Johnson, 1975, 1977a). Corals, stromatoporoids, echinoderms, and trilobites are characteristically absent in the Mosalem. Where the Mosalem Formation is thin, a basal zone of stromatolitic algal mats is observed (ibid.). Skeletal grains in the Mosalem are non-abraded, suggesting generally quiet depositional conditions. The thinly-bedded argillaceous dolomites and shales and horizontally-laminated stromatolites in the Mosalem are also consistent with relatively quiet depositional environments. The preservation of organic matter in the Mosalem, including plant filaments (ibid.), graptolites, and soft-bodied worms (T. Frest, 1982, personal comm.), also suggests a non-agitated depositional setting.

The restricted fauna and low-energy B.A. 1 environment of the Mosalem Formation in Iowa are characteristic of the "low-energy zone" of Irwin (1965) and "restricted subtidal" environment of Anderson (1971). Wave current activity was probably damped somewhere offshore (B.A. 2 position), restricting circulation in the nearshore zone (see Fig. 4). The discovery of possible halite pseudomorphs in the Iowa Mosalem suggests that elevated salinities may have been present at times during Mosalem deposition. However, some currents were occasionally present in the nearshore Mosalem environments, as evidenced by rare ripple marks low in the sequence.

Stegerhynchus Association

The uppermost portion of the Scotch Grove Formation (upper Waubeek and Buck Creek Quarry facies) and basal Gower Formation (Anamosa facies) in Linn and Jones Counties, Iowa (Fig. 2 map) contain benthic associations of considerably different composition from those in underlying Scotch Grove strata. Block collections have produced a relatively low diversity assemblage characterized by brachiopods and, locally, small tabulate and solitary rugose corals. This assemblage is termed the *Stegerhynchus* association. In addition to *Stegerhynchus,* other brachiopods, commonly *Protathyris, Spirinella,* and *Meristina,* are prominent members of this association. Of special interest is the absence of bryozoans and trilobites and general absence of echinoderms, which renders the association considerably different from the underlying Scotch Grove associations. *Protathyris* is known only from a B.A. 2 position (Boucot, 1975), and the presence of *Protathyris* in the *Stegerhynchus* association suggests the same position.

The lowest occurrence of the *Stegerhynchus* association in the upper Scotch Grove Formation is interbedded with strata containing scattered small echinoderm debris. Collections recovered from this position contain a slightly more diverse assemblage than *Stegerhynchus* association collections identified a few meters higher stratigraphically, and small colonial rugosans (*Heliolites*), gastropods, bivalves, and additional brachiopod taxa are present (Witzke, 1981c, p. 409). However, *Protathyris* is absent in these collections. Higher in the sequence, the uppermost Scotch Grove *Stegerhynchus* association is further reduced in diversity, contains fewer brachiopod taxa, and completely lacks echinoderm debris. Brachiopods are the only benthic group represented in some uppermost Scotch Grove collections. This general change in benthic association diversity in the uppermost Scotch Grove is also marked by the appearance of two brachiopod genera, *Protathyris* and ?*Nalivkinia,* not represented lower in the sequence. The presence of an atrypid tentatively identified by Boucot (1981, personal comm.) as ?*Nalivkinia* is noteworthy, as the genus has previously been identified only in central Asia. Elements of the uppermost Scotch Grove *Stegerhynchus* association survived past the close of Scotch Grove deposition, and *Protathyris* and rhynchonellids are prominent throughout much of the Gower Formation.

The disappearance of several probable stenohaline groups (most notably the bryozoans, trilobites, echinoderms) in the uppermost Scotch Grove Formation in the western portion of the East-Central Iowa Basin (Linn-Jones counties) suggests that elevated salinities may be, in part, responsible for the biotic changes. The major changes in benthic association structure evident in the uppermost Scotch Grove Formation immediately preceded, or were coincident with, the appearance of laminated Gower carbonate deposition in eastern Iowa, and there appears to be a close link between the appearance of the *Stegerhynchus* association and major changes in the patterns of carbonate deposition in Iowa. As will be discussed later, the appearance of laminated carbonate deposition in eastern Iowa probably marked a significant change in the patterns of water circulation that led to elevated salinities. Uppermost Scotch Grove *Stegerhynchus* associations, assigned a B.A. 2 position, overlie normal-marine B.A. 3 associations, and a relative drop in sea level towards the close of Scotch Grove deposition in Iowa is inferred. Unlike relative sea level drops earlier in the Silurian, the probable drop in sea level at the close of Scotch Grove deposition created physiographic conditions that led to the restriction of normal-marine epeiric circulation in eastern Iowa. This change is not only reflected in the patterns of carbonate deposition, but also by a general reorganization of benthic community structure.

Laminated Carbonate Environments and Associations

The onset of Gower deposition was marked by the widespread appearance of laminated carbonate sediments over much of east-central Iowa. Although three general facies are recognized in the Gower Formation of Iowa, flat-lying sequences containing laminated dolomites (Anamosa facies) typify much of the formation. The bulk of the Anamosa facies is comprised of laminated dolomites; individual laminae generally range between about 0.3 and 3 mm thick, and laminae as thin as 30 microns are noted. The laminated rocks include three general lithologies: 1) wavy- or crinkly-laminated rocks interpreted as subtidal algal stromatolitic mats (Philcox, 1972; Henry, 1972); 2) planar-laminated rocks, possibly representing varved carbonate accumulations deposited by episodic or seasonal carbonate precipitation (Witzke, 1981c); and 3) faintly-laminated dolomites. In addition, the Anamosa facies includes a variety of secondary rock types: thinly-bedded dolomites, dense to porous non-laminated dolomite mudstones, intraclastic dolomites, dolomites with evaporite crystal molds, and fossiliferous dolomites with skeletal wackestone to packstone textures. Individual laminae and dolomite mudstone beds are laterally persistent on outcrop (up to distances of 3 km or more), suggesting widespread quiet-water depositional environments. The rare presence of evaporite crystal molds (Henry, 1972), probably gypsum, along with the general absence of benthic faunas, indicates that the Anamosa facies was, at least in part, deposited under conditions of elevated salinity. Similar laminated carbonate intervals are present in evaporitic sequences in the Salina Group of the Michigan Basin. Although the bulk of the Anamosa facies was probably deposited under quiet conditions, the occasional presence of truncated laminae and intraclast beds in the sequence suggests that periodic turbulent conditions, perhaps generated during storm events, occurred during deposition.

The Anamosa facies is characterized by a general absence of benthic invertebrates (including burrowers), although a few low-diversity associations are scattered within some Anamosa sequences. The beds containing benthic faunas are typically quite thin, indicating that benthic faunas lived in the Anamosa environments for relatively short periods of time. Benthic faunas are most commonly encountered in the Anamosa facies in the general vicinity of the Brady facies mounds, where abundant brachiopod and coral faunas thrived in the shallower mound environments. These faunas are included in the *Protathyris*-rhynchonellid association, an association best developed in the mound facies. This association interfingers with laminated Anamosa dolomites near the mound margins. However, thin beds bearing the *Protathyris*-rhynchonellid associations are occasionally present within the Anamosa facies at localities removed from areas of Brady facies mound developments; thus at times when laminated

Anamosa deposition was interrupted, this association may have briefly lived in the intermound environments. In general, the *Protathyris*-rhynchonellid association typically includes an abundance of few taxa, most notably athyrid (*Protathyris, Hyattidina*) and indeterminate rhynchonellid brachiopods and small tabulate and solitary rugose corals. Gastropods, bivalves (*Pterinea*), and ostracodes have also been observed. Echinoderm debris is characteristically absent throughout the Anamosa facies, although some small echinoderm debris has been locally noted, most commonly near the contact with the underlying Scotch Grove Formation.

A second benthic association, termed the "rod"-algal mat association, is also identified in the Anamosa facies. This association is not only noted at a position where the Brady and Anamosa facies interfinger, but also at localities far removed from any carbonate mounds. The "rods" are enigmatic cylindrical fossils generally about 1 cm by 2 mm in size, but occasionally reaching lengths of up to 4 cm. They are usually associated with algal-laminated beds. The "rods" were apparently soft when deposited, as indicated by draping of individual "rods" to conform to bedding surface undulations (Henry, 1972). The "rods" have been variably interpreted as fecal pellets or dwelling tubes of an unknown benthic invertebrate. However, the "rods" are exceptionally large for most known fecal pellets. Gill (1977) illustrated "rods" from algal-laminated dolomites of the A-1 carbonate in the Michigan Basin which he interpreted as being of "fecal origin," probably produced by unknown "mat-grazing organisms." However, if the abundant "rods" were produced by burrowing or grazing organisms, there should be evidence of burrowing within the laminated dolomites or truncated grazed surfaces on individual algal laminae adjacent to the "rod"-bearing beds. Such features have not been observed in the laminated Gower dolomites. In addition, well-preserved "rods" have a hollow central chamber, a feature not easily explained if they are of fecal origin. Henry (1972) alternatively suggested that the "rods" were soft, gelatinous dwelling tubes of an unknown "worm"-like organism. The organisms that lived in these tubes may have been filter feeders. The general exclusion of a benthic fauna in most laminated Anamosa environments suggests that benthic conditions were hostile to most invertebrates, probably due to elevated salinities. However, the "rod" organisms were apparently uniquely adapted for survival in some of the subtidal organic-mat environments.

Carbonate Mound (Reef) and Related Associations

Carbonate mound facies interfinger with laminated dolomites of the Anamosa facies within the Gower Formation of eastern Iowa. Two mound facies are recognized, each generally occupying a distinct geographic region of eastern Iowa. The Brady facies includes coral- and brachiopod-rich mounds typically developed in the western and central portions of the East-Central Iowa Basin. Stratigraphic relations indicate that the Brady mounds were deposited in shallower-water environments than the adjacent flat-lying Anamosa beds (Witzke, 1981a). Brady facies mounds and mound complexes vary in size from about 150 m to 1 km in diameter; maximum vertical dimensions are unclear due to post-Silurian erosion (up to 25 m preserved). Dips average about 20 to 50° in the mounds, and slump-folds locally achieve dips up to 90° (Hinman, 1968).

The Brady facies is characterized by fossiliferous dolomite with skeletal wackestone-packstone (some grainstone and boundstone) textures. Dense non-laminated to laminated dolomites, in part with prominent stromatolites, are interbedded with the fossil-rich beds. Although, in a general sense, Brady rock types resemble those of the Anamosa facies, the Brady facies is *markedly* more skeletal rich. The Brady mounds lack a rigid skeletal framework, and, as evidenced by abundant relict fibrous isopachous cements, the mounds apparently became rigid features on the sea floor primarily through submarine cementation processes.

A profusion of fossils is evident in the Brady facies, but the faunas are of relatively low diversity. As previously discussed, dense brachiopod accumulations of the *Protathyris*-rhynchonellid association comprise much of the Brady facies. The abundant small brachiopods are normally articulated, and dolomite-replacement of delicate athyrid spiralia is not uncommon. The *Fletcheria* association is well developed within some Brady facies mounds, commonly intimately associated with *Protathyris*-rhynchonellid beds. This association is dominated by clusters of the solitary rugose coral, *Fletcheria* sp., and small colonies (usually less than 20 corallites) of an indeterminate tabulate coral are commonly encountered. Small solitary rugosans, *Halysites,* and *Favosites* are locally present. The coral-rich *Fletcheria* association intergrades with the *Protathyris*-rhynchonellid association in the Brady facies, and *Fletcheria* and small tabulates are locally represented in the brachiopod-rich beds. The abundance of corals and *Protathyris* in these associations suggests a B.A. 2 position. Toward the edges of the Brady facies mounds, the *Protathyris*-rhynchonellid association interfingers with laminated dolomites of the Anamosa facies. At this general position, algal-laminated dolomites, in part containing "rods," become prominent, and domal stromatolites are locally observed. "Rod" packstones are noted near the mound edges.

A distinct benthic association is locally present in the central mound areas of the Brady facies, stratigraphically below *Fletcheria* and *Protathyris*-rhynchonellid associations. Large pentamerid (*Harpidium*) and trimerellid brachiopods are conspicuous in this association, forms generally characteristic of a B.A. 3 position (Boucot, 1975). In addition, spiriferid, strophomenid, and rhynchonellid brachiopods are also represented, although athyrids are absent. Gastropods, bivalves, and nautiloids are present, but corals are generally rare. The *Harpidium*-trimerellid association locally contains rare echinoderm debris, but trilobites, bryozoans, and stromatoporoids have not been observed.

The LeClaire facies occupies a position near the southeast margin of the East-Central Iowa Basin, and is best developed in Scott County, Iowa (see Fig. 2 map) and adjacent areas of Illinois. The LeClaire facies includes mounded and flat-lying strata that interfinger with the Anamosa facies in a complex manner. The LeClaire facies contains several different benthic associations. Unlike benthic associations in the Brady facies, the LeClaire facies locally includes associations with an abundance of crinoidal debris, both in flat-lying and mounded sequences. Large crinoid debris, including identifiable cups (especially *Eucalyptocrinites, Crotalocrinites*), is locally common in some LeClaire mounds, and small indeterminate crinoid debris is present in some flat-lying LeClaire sequences. Trilobites also occur in some LeClaire mounds. The presence of crinoid debris and trilobites in the LeClaire facies (these groups commonly regarded as stenohaline) suggests that LeClaire environments were developed, in part, in water of generally normal-marine salinity. Crinoidal rocks in the LeClaire facies resemble typical lithologies in the Palisades-Kepler Mound facies, although, unlike the Palisades-Kepler mounds, the LeClaire facies occurs higher stratigraphically and is laterally equivalent to laminated dolomites. However, the LeClaire facies also includes lithologies and benthic associations that closely resemble those in the Brady-Anamosa facies.

Fletcheria associations are well developed in the LeClaire facies, both in flatlying and mounded sequences, and are locally interbedded with crinoidal or laminated dolomites. The LeClaire *Fletcheria* associations contain rugose and tabulate corals, brachiopods (rhynchonellids, atrypids), and rare gastropods, but echinoderm debris is absent. Additional brachiopod-dominated associations, commonly containing rhynchonellids and atrypids (aff. ?*Nalivkinia*), occur in the facies. The LeClaire mounds also locally contain a brachiopod association characterized by large pentamerids (*Conchidium*) and trimerellids; large bivalves ("*Megalomus*"), gastropods, and solitary rugose corals also occur. The LeClaire rhynchonellid-atrypid and *Conchidium*-trimerellid faunas resemble, in a general sense, the *Protathyris*-rhynchonellid and *Harpidium*-trimerellid associations, respectively, in the Brady facies. A degree of faunal similarity between the Brady and LeClaire mounds is apparent, although important faunal differences, particularly with respect to the crinoidal component, need to be stressed.

As with the upper Scotch Grove mounds, mound facies in the Gower Formation were subjected to water currents during deposition to varying degrees. These currents brought a continuing supply of nutrients to the abundant suspension-feeding invertebrates that lived on the mounds, and also facilitated the movement of water through the mound promoting submarine cementation. However, the characteristic preservation of abundant articulated brachiopods implies that agitated wave-washed conditions were not continually present in the mound environments. Although the LeClaire mounds, in part, contain crinoidal faunas suggestive of open-marine conditions, more Gower mound faunas, especially those in the Brady facies, are characterized by low-diversity associations lacking several biotic groups commonly interpreted as having stenohaline normal-marine environmental requirements (most notably echinoderms, trilobites, bryozoans). In addition, the Gower mound facies interfinger with laminated Anamosa carbonates that were probably deposited in environments of elevated salinity. It is consistent with those observations to suggest that the Gower mound environments were also subjected to conditions of fluctuating or elevated salinities during their deposition.

Upper Gower Faunas and Environments

The final phases of Silurian sedimentation in Iowa have been largely erased by pre-Middle Devonian erosion. However, the uppermost Gower rocks examined contain faunal and lithologic characteristics distinct from those in underlying strata. The uppermost portion of the Anamosa facies at one locality in Jones County (see Fig. 2 map) includes non-laminated to faintly-laminated dolomites that are locally intraclastic. Specimens of a large ostracode, *Leperditia* sp., were found in this interval. No other fossils were recovered, and the fauna was undoubtedly one of very low diversity. The presence of intraclastic rocks suggests the development of shallower water conditions during upper Gower deposition. Intraclasts may have been incorporated into the enclosing fine-grained carbonate sediments during episodic incursions of agitated conditions. This shallowing trend evident in the upper Gower led to eventual offlap of the Silurian sea from eastern Iowa.

Gower Depositional Model

The progression of normal-marine benthic associations in the middle Llandoverian through middle Wenlockian sequence in Iowa bespeaks long-term maintenance of stable salinities and effective circulation in the Iowa portion of the epeiric sea. However, a profound change in benthic association structure and carbonate depositional patterns occurred during the middle to late Wenlockian. Epeiric water circulation patterns in Iowa were apparently disrupted at that time. Diverse marine B.A. 3 associations in the upper Scotch Grove are replaced by relatively low-diversity restricted-marine B.A. 2 associations near the contact with the Gower Formation. A relative drop in sea level may have contributed to these changes.

What other factors contributed to the restriction of water circulation in eastern Iowa during the late Wenlockian? I previously suggested that the late Wenlockian drop in sea level "left central Iowa emergent at the beginning of the Gower deposition, and open circulation across the carbonate shelf was thereby cut off" leaving "east-central Iowa as a restricted embayment of the Silurian sea" (Witzke, 1981a, p. 17). During marine regression, the seas would retreat first from the structurally elevated areas and be retained longest within the basinal areas (in this case, the East-Central Iowa Basin). A tentative model of Gower deposition is proposed in which a restricted embayment of the Silurian sea in east-central Iowa opened eastward into Illinois where better circulation and more normal marine salinities prevailed.

The onset of Gower deposition was marked by the widespread appearance of laminated carbonate sediments (Anamosa facies) over much of east-central Iowa. I concur with Henry (1972, p. 78) and Philcox (1972, p. 701) in interpreting the depositional environment of the laminated Gower carbonates as one of quiet conditions of restricted circulation and high salinities. However, equivalent carbonate mound facies developed in waters that were generally shallower than the laminated Anamosa facies. The nearer-surface water conditions in the mound environments were apparently more favorable for the flourishing of benthic organisms than the slightly deeper environments where subtidal organic mats and "evaporitic" carbonates were deposited. These interpretations suggest that a vertical stratification of the water column was developed during Gower depositional in eastern Iowa. The probability of hypersaline conditions in the Gower environments further suggests that the water column may have been divided into two water masses by a halocline. The halocline marked the boundary between the denser, more saline bottom waters and an upper surface layer of less saline and better aerated waters. The Brady facies mounds apparently developed in the shallower and more hospitable surface waters, whereas deposition of the Anamosa facies predominated beneath a halocline (Witzke, 1981a, p. 21). Because the Brady faunas, while extremely abundant, are generally of low diversity and characteristically lack several normally stenohaline groups, the waters of the upper surface layer apparently still posed stresses that tended to exclude several groups of marine organisms, and somewhat elevated salinities are suggested. Skeletal-rich Brady facies beds may have spread laterally into the flat-lying Anamosa facies at times when the halocline became depressed or disrupted.

The LeClaire facies includes a more diverse benthic fauna compared to the more restricted faunas of the Brady facies, suggesting that surface water conditions were more favorable for marine faunas in the eastern portion of East-Central Iowa Basin than farther west. This can be explained if surface water salinities increased westward within the basin. Carbonate buildups and skeletal/mud banks of the LeClaire facies in the eastern portion of the basin may have served to attentuate open marine circulation between Illinois and eastern Iowa. The LeClaire facies may thereby have formed an effective circulation barrier, promoting the development of a stratified water column in the East-Central Iowa Basin. The halocline must have vanished eastward into Illinois, where saline bottom waters presumably mixed with more open-marine waters. The LeClaire-Anamosa facies belt lies at a position transitional between the western Brady-Anamosa facies belt, where a relatively stable and long-lived halocline was apparently developed, and an open-marine facies belt in Illinois. The LeClaire facies, occupying this intermediate environmental position, contains both open-marine and restricted-marine benthic associations.

CONCLUSIONS

The central objective of this report was to evaluate the distribution of the Iowa Silurian benthic associations in terms of possible controlling paleonvironmental parameters. The Iowa Llandoverian depth-related benthic paleocommunity model of Johnson (1975, 1980) was tested using additional petrographic and stratigraphic information. In general, the distribution of the three basic level-bottom open-marine benthic associations (coral-stromatoporoid, pentamerid, stricklandiid) was found to be highly correlated to depth-related paleoenvironmental parameters, in particular the relative position of effective wave base. Open-marine epeiric circulation patterns were maintained across the carbonate shelf in Iowa during the middle Llandoverian through middle Wenlockian, and the temporal sequence of benthic asociations and facies is linked to widespread depth-related environmental changes. Open-marine environments and faunas are correlated to general Benthic Assemblage positions within the epeiric sea, and the change from one B.A. type to another in the Iowa stratigraphic sequence can be consistently interpreted in terms of relative changes in sea level. As illustrated in Figure 1, several transgressive (deepening) and regressive (shallowing) trends are evident. However, the change from one B.A. type to another only documents *relative* changes in sea level, and absolute changes in water depth may not be accurately reflected. This is particularly evident in the open-marine mound facies. Although the mounds typically contain B.A. 3 associations, water depths and environmental conditions in the mound facies were considerably different than in the intermound environments where B.A. 3 associations also occur. In many respects, the environmental factors operating during mound deposition share more similarities with flat-lying B.A. 2 environments than with the B.A 3 intermound environments.

The disruption of open-marine epeiric circulation patterns during the late Wenlockian and Ludlovian resulted in a dramatic reorganization of benthic association structure and carbonate depositional patterns. The temporal and geographic distribution of the Late Silurian benthic assemblages was related, not only to relative changes in sea level, but more importantly, to salinity stresses within the restricted eastern Iowa sea. As salinity stresses increased within the eastern Iowa seaway, several stenohaline groups, notably the echinoderms, trilobites, and bryozoans, were excluded from the benthic associations. Although Benthic Assemblage analysis, when utilized with additional stratigraphic and sedimentologic evidence, provides a basis for evaluating relative changes in sea level, a strict correlation of Benthic Assemblages with specific water depths is overly simplistic. Additional environmental parameters operating on epeiric carbonate shelves, especially those related to salinity, also exerted significant influence on the distribution of Benthic Assemblages and their contained biotic associations. In general, relative changes in sea level affected carbonate deposition by modifying the position of storm and fair-weather wave base and, in combination with physiographic and climatic factors, water circulation patterns.

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OBSERVATIONS ON THE COMMENSALISM OF SILURIAN PLATYCERATID GASTROPODS AND STALKED ECHINODERMS

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Abstract

Commensalism of coprophagous platyceratid gastropods and stalked echinoderms persisted from the Ordovician through the Permian. Reported examples from the Silurian are few although this association was well established by that time.

Among Silurian crinoids only camerates are involved in this commensalism. These taxa comprise only nine genera from seven families among the 57 genera represented by 21 Silurian camerate families. Four of these genera (*Dimerocrinites, Lyriocrinus, Macrostylocrinus, Saccocrinus*) are found in the Rochester Shale of New York and Ontario. Other host crinoid genera include *Ptychocrinus* (Power Glen Shale, New York and Ontario), *Periechocrinus* (Waldron Shale, Indiana), *Scyphocrinites* (Silurian-Devonian boundary, Morroco), and *Marsupiocrinus* and *Clematocrinus* (Wenlock Limestone, England). *Dimerocrinites* with attached platyceratids are also known from the Högklint beds at Häftingsklint, Gotland, Sweden.

The cystoid *Caryocrinites* from the Rochester Shale is also found as a platyceratid host. This is the only cystoid known as a host in the Silurian. *Caryocrinites* is unique among cystoids because of its morphologic similarity to crinoids, particularly camerates.

The non-camerate host crinoids (six genera of poteriocrinine inadunates and one taxocrinid flexible) in the geologic record bear morphologic and behavioral similarities to camerates, and these characteristics may influence host selectivity. The tegmen and anus morphologies of host crinoids are variable, and the degree of control which these features exert on host selectivity is uncertain.

INTRODUCTION

Platyceratid gastropods are found attached to the tegminal area of certain Paleozoic stalked echinoderms, primarily crinoids and rarely cystoids and blastoids. Presumably, the platyceratid settled during its larval stage onto a young host echinoderm and led a sedentary life situated over the echinoderm's anal opening where it fed on discharged fecal material. This commensalism was apparently successful since it persisted from the Ordovician, when platyceratids first appeared, through the Permian, when both platyceratids and the echinoderms which served as hosts became extinct (Bowsher, 1955). This platyceratid-echinoderm relationship has been reviewed in general by several authors (Keyes, 1888; Clarke, 1921; Bowsher, 1955; Lane, 1978) but little has been previously published about Silurian occurrences even though this association was well established by that period. This paper will relate the known Silurian commensal occurrences, describe the types of echinoderms that serve as hosts, and suggest some possible factors in host selectivity by platyceratids.

SILURIAN OCCURRENCES

The existence of this commensalism in Silurian time has been known at least since 1851 when Hall figured (1851), Pl. 49, fig.

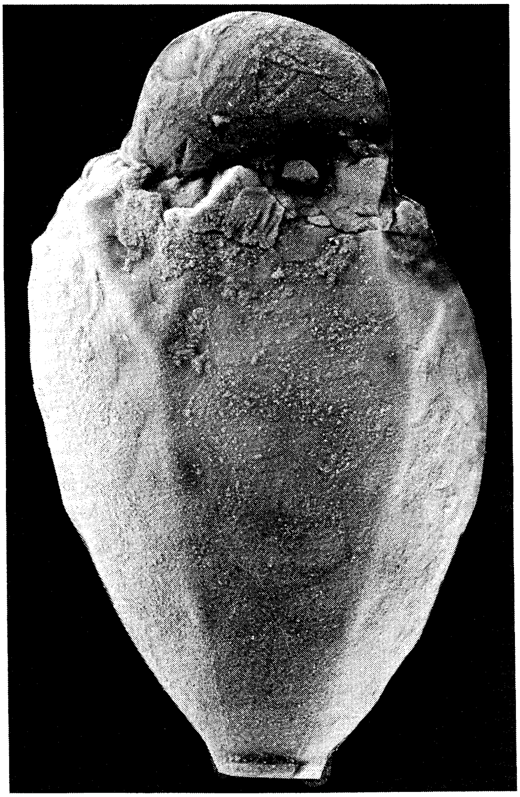

Fig. 1 *Naticonema* in place on the crinoid *Saccocrinus* (ROM 35797, Royal Ontario Museum) from the Rochester Shale of Ontario. Photo courtesy of C. E. Brett. (x2)

Fig. 2. *Platyceras* on the theca of the cystoid *Caryocrinites ornatus* (E25477, Buffalo Museum of Science) from the Rochester Shale of New York. Photo courtesy of C. E. Brett. (x2)

1d) the cystoid *Caryocrinites ornatus* from the Rochester Shale of Lockport, New York, with a platyceratid firmly attached to it. Hall did not attempt an interpretation of this relationship, but he concluded that it represented an association in life and was not just a fortuitous occurrence. The earliest report of a Silurian crinoid host was provided by Murchison (1854) who figured a specimen of *Marsupiocrinus caelatus* with attached platyceratid from the Wenlock Limestone of Dudley, England. Murchison believed that this crinoid was carnivorous and the gastropod was its prey.

The oldest Silurian occurrence of the platyceratid-echinoderm relationship is known from the Llandoverian Power Glen Shale of New York and Ontario (Brett, 1978a). Brett reported a high density of platyceratids at one locality where *Naticonema niagarense* was found attached to many of the more than 100 crowns of the crinoid *Ptychocrinus medinensis* present.

Additional Silurian examples of this commensalism were found in the Wenlockian Rochester Shale of New York and Ontario. Bowsher (1955) and Brett (1978b) reported *Naticonema niagarense* attached to the crinoid *Macrostylocrinus ornatus* from this unit. *Naticonema* was also found attached to the cystoid *Caryocrinites ornatus* (Hall, 1851); Bowsher, 1955; Brett, 1978b) and to the crinoids *Lyriocrinus, Saccocrinus,* and *Dimerocrinites* (C. Brett, 1977, pers. comm.) in the Rochester Shale. The Wenlockian Högklint beds at Häftingsklint, Gotland, Sweden, have also yielded *Dimerocrinites* with attached platyceratids (C. Franzén, 1978, pers. comm.). *Saccocrinus* and *Caryocrinites* from the Rochester Shale are illustrated as playceratid hosts in figures 1 and 2, respectively.

Platyceras haliotis has long been known as a commensal on the crinoid *Marsupiocrinus caelatus* from the Wenlock Limestone of Dudley, England (Murchison, 1854); Springer, 1926; Bowsher, 1955; Watkins and Hurst, 1977). The crinoid *Clematocrinus*

Fig. 3. Slab of abundant well-preserved *Clematocrinus retiarius* showing two crowns with attached platyceratids. This slab (A12749, Fletcher Collection, Cambridge University) is from the Wenlock Limestone of Dudley, England. (x2)

retiarius (figs. 3 and 4), previously unreported as a host, also occurs with attached platyceratids in the Wenlock Limestone at Dudley. Watkins and Hurst (1977) described this monotaxic crinoid assemblage in detail (under the name *Hapalocrinus*) but did not report the presence of platyceratids. Several slabs of abundant well-preserved *C. retiarius* from Dudley in the Fletcher Collection (Cambridge University) show a rather common occurrence of small commensal platyceratids. The incomplete preparation of the slabs and the small size of the gastropods make it difficult to observe the relationship, therefore, an even higher density of platyceratids possibly exists here.

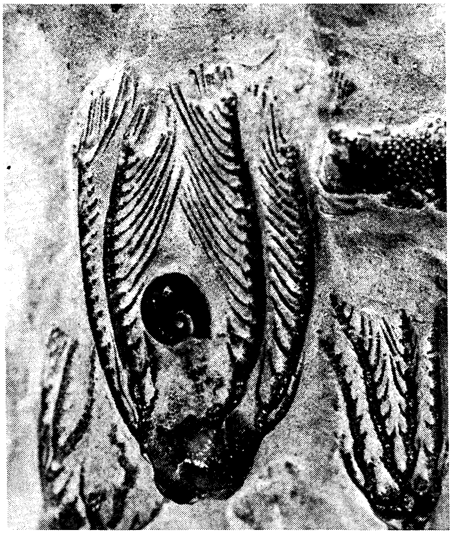

Fig. 4. Crown of the crinoid *Clematocrinus retiarius* (A12743, Fletcher Collection, Cambridge University) with attached platyceratid, also from Wenlock Limestone at Dudley, England. (x4)

Another previously unreported Silurian example of this commensal behavior was found in the Wenlockian Waldron Shale near Waldron, Indiana, and was brought to my attention by Jeff Aubrey and Kenneth Sever. In this unit platyceratids are found *in situ* on the crinoid *Periechocrinus christyi.* Both the platyceratid and *Periechocrinus* individuals are unusually large for Silurian occurrences of this relationship. One unique specimen of *Periechocrinus,* collected by Kenneth Sever and loaned to me for this study, bears two platyceratids (figs. 5-7). The larger of the two gastropods has an irregular apertural margin corresponding to the distribution of the crinoid arm facets,

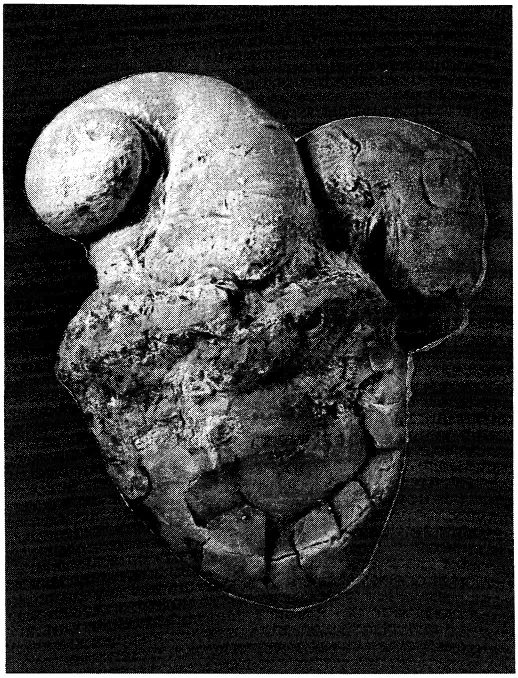

Fig. 5. Large *Periechocrinus christyi* aboral cup associated with two platyceratid gastropods, from the Waldron Shale, near Waldron, Indiana. Specimen in figs. 5-7 is in the collection of Kenneth Sever. Figs. 5 and 6 are x 0.8.

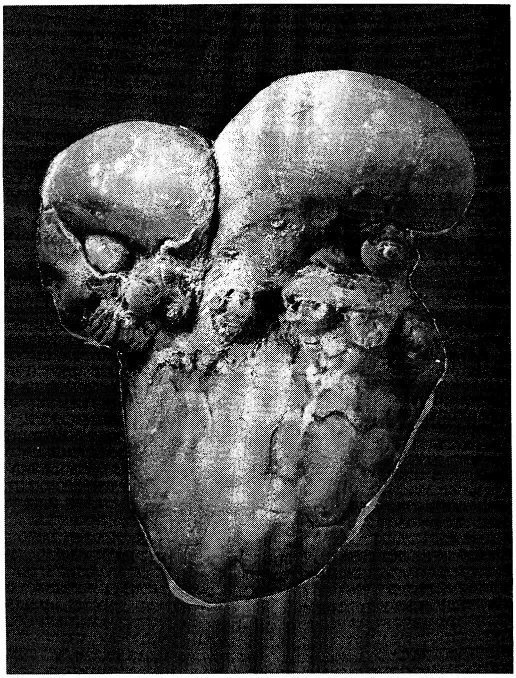

Fig. 6. Another view of the *Periechocrinus* specimen in fig. 5.

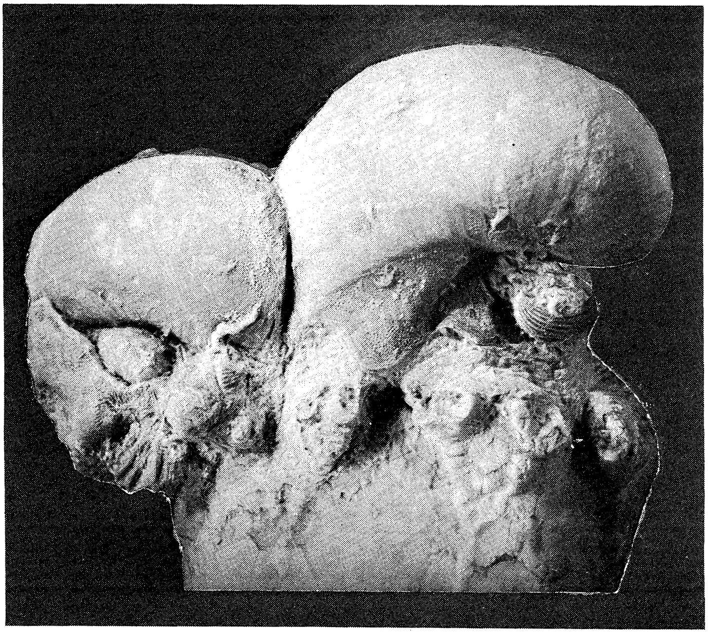

Fig. 7. Close-up of the attachment area on the *Periechocrinus* specimen in figs. 5 and 6. Note the irregular growth lines and apertural margin of the larger gastropod and also the epifaunal organisms which are present on both platyceratid shells. (x1.2)

and its aperture is oriented over the crinoid tegmen. The smaller gastropod is displaced with its aperture partly facing the other gastropod. The apertural margin of the smaller gastropod shows no modification to accommodate the larger shell, but a portion of its margin is irregular in outline, suggesting it may once have been attached to this or another crinoid, but dislodged at the time of burial. Several rhynchonellid brachiopods are associated with the gastropods, three of which are oriented with their pedicles towards the smaller gastropod, suggesting that they may have been attached to it in life. The platyceratid shells are heavily encrusted by ectoproct bryozoans, however, and the brachiopod attachment site is concealed. Several cornulitids are also attached to the gastropod shells. The presence of the same epifaunal organisms on both shells suggests a living association may have existed between the two platyceratids; however, it is also possible that the presence of the smaller gastropod is only fortuitous.

Examples of this commensalism have also been found at the Silurian-Devonian boundary in southeastern Morocco. Lierl (1982) reported both *Platyceras (Orthonychia) elegans* and *Ptychospirina* sp. attached to specimens of the crinoid *Scyphocrinites elegans* there.

No examples of this commensal behavior are known from the diverse North American Silurian reef echinoderm faunas. Many of the camerate host crinoids *(Dimerocrinites, Lyriocrinus, Macrostylocrinus, Marsupiocrinus, Periechocrinus)* and the cystoid *Caryocrinites* commonly occur in Silurian reefs, as do platyceratids. The absence of this relationship from the reef environment appears to be an artifact of preservation because the high energy and low sedimentation rates characteristic of reefs are not conducive to the type of rapid burial needed to preserve articulated echinoderms. Once an echinoderm begins to disarticulate any attached platyceratids could be mechanically detached from it, destroying evidence of the original association. A brief survey of the Greene Museum collections (University of Wisconsin-Milwaukee) has revealed several loose platyceratid specimens from the Hawthorne and Bridgeport Silurian reefs (Chicago, Illinois) with irregular apertural margins suggesting that they may have been attached to crinoids or cystoids.

RELATION OF COMMENSALISM TO CRINOID MORPHOLOGY AND BEHAVIOR

Several of the Silurian crinoid taxa which serve as hosts to platyceratids are not anchored by holdfasts or roots and are capable of some mobility. Some, such as *Dimerocrinites,* had prehensile distally-coiling stalks to provide limited mobility. One of the host crinoids, *Scyphocrinites,* was eleutherozoic and drifted by means of an air-filled, bulbous float (Strimple, 1963; Lierl, 1982). *Clematocrinus* had nodal rings of cirri on its stem suggesting it had the ability to reorient itself on the soft sediments on which it lived (Watkins and Hurst, 1977). The lack of direct contact with the substrate and the mobile lifestyles of some of the Silurian host crinoids lend support to the idea that platyceratids settled on their hosts as free-swimming larvae.

Evidence for the sedentary lifestyle of platyceratids is provided by several Silurian examples in which the attached gastropod has an irregular apertural margin which conforms to irregularities on the host at the attachment site. The large platyceratid attached to the *Periechocrinus* specimen in figure 7 provides a fine example of this apertural modification.

The presence of a large, smooth, flat tegmen has been proposed as the principal factor in host selectivity by platyceratids (Bowsher, 1955; Lane, 1978). The Silurian crinoids which serve as hosts, however, exhibit a variety of tegmen morphologies ranging from flat to conical to depressed. The type of anal area also varies among these crinoids. The anus may be a simple opening on the tegmen (e.g., *Marsupiocrinus*) or marginal to the tegmen (e.g., *Macrostylocrinus*). In some taxa an anal ridge (e.g., *Ptychocrinus*) or anal tube (e.g., *Periechocrinus*) exists. The length of the anal tube increases dramatically in some later hosts, particularly in Carboniferous taxa such as *Stellarocrinus*. No matter what the structure of the anus or the morphology of the tegmen the platyceratid is always associated with the anal opening. In those taxa with a long anal tube or marginal anus the platyceratid may have had no contact with the tegmen at all. Factors other than tegmen morphology apparently are significant in controlling host selectivity.

Camerate crinoids and feeding adaptations

All of the Silurian crinoids to which platyceratids are found attached belong to the subclass Camerata. Among 57 genera (21 families) of known Silurian camerates nine genera (seven families) are involved in this commensalism (Table 1). The earliest known example in the Ordovician also involved a camerate host (*Glyptocrinus*) (Bowsher, 1955), and of the numerous post-Silurian host crinoid genera all are camerates except for six genera in the inadunate suborder Poteriocrinina and one genus *(Taxocrinus)* from the subclass Flexibilia. This relationship occurs rarely in the fossil record among known host taxa; however, many other camerates were possible platyceratid hosts, but specimens exhibiting this commensal association have yet to be found.

TABLE 1. Classification of Silurian crinoids serving as platyceratid hosts.

- Subclass Camerata
  - Order Monobathrida
    - Family Hapalocrinidae
      - *Clematocrinus*
    - Family Marsupiocrinidae
      - *Marsupiocrinus*
    - Family Patellocrinidae
      - *Macrostylocrinus*
    - Family Scyphocrinitidae
      - *Scyphocrinites*
    - Family Periechocrinidae
      - *Periechocrinus*
      - *Saccocrinus*
  - Order Diplobathrida
    - Family Rhodocrinitidae
      - *Lyriocrinus*
    - Family Dimerocrinitidae
      - *Dimerocrinites*
      - *Ptychocrinus*

The three groups of crinoids which were hosts to platyceratids shared similar morphologic and behavioral adaptations. Most camerate and some flexible crinoids, particularly taxocrinids, are considered to have been rheophilic, filtration-fan feeders (Breimer, 1978). These crinoids maintained a passive feeding posture with their highly pinnulated or ramulated arms forming a filtration net oriented normal to the horizontal current (Macurda and Meyer, 1974). This feeding method provided an efficient means of capturing plankton and other detritus. In this orientation the crinoid had to have some means of supporting its heavy crown. This balance control necessitated a stalk which was flexible enough to bend in the feeding posture but rigid enough to provide elevation and anchorage. Most camerates possessed a stalk capable of considerable flexure in the middle while rigidity at the proximal and distal ends provided maximum leverage. The distally-coiling stalks of dimerocrinitids (e.g., *Dimerocrinites*) and rhodocrinitids (e.g., *Lyriocrinus*) may have been very useful in balance control because they were able to yield somewhat to prevent too much longitudinal stress in the stalk (Breimer, 1978). Movement of the pinnules provided additional control. This passive rheophilic feeding method did not require complicated movements and was well suited to camerates which lacked muscular contacts between brachials (Breimer, 1978). Breimer (1978) has also suggested that advanced inadunate crinoids possessed pinnulate arms capable of muscular control and could actively orient their crowns into the current at a specific angle in a rheophilic posture in order to derive lift from the current. Although not all poteriocrinine inadunates (the only inadunates known as platyceratid hosts) had developed muscular articulation, they had earlier evolved pinnulate arms and were capable of the rheophilic feeding posture

(Lane and Breimer, 1974; Breimer and Webster, 1975).

Crinoids adapted to the alternative, rheophobic feeding posture either rested directly on the substrate or were supported by a short, rigid stalk. Rheophobes are thought to have lived in areas with very slight currents, or none, where they fed on plankton and other detritus which settled gravitationally through the water column onto their outstretched non-pinnulated arms (Breimer, 1978). No rheophobes have been reported as platyceratid hosts.

What in particular made rheophiles attractive, or rheophobes unattractive, to platyceratids as hosts is unknown. Platyceratids may have selected rheophilic hosts because these crinoids could effect some balance control and were capable of supporting a gastropod while maintaining their feeding postures. The most effective rheophiles may have been camerates such as dimerocrinitids and rhodocrinitids with prehensile stalks, and several of the Silurian host crinoids are of this type. The sessile rheophobic crinoids may have possessed some chemical or mechanical means of preventing organisms from settling on them in order to keep their feeding surfaces clear. Utilizing different feeding methods at different feeding levels rheophobes and rheophiles may have had different food sources. Rheophiles may have fed on smaller sized plankton and detritus than rheophobes (Meyer and Lane, 1976; Watkins and Hurst, 1977). The difference in food source may have been reflected in the crinoid's fecal contents. Rheophobes were probably less efficient feeders than rheophiles. Also they may have had a lower metabolic rate resulting in lower feces production than rheophiles (D. B. Macurda, 1983, pers. comm.).

MORPHOLOGY OF *CARYOCRINITES*

The rhombiferan cystoid *Caryocrinites ornatus* is the only Silurian cystoid known to host platyceratids. *Caryocrinites* is an unusual cystoid having many morphologic similarities to crinoids, particularly camerates. A "tegmen" of specialized plates covers the mouth of *Caryocrinites* and bears a morphologic similarity, but is not homologous, to the tegmen of crinoids (Kesling, 1967). The long flexible stalk of *Caryocrinites* is also very crinoid-like and dissimilar to most other cystoids which are eleutherozoic or possess very short rigid columns. Brett (1978b) compared the radix-type root of *Caryocrinites* to that of some camerate crinoids. The biserial arrangement and pinnulation of *Caryocrinites* arms is unlike most other cystoids, which have simple unbranched brachioles, but is reminiscent of camerate crinoid arm structure. Sprinkle (1975) suggested that the development of such arms in *Caryocrinites* increased its food-gathering capacity. Also, the theca of *Caryocrinites* is similar in appearance to many camerate crinoid calices (Kesling, 1967). The commensal platyceratid is commonly situated on the upper surface of the *Caryocrinites* theca in a position corresponding to that occupied on many crinoids. Based on its general morphology Sprinkle (1975) believed that *Caryocrinites* was a top layer rheophilic filter-feeder.

Caryocrinites is the only Silurian cystoid known to be involved in this commensalism, and it is the only one to possess numerous camerate crinoid morphologic characteristics. This morphologic similarity to camerates (which are the only Silurian crinoids that host platyceratids) may have been the reason that *Caryocrinites* was a suitable host for these gastropods.

SUMMARY

All Ordovician and Silurian host crinoids as well as the majority of post-Silurian hosts are camerates. The non-camerate hosts comprise only six genera of poteriocrinine inadunates and one flexible. These inadunate and flexible crinoids bear resemblance to camerates, and all three groups are thought to have been rheophilic filter-feeders. The only Silurian cystoid *(Caryoc-*

rinites) known to be a platyceratid host mimics many camerate crinoid traits. This evidence suggests that echinoderms possessing certain morphologic or behavioral characteristics of camerate crinoids were selected as hosts by platyceratids. What specific characteristics possessed by these echinoderms influenced host selectivity is uncertain, but possibly this selectivity was related to particular morphologic or behavioral adaptations associated with rheophilic feeding. The variety of tegmen and anus types exhibited by Silurian and later crinoid hosts suggests that factors other than the morphology of these features were critical in host selection.

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MICROFAUNA OF THE MIDDLE SILURIAN WALDRON SHALE, SOUTHEASTERN INDIANA

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Abstract

A distinctive microfauna developed around crinoid holdfasts on the soft-bottomed environment of the Middle Silurian Waldron Shale of southeastern Indiana. This microfauna was less diverse than the microfauna outside of the crinoid meadows. The echinoderms exerted an unknown control on the microfauna, that permitted selected foraminiferid (*Psammosphaera* and *Saccamina*) and ostracode (?*Cyrtocyprus* and *Leperditia*) genera to monopolize the micro-environment. Scolecodonts were the faunal group least affected by the presence of crinoids.

INTRODUCTION

This study examines the influence of crinoids upon the distribution of microfossils in the Middle Silurian (Wenlockian) Waldron Shale of southeastern Indiana. Most crinoids inhabiting the shallow sea during deposition of the Waldron muds possessed root systems (holdfasts) that attached to the sea bottom. The attachment device was composed of cirri and radial rootlets located at the base of the stem (Fig. 1). The animals anchored themselves by wrapping the roots around firm objects, such as brachiopods, or by attaching directly to the sea bottom. Because two species of *Eucalyptocrinites, E. crassus* (Hall) and *E. tuberculatus* (Miller and Dyer), are the most abundant crinoids in the Waldron Shale, the root systems examined in this study are assumed to be of these species (Macurda, 1968; Halleck, 1973) (Fig. 2).

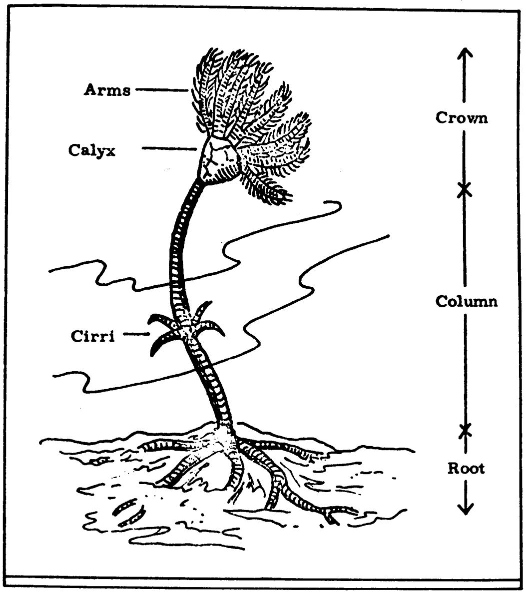

Fig. 1. Diagrammatic sketch of *Eucalyptocrinites* illustrating the basic structured parts of the animal.

According to Halleck (1973, p. 239), *Eucalyptocrinites* was so abundant locally during Waldron deposition that they formed crinoid "meadows," which, along with algal growths, acted as sediment traps. This unique environment could have a microfauna distinctive from that of adjacent areas without major crinoid beds. Furthermore, because the crinoids acted as sediment traps, the microfossils recovered from sediment around the root systems should provide a good record of the forms that existed in the

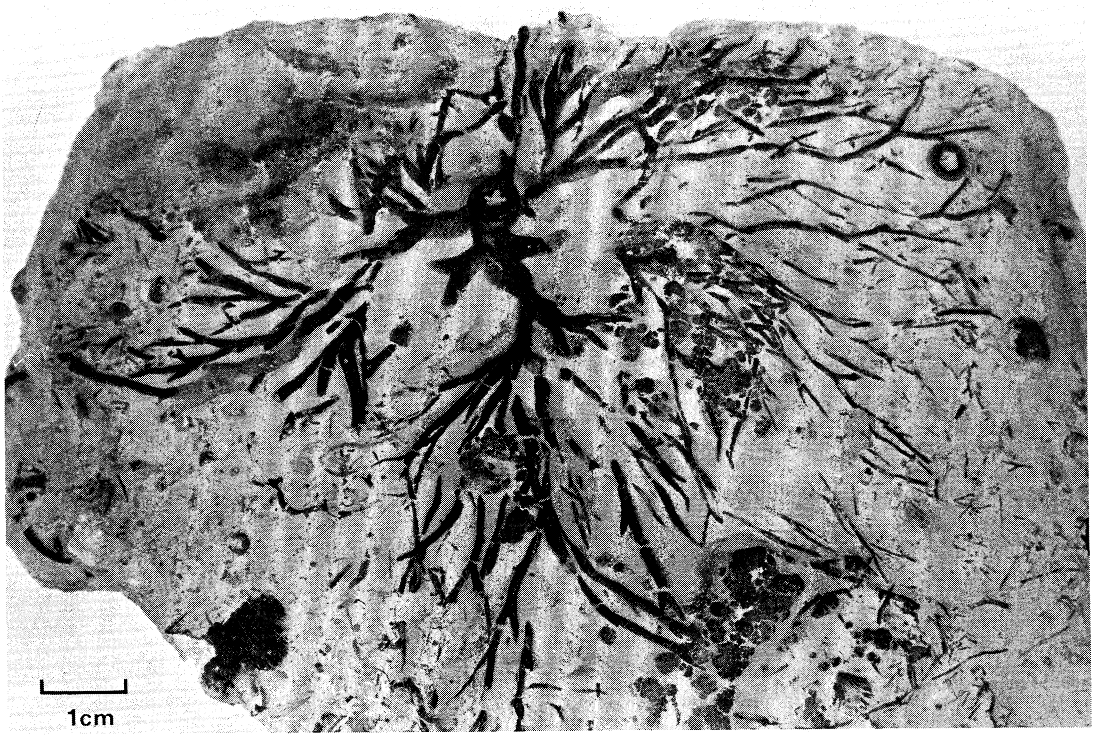

Fig. 2. *Eucalyptocrinites* holdfast or root system from the Middle Silurian Waldron Shale in southeastern Indiana. Greene Museum specimen G27371.

crinoid "meadows" at time of deposition. This study was designed to evaluate these assumptions.

Previous Investigations

The celebrated invertebrate fauna in the Waldron Shale of southeastern Indiana was first detailed in the literature by James Hall (1864). Elrod (1883) applied the name Waldron Shale to the upper part of the Middle Silurian (Wenlockian) calcareous shales cropping out in southeastern Indiana, in order to distinguish it from the underlying Laurel Limestone. Reports on the Waldron Shale during the early 1900s were completed by Price (1900), Cumings (1900), and Kindle and Barnett (1909).

Studies of ostracodes from the Waldron Shale include the work of Berry (1931), Coryell and Williamson (1936), and Morris and Hill (1951, 1952). Other paleontological work on the Waldron included foraminiferal studies by Hattin (1960) and McClellan (1966), and a study of acritarchs by Krebs (1972).

Evolution and paleoecology of the Waldron fauna were evaluated by Tillman (1962), McClellan (1966), Macurda (1968), and Halleck (1973). Macurda (1968) described the ontogenetic development of the crinoid *Eucalyptocrinites,* while Halleck (1973) studied the relations of crinoids to the existence of a hardground at the Laurel-Waldron contact.

Stratigraphy

The Waldron Shale crops out along a discontinuous, elongated strip extending from northern Indiana to western Tennessee, where it was originally called the Newsom

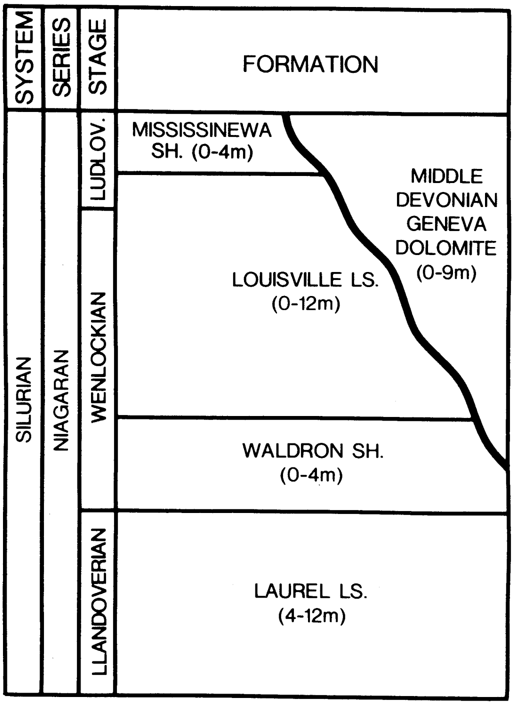

Fig. 3. Part of the Middle Silurian stratigraphic section for southeastern Indiana. The relative position of Middle Devonian Geneva, which unconformably overlies Silurian rocks, is also shown. The thickness of all units is given in meters. Modified from McClellan (1966, p. 451).

Shale. In the study area of southeastern Indiana, the Waldron Shale is generally underlain by the Laurel Limestone, and overlain by the Louisville Limestone (Fig. 3). However, at several localities, the Waldron Shale is unconformably overlain by the Middle Devonian Geneva Dolomite due to erosion during Early Devonian time. The Laurel, Waldron, and Louisville formations are all of Middle Silurian (Wenlockian) age, as established by the presence of ostracodes of the *Drepannellina clarki* zone in both the Laurel and the Waldron formations, and the presence of the brachiopod *Rhipidium* in the Louisville Limestone (Berry and Boucot, 1970).

The Waldron consists of nonresistant, blue-gray, silty shale, which is easily differentiated from resistant carbonates of the underlying Laurel or the overlying Louisville or Geneva formations (Fig. 4). The blue-gray shale pales to a buff-gray where it is weathered or more calcareous, as at Sandusky, Indiana. The parting changes from blocky to very fissile, depending on the amount of carbonate present. The Waldron is locally fossiliferous, especially where it is

Fig. 4. Waldron Shale at Tunnel Mill near Vernon, Indiana.

highly calcareous. According to Heele (1963), the shale is composed of calcite and dolomite, with lesser amounts of feldspar, illite, kaolinite, pyrite and quartz.

The Waldron varies in total thickness from 0 to 4 m, and thins to the north and east. In western exposures, the formation is about 2.5 m thick, and it reaches a maximum of 4 m near Louisville, Kentucky (McClellan, 1966).

PALEOGEOGRAPHIC SETTING

During Wenlockian time, present-day Indiana was covered by a tropical epicontinental sea with an extensive reef system. These reefs developed in the southeastern Trade Wind belt of the southern latitudes, and formed around the margins of the proto-Michigan basin and the Vincennes basin in southern Illinois and Indiana (Shaver, 1977) (Fig. 5). The Waldron muds were deposited in shallow water on the Wabash platform between the developing basins (Shaver, 1977).

METHODS

Samples

Twenty-eight of the 36 crinoid holdfasts used in this study came from the Greene Memorial Museum Collection at the University of Wisconsin-Milwaukee. These samples were purchased by Thomas A. Greene, a Milwaukee pharmacist and amateur paleontologist, from J. T. Doty, a fossil collector from Waldron, Indiana in the early 1880s. Other samples were collected from 4 expo-

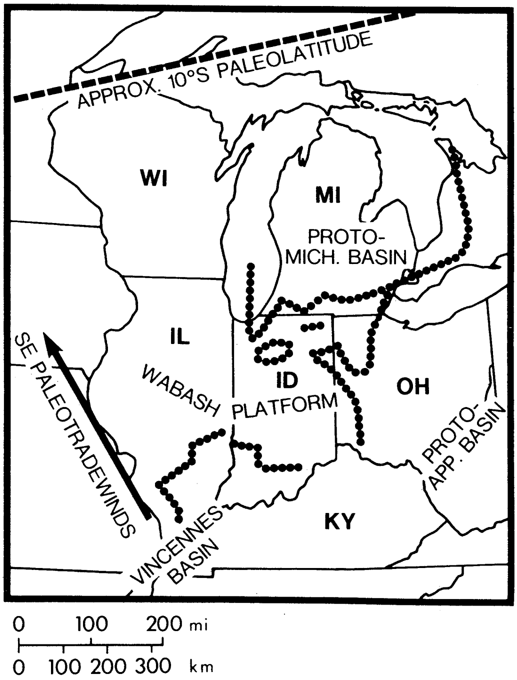

Fig. 5. Major reef systems (dotted lines) and paleogeographic features in the central Great Lakes region during the Silurian. Adapted from Shaver (1977, p. 1409 and p. 1422).

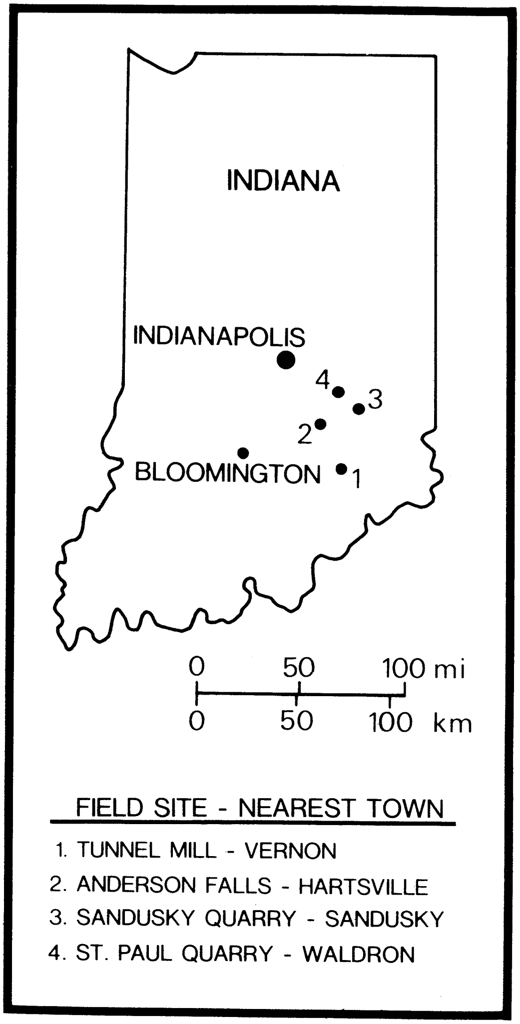

Fig. 6. Location of field localities discussed in the text.

sures of Waldron Shale in southeastern Indiana. The 4 field localities were: Tunnel Mill, Anderson Falls, Sandusky quarry, and St. Paul quarry (Fig. 6). The only 2 crinoid holdfasts found in place were collected at Tunnel Mill, although 6 displaced specimens were collected at the St. Paul quarry. Other localities provided control samples from areas where holdfasts were not present.

Laboratory Work

In order to recover microfossils, samples were crushed to approximately 3 cm prior to chemical treatment. The most satisfactory

TABLE 1. Summary of samples utilized in this study.

Holdfast Samples from Greene Museum	*Weight in Grams*
GM-1 (17744, 17745, 17750, 17754)	97
GM-2 (1162, 17743, 17751, 17755)	95
GM-3 (17746, 17747, 17748, 17753)	96
GM-4 (17741, 17749, 17752)	97
GM-5 (1008, 1660)	123
GM-6 (17758, 17762)	116
GM-7 (1630, 17756, 17757, 17759, 17760, 17761)	119
GM-8 (17740)	130
GM-9 (17742)	122
TOTAL OF 9 HOLDFAST SAMPLES FROM GREENE MUSEUM	743
Holdfast Samples Collected in the Field	
TM-4	122
SPQ-5	188
SPQ-6	56
SPQ-7	251
SPQ-8	82
SPQ-9	91
SPQ-10	33
TOTAL OF 7 HOLDFAST SAMPLES COLLECTED IN THE FIELD	823
TOTAL OF ALL 16 HOLDFAST SAMPLES	1566
Nonholdfast Samples Collected in the Field	
TM-1	300
TM-2	300
TM-3	300
AF-1	100
AF-2	300
AF-3	300
AF-4	200
SQ-1	300
SQ-2	300
SQ-3	300
SPQ-1	300
SPQ-2	300
SPQ-3 & 4	300
TOTAL OF 13 NONHOLDFAST SAMPLES COLLECTED IN THE FIELD	3600

Explanation for Table 1: GM numbers 1 through 7 are composite samples of the Greene Museum cataloged specimens listed in parentheses. There was sufficient material of Greene Museum samples 17740 and 17742 to run them separately. Indiana field sites are shown on Fig. 5. Sample locations are: TM-Tunnel Mill, AF-Anderson Falls, SQ-Sandusky quarry, and SPQ-St. Paul quarry.

disaggregation technique utilized Quaternary 0, a detergent with a good wetting character. Although Zingula (1968, p. 102) recommended a 20% solution of Quaternary 0, a concentration of 33% produced better results for samples used in this study. The disaggregated material was washed through nested sieves of 35, 60, 120, and 170 mesh. The 35 mesh fraction represented rock material that did not break down, and it was discarded. The other 3 fractions were manually picked for microfossils, although the 170-mesh fraction proved to be unfossiliferous. Over 1500 microfossils were recovered, and 1328 of these could be identified to generic level.

The size of the samples processed was dependent upon availability of material. Holdfast samples were generally limited to about 100 gm, while 300 gm of non-holdfast field samples were used. To have sufficient material to process most of the Greene Museum holdfast specimens, samples of similar lithology from the same locality were combined (Table 1).

As shown in Table 1, a total of 16 holdfast samples totaling 1566 gm was processed. Of these, 7 were composite samples. A total of 3600 gm from 13 field samples not associated with holdfasts was also processed. This disparity in sample number and amount created some problems in interpreting the results of microfauna analysis. Furthermore, the stratigraphic position of Greene Museum samples within the Waldron was unknown. Hence, the microfauna recovered must be considered to be "time averaged" in that they probably represent the accumulation of fossils throughout the time represented by deposition of the Waldron Shale.

MICROPALEONTOLOGY

Analysis

The microfossils recovered included 656 foraminifera, 443 ostracodes, 181 brachiopod fragments, 35 scolecodonts, 13 gastropods, and lesser numbers of echinoid spines, bryozoan fragments, and crinoid parts.

Sources used in the identification of the microfossils included: Coryell and Williamson, 1936; Stewart and Priddy, 1941; Morris and Hill, 1951, 1952; Hattin, 1960; Moore, 1961, 1962, 1964; McClellan, 1966; Lundin and Newton, 1970; and Glaessner, 1972. Generic identification was difficult in many cases, because a majority of the brachiopods, gastropods and ostracodes were internal casts.

Because the gastropod casts probably represent juvenile forms, no attempt was made to classify them to genera. However, the coiling pattern and shell shape were distinctive enough to infer that at least 3 genera were present. The three gastropod "form genera" were identified as "Bellerophontiform," "Conispiral," and "Planispiral" (Fig. 7).

The brachipods presented the same problem as the gastropods. Although distinctive variations in the valves were evident, the internal casts were not definitive enough to identify genera. Based on valve shape and the presence or absence of ribbing, at least three "form genera" were inferred to be present. These were designated as "Ribbed," "Spatulate," and "Sulcate" (Fig. 7).

For each sample studied, the 60 and 120 mesh fractions were analyzed individually. In general, the 120 mesh yielded relatively few microfossils and the forms were similar to those present in the 60 mesh fraction.

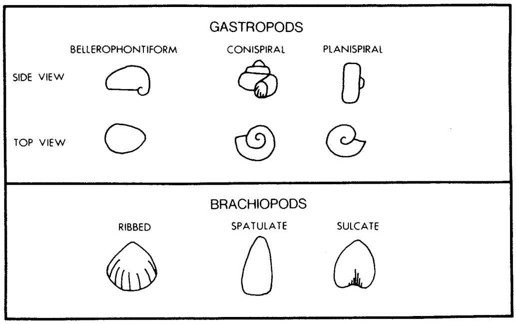

Fig. 7. "Form genera" for microbrachiopods and microgastropods described in this study.

Siemann-Gartmann (1979, p. 33-34) provided detailed counts of the microfauna for each sieve size and for each sample processed. However, this information only served to establish that all the samples processed could be combined into holdfast samples and nonholdfast samples. Table 2 provides this summary.

Abundance and Diversity

Table 2 lists the individual genera identified from the two basic lithogenetic

TABLE 2. Summary of the number of microfauna genera ("form genera" of brachiopods and gastroods) and individuals recovered from 16 holdfast samples totaling 1566 gm and 13 nonholdfast samples totaling 3600 gm. The difference in the number and weight of samples in each category must be considered in this comparison.

Holdfast Microfauna (Genera) - Individuals		*Nonholdfast Microfauna (Genera) - Individuals*	
Brachiopods (3)	61	*Brachiopods* (3)	120
Ribbed	9	Ribbed	9
Spatulate	6	Spatulate	11
Sulcate	46	Sulcate	100
Foraminifera (6)	356	*Foraminifera* (9)	300
Metamorphina	2	Hemisphaeramina	2
Psammosphaera	128	Metamorphina	7
Saccammina	222	Psammonyx	1
Sorosphaera	1	Psammosphaera	108
Sorostomasphaera	2	Saccammina	156
Webbinelloidea	1	Sorosphaera	14
		Sorostomasphaera	8
		Thurammina	2
		Webbinelloidea	2
Gastropods (2)	2	*Gastropods* (3)	11
Bellerophontiform	1	Bellerophontiform	1
Planispiral	1	Conispiral	6
		Planispiral	4
Ostracodes (10)	213	*Ostracodes* (14)	228
Bairdia	26	Bairdia	20
Beyrichia	4	Beyrichia	3
Buthocyrus	11	Bythocyrus	20
?Cyrtocyprus	97	?Cyrtocyprus	84
Entomozoe	4	Entomozoe	4
Eridochoncha	13	Eridochoncha	2
Euprimitia	4	Euprimitia	15
Halliella	2	Halliella	4
Leperditia	48	Hemiaechminoides	2
Primitia	4	Leperditia	43
		Primitia	22
		Schmidtella	3
		Thlipsuroides	3
		Waldronites	3
Scolecodonts (2)	17	*Scolecodonts* (4)	18
Arabellites	4	Arabellites	3
Nereidavus	13	Nereidavus	13
		Staurocephalites	1
		Ungulites	1
TOTAL GENERA: (23)	649	TOTAL GENERA: (33)	677

associations described above. The total genera present is also provided in this table. The holdfast samples yielded 23 genera, while 33 genera were present in nonholdfast samples. In spite of a large bias in the weight of nonholdfast samples, it seems that they contain a more diversified microfossil assemblage than the holdfast samples.

All three brachiopod "form genera" are present in the grouping of microfossil forms from both primary lithologic associations. Since more than twice as much nonholdfast material was processed, it seems that microbrachiopods were present in essentially equal numbers in the two groups under study. In both instances, the most common brachiopod form was the "Sulcate."

All six genera of foraminifera which are present in the holdfast samples are also present in the nonholdfast samples. Although 3 more genera are present in the latter lithologic association, they are represented by only 5 specimens. Although the foraminiferal fauna is dominated by *Psammosphaera* sp. and *Saccammina* sp. in both associations, it is more abundant with holdfasts. When one considers the biased sampling against holdfast lithologies, this difference is given more significance. Other foraminiferal genera common to both lithologic associations are lower in total number of individuals per genus in the holdfast samples. However, the total number of foraminifera individuals is still higher in holdfast samples (356) than in nonholdfast rocks (300). This indicates that the holdfasts contain more foraminifera, although the fauna was less diverse, than the samples without holdfasts.

Only two of the gastropod "form genera" were found in association with holdfasts, and these were each represented by only one specimen. Eleven gastropods representing 3 "form genera" were identified from nonholdfast samples.

Holdfast samples contained only 10 of the 14 ostracode genera recovered during this study. Of these 10 genera, 5 (*Bairdia, Beyrichia, ?Cyrtocyprus, Eridochoncha* and *Leperditia*) occurred in greater numbers than in the nonholdfast control samples, and one (*Entomozoe*) was represented by 4 specimens in each rock type. The total number of individual ostracodes recovered was 213 from holdfast samples and 230 from nonholdfast rocks. However, these numbers are misleading if one does not consider that approximately 2.3 times more nonholdfast rock was processed.

Two genera of scolecodonts were found in holdfast material, whereas four genera were recovered from nonholdfast samples. However, the 2 unique genera were each represented by a single specimen. The two scolecodont genera, *Arabellites* and *Nereidavus,* that occur in both sample types are present in almost equal numbers. Furthermore, the total number of scolecodonts is similar in both associations (17 in holdfast samples and 18 in nonholdfast rocks). Once again, if sample bias is considered, the holdfast samples are characterized by more individual scolecodonts, but fewer genera.

The holdfast and nonholdfast faunas described above were tested with the Shannon index, which provides a measure of diversity for nominal scale data. The Shannon index for each group was then utilized to determine relative diversity of each group (Zar, 1974, p. 35). These tests verified the apparent diversity differences noted in a visual examination of Table 2. Although both faunas have a moderately high diversity, the holdfast fauna is relatively less diverse.

INTERPRETATION

When I began this study, I presupposed that the microfauna associated with crinoid holdfasts would be more diverse and abundant than the control fauna. This assumption was based on the view that the Waldron crinoids supposedly lived in well-circulated marine waters with a constant supply of food. Such an environment should also allow a diverse microfauna to flourish. Furthermore, I visualized effective entombment of these organisms upon death because the crinoids, along with algal mats, would act as effective sediment traps (Halleck, 1973; Abbott, 1975). My conceptual model was only half right. As previously described, the microfauna associated with the crinoid holdfasts is more abundant, than with nonholdfast rocks, but it is less diverse.

The percentage of each faunal group present in the total microfossil assemblage in the holdfast and nonholdfast samples is summarized in Table 3. Based on these figures, it is evident that brachiopods are relatively less abundant in association with holdfasts than they are in nonholdfast rocks. More than half (54.9%) of the microfauna associated with holdfasts consists of foraminifera, while they comprise only 44.1% of the microfauna in nonholdfast rocks. Gastropods are a minor element in both microfaunas, but they are more abundant in nonholdfast samples. Ostracodes made up approximately one third of all the microorganisms in both holdfast and nonholdfast groups. Scolecodonts are present in equal percentages in both rock types.

TABLE 3. Percentage of microfaunal groups in holdfast and nonholdfast samples utilized in this study.

	Holdfast	*Nonholdfast*
Brachiopods	9.4%	17.7%
Foraminifera	54.9%	44.1%
Gastropods	.3%	1.6%
Ostracodes	32.8%	33.9%
Scolecodonts	2.6%	2.7%
Total	100.0	100.0

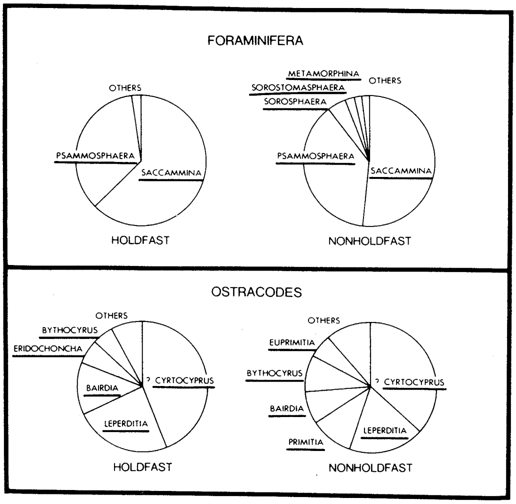

Fig. 8. Percent of genera for the foraminifera and ostracode faunal groups.

As described above, the foraminifera constitute 54.9% of holdfast samples, and 98.2% of this fauna is composed of two genera, *Psammosphaera* (35.9%) and *Saccammina* (62.3%) (Fig. 8). The remaining 1.8% includes four genera (*Metamorphina, Sorosphaera, Sorostomasphaera,* and *Webbinelloidea*). Foraminifera make up 44.1% of the microfauna of nonholdfast samples, with five genera constituting 97.5% of the fauna. These genera are *Psammosphaera* (36%), *Saccammina* (52%), *Sorosphaera* (4.7%), *Sorostomasphaera* (2.7%) and *Metamorphina* (2.3%) (Fig. 8). The remaining 2.4% consist of the following genera: *Hemisphaeramina, Psammonyx, Thurammina* and *Webbinelloidea.*

Although the percentage of ostracodes in both groups is similar, the relative amounts of the genera represented are different. Genera present in holdfast samples consist of *?Cyrtocyprus* (45.5%), *Leperditia* (22.5%), *Bairdia* (12.2%), *Eridochoncha* (6.1%), and *Bythocyrus* (5.2%) (Fig. 8). These 5 genera represent 91.5% of the ostracode fauna, while the remaining 8.5% consists of *Beyrichia, Entomozoe, Euprimitia, Halliella,* and *Primitia.*

In nonholdfast samples, 88.7% of the ostracode fauna is composed of six genera. These are: ?*Cyrtocyprus* (36.5%), *Leperditia* (18.7%), *Primitia* (9.6%), *Bairdia* (8.7%), *Bythocyrus* (8.7%), and *Euprimitia* (6.5%) (Fig. 8). The remaining 11.3% consists of the following nine ostracode genera: *Beyrichia, Entomozoe, Eridochoncha, Halliella, Hemiaechminoides, Schmidtella, Thlipuroides,* and *Waldronites.* The two most abundant ostracode genera, ?*Cyrtocyprus* and *Leperditia,* comprise 68% of the total ostracode fauna in the holdfast samples compared with only 55% in nonholdfast rocks (Fig. 8).

Two foraminifera genera (*Psammosphaera* and *Saccammina*) and two ostracode genera (?*Cyrtocyprus* and *Leperditia*) dominate the microfauna. These forms may have been generalists, who occupied an environment that was not highly specialized. Since the 4 taxa listed above comprise 76.3% of the total population of microorganisms present in the holdfast assemblage, this might indicate the environment associated with the crinoid roots was not partitioned into narrow ecological niches which would have favored a wider range of microorganisms. Once established in this nonspecialized environment, generalists would flourish and probably crowd out other genera. Hence, environmental factors favoring a large population of nonselective microorganisms could explain the lower diversity previously described. However, it may be that the most abundant taxa were merely better adapted to the environment associated with the holdfasts.

It is also possible the crinoids themselves were responsible for lower diversity in the microfauna associated with the holdfasts. Watkins and Hurst (1977) constructed a model of crinoid ecology for the Middle Silurian Wenlock Limestone of Dudley, England. These workers concluded that crinoids affected the associated fauna by their high-level suspension feeding habits. A dominance of crinoids resulted in "high crinoid species diversity, partitioning of planktonic resources, and maintenance of suspension feeding height over other fauna" (Watkins and Hurst, 1977, p. 216). Lane (1973), who reported on Carboniferous crinoids from Crawfordsville, Indiana, arrived at similar conclusions in a study that focused on a depositional environmental receiving terrigenous sediment.

According to Watkins and Hurst (1977), one key to the successful dominance of the crinoids was their diversity, which allowed for stratified feeding heights. Although species diversity in crinoids of the Waldron Shale was probably inhibited by the soft bottom environment, they may have exerted some control on the associated microfauna.

Size comparisons between the holdfast and nonholdfast foraminifera and ostracodes do not indicate that crinoids selectively filtered out some forms for food. Furthermore, the rooted crinoids would feed well above the level of the substrate where the microfauna lived (Fig. 1).

The scolecodonts were the faunal group that appears to be least affected by the presence of crinoids. These microfossils are the jaws of worms that inhabited the substrate at least part of the time, and this would minimize any influence by crinoids.

Based on the discussion above, there is a difference between the microfaunas associated with holdfast and nonholdfast samples. However, my work does not establish what caused this difference. Certainly the controls are somehow related to the presence of crinoids, or crinoid holdfasts.

CONCLUSIONS

This study establishes that the microfauna associated with crinoid holdfasts in the Middle Silurian Waldron Shale of southeastern Indiana is distinctive from control samples not associated with holdfasts. The crinoid holdfast microfauna is characterized by a large percentage of foraminifera and ostracodes. A small percentage of the microfauna is composed of brachiopods, scolecodonts and gastropods. A total of only 23 genera represents the five faunal groups present in the crinoidal microfauna, whereas 33 genera are present in the same 5 faunal groups in nonholdfast samples. Thus, the holdfast faunal assemblage is characterized by a relatively abundant microfauna with lower diversity than that recovered from the control samples.

Crinoids, or crinoid holdfasts, exerted an unknown controlling influence over the microfauna, although several possibilities are discussed. The genera that make up 76.5% of the crinoidal microfauna were *Psammosphaera* and *Saccammina* (foraminifera), and ?*Cyrtocyprus* and *Leperditia* (ostracodes). The only faunal group that was not significantly affected by the rooted crinoids were the scolecodonts. These conclusions support the findings of Watkins and Hurst (1977), who also concluded that crinoids exerted a control on the associated fauna.

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EVOLUTION OF A BIOSTRATIGRAPHIC ZONATION; LESSONS FROM LOWER TRIASSIC CONODONTS, U.S. CORDILLERA

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Abstract

Condonts have exceptional value as biostratigraphic tools, and more than 100 conodont biozones are recognized in Ordovician through Triassic rock. They facilitate correlation in Triassic strata where stratigraphically significant ammonoids are rare or absent. A biostratigraphic zonation for the entire Triassic System was first developed in 1971 by integrating parts of a Lower Triassic zonation developed in West Pakistan with zonations from the Cordillera of the western United States.

Conodonts were considered to be 'facies breakers,'' and paleoecologic influences were not recognized in the Great Basin and Middle Rocky Mountains by many earlier workers. This resulted in a number of proposed modifications for the Smithian Stage. Additional conodont biostratigraphic studies extended the total ranges of some conodont species and eliminated the utility of several overlapped biozones. As regional biostratigraphic work on Lower Triassic conodonts continued, it became apparent that simplification of the zonal scheme would make it more useful in a variety of marine depositional environments on a worldwide basis, if the spirit of Albert Oppel's ''ideal profile'' were followed.

Lower Triassic conodont biozones are based on: *Hindeodus typicalis* for the Griesbachian Stage, *Neospathodus kummeli* and *Neospathodus dieneri* for the Dienerian Stage, and *Neospathodus waageni* for the Smithian Stage. The uppermost Early Triassic Spathian Stage biozones are based on: *Neospathodus triangularis, Neospathodus collinsoni, Neogondolella jubata,* and *Neospathodus timorensis.*

The refined Lower Triassic zonation presented here is a progress report that extends the generic ranges of *Gladigondolella* and *Platyvillosus* downward into the Smithian. Further biostratigraphic studies will modify this contemporary effort, as total ranges of zone diagnostic conodonts are ultimately defined.

INTRODUCTION

Conodonts were widespread in early oceans for a span of 400 million years, from the latest Precambrian or earliest Cambrian into the latest Triassic (Sweet and Bergström, 1981). Their resistant, phosphatic, microskeletal components, while providing very limited clues as to the biologic nature of the conodont animal, possess exceptional value as biostratigraphic tools.

Conodonts were probably small (up to several centimeters in greatest dimension), bilaterally symmetrical, free-moving organisms which occupied pelagic to benthic marine environments. A recently described, elongate, soft-bodied animal with an apparatus of conodont elements, apparently in place, shows similarities to both chordates and chaetognath marine worms (Briggs and others, 1983). The microscopic elements served as teeth or as supports for respiration or feeding activities, and were embedded in, or covered by, fleshy tissue (Bengston, 1976; Jeppsson, 1979; Clark, 1981a). After death, these carbonate-apatite structures became dissociated, so natural assemblages of hard parts are rare. Crushing and processing rock for recovery of conodonts further isolate individual elements.

Within the past 35 years, coincident with the use of the acetic acid method for dissolution of carbonate rocks, conodont study accelerated and the literature burgeoned. Work during this period focused primarily upon the stratigraphic distribution of diagnostic forms. As a result, more than 100 conodont biostratigraphic units are recognized from Ordovician through Triassic rock (Sweet and Bergström, 1981).

The widespread occurrence of conodonts in diverse lithologies led to the general belief that they were largely independent of environmental influences, and stratigraphers envisioned a universal spread of individual taxa in marine environments. The same species were observed, for example, in Ordovician lithofacies that included shelly shelf limestone, black graptolitic shale, and deep water chert-shale sequences containing sponge spicules and radiolaria. The ubiquitous nature of some forms prompted an unnamed geologist to remark that "Conodonts are like God—they are everywhere" (Lindström, 1976).

By 1950, conodont faunas from Ordovician through Permian rocks were described for the United States. Müller (1956) described the first fully-documented North American Lower Triassic conodont fauna from strata in Nevada. Clark (1957) pioneered the use of conodonts to establish the Triassic age for marine strata in the eastern Great Basin. However, documentation of Triassic conodonts lagged behind Paleozoic efforts. Factors contributing to this situation include the limited areal extent of marine Triassic rocks, the remote, often desolate, character of the Great Basin outcrop area, the limited abundance of most Lower Triassic conodont faunas, and a small number of persistent workers. Apparently, the paucity of knowledge about the Triassic in the western United States is only part of a worldwide problem, for Derek Ager states, "Much is hidden in the mists of the early Triassic, which is probably the least known episode in the long history of Phanerozoic time" (1981, p. 99).

Conodont faunas of both the Late Permian and Early Triassic lack diversity, but include distinctive forms. An evolutionary crisis in Early Permian time eliminated many long-ranging Paleozoic taxa, and only four or fewer major superfamilies survived (Clark, 1972; Sweet, 1973; Sweet and Bergström, 1981). The cosmopolitan nature of Lower Triassic marine faunas reflects the assembly of a single supercontinent, with the Pacific and Tethyan oceans forming a continuous water body around the shores of Pangaea (Valentine and Moores, 1973).

BIOZONES AND CORRELATION

Worldwide biostratigraphic zonation and correlation of Permian and Triassic marine rocks are historically based on ammonoid faunas, which are arranged in a standard succession. In North America, at least 35 ammonoid zonal units provide a biostratigraphic framework for the marine Triassic (Silberling and Tozer, 1968). Although ammonoids were widely distributed in late Paleozoic and Mesozoic seas, they are rare fossils in many geographic areas. More recently, conodonts were used to facilitate or refine correlation where ammonoids are scarce or absent (Clark and Behnken, 1971; Sweet and others, 1971).

Regardless of the fossil content utilized, the purpose of biostratigraphic zonation is to provide a means by which the relative timing of biologic and geologic events can be determined and correlated on a worldwide basis. These biozones must necessarily have time significance, and may involve evolutionary changes, migrations, and extinctions (Eicher, 1968).

Three principal categories of biostratigraphic units are used, depending upon circumstances and available fauna (North

American Commission on Stratigraphic Nomenclature, 1983). However, range (interval) zones of various types are the most widely employed. Interval zones are defined by the lowest and/or highest, documented occurrences of less than three taxa (Fig. 1). They include: the interval between the lowest and highest occurrences of a single taxon (taxon range zone), the interval between the lowest occurrence of one taxon and the highest occurrence of another taxon (concurrent range zone or partial range zone), or the interval between successive lowest or highest occurrences of two taxa (lineage zone or interval zone). Unfossiliferous intervals are also recognized between or within biozones (barren interzones and intrazones).

An assemblage zone is characterized by the association of three or more taxa, and in practice, two different concepts are used

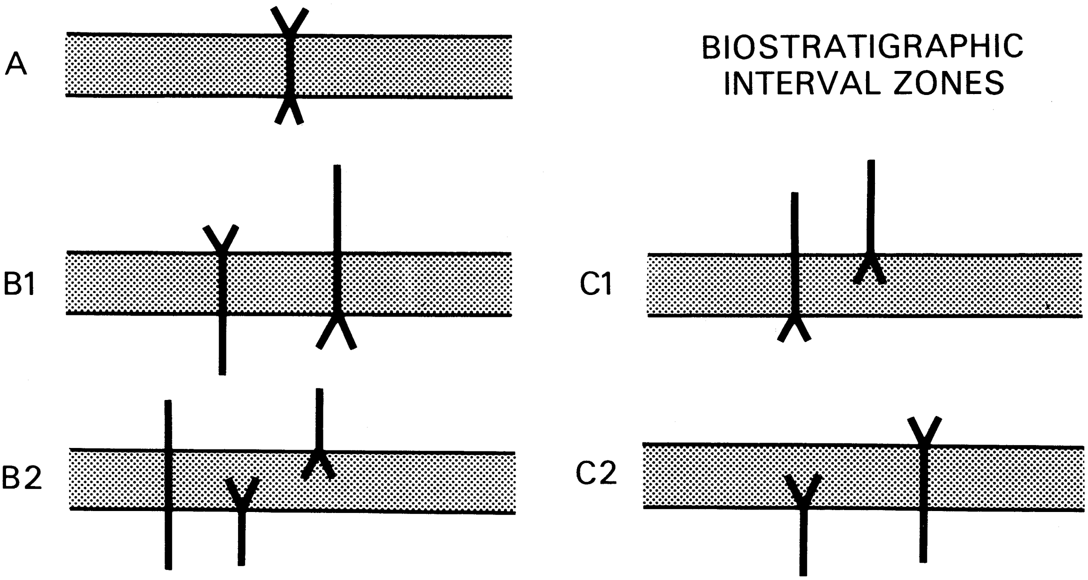

Fig. 1. Biostratigraphic interval zones, as defined by the North American Commission on Stratigraphic Nomenclature (1983). Examples include: A) taxon range zone, B1) concurrent range zone, B2) partial range zone, C1) lineage zone, C2) interval zone.

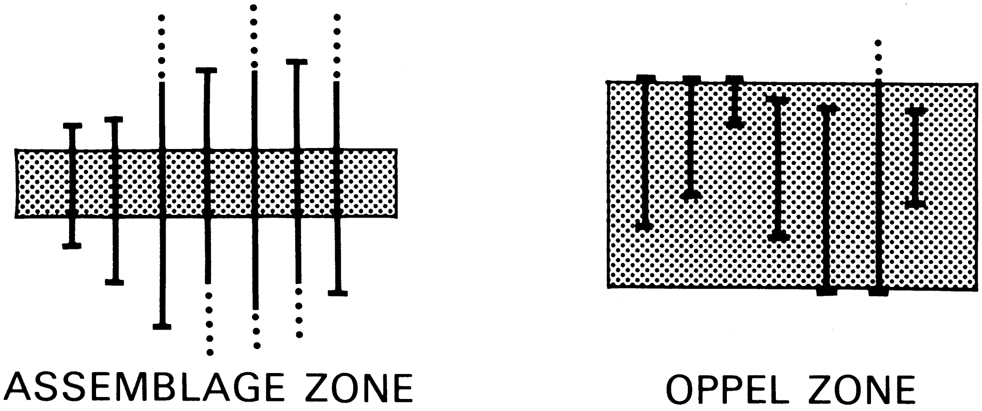

Fig. 2. Assemblage zones, as defined by the North American Commission on Stratigraphic Nomenclature (1983). Examples include: Left) assemblage zone, not based upon the ranges of the included species; Right) Oppel zone, a concurrent range zone defined by more than two taxa.

(Fig. 2). One, the assemblage zone, is characterized by a certain association of taxa without regard to their range limits. The second type is an Oppel zone, with boundaries based on two or more documented, first and/or last occurrences of the taxa characterizing the zone. This is also a form of concurrent range zone.

The third category, or abundance zone, is characterized by quantitatively distinctive maxima of relative abundance of one or more taxa (Fig. 3). This is the acme zone of the International Subcommission on Stratigraphic Classification (Hedberg, 1976).

Although all fossils, in a general sense, may be considered "facies fossils" (Ager, 1981), some assemblage and abundance biozones may reflect strong local ecologic control, and are not necessarily time significant. The appearance of the included taxa in these cases may be due to the shift or return of favorable, or optimal environmental conditions within a geographic area.

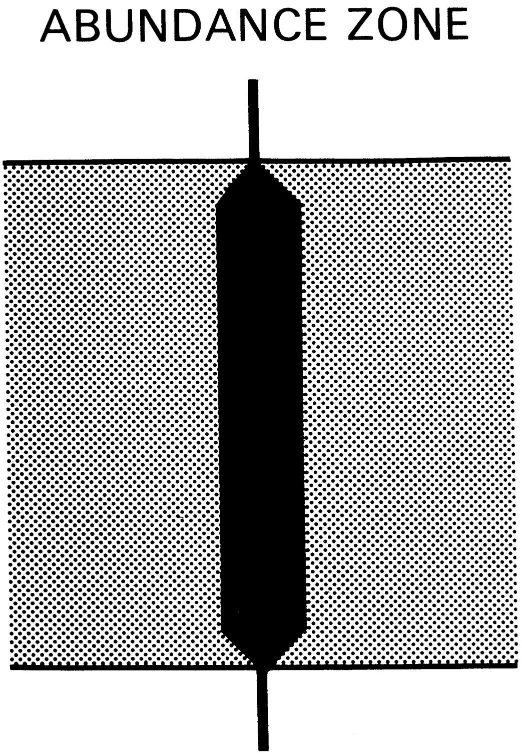

Fig. 3. Abundance zone, as defined by the North American Commission on Stratigraphic Nomenclature (1983). This biozone is based on a marked increase in abundance of the defining taxon or taxa.

Whether based on the range of a single taxon or of a specific combination of taxa, a biozone conceptually includes all the rocks deposited anywhere during the entire time the defining taxon or taxa existed (total range), whether their remains are recognized or not. Most local range zones (teilzones) are only fragments of the total taxon/taxa record. The development and application of biozones were elegantly detailed in 1856 by young Albert Oppel during his study of Jurassic biostratigraphy. Oppel visualized the general succession of fossils as independent of the actual paleontologic or lithic succession at any one place (Hancock, 1977). In discussing correlation based on fossil content, Oppel observed:

> "This task is admittedly a hard one, but it is only by carrying it out that an accurate correlation of a whole system can be assured. It necessarily involves exploring the vertical range of each separate species in the most diverse localities, while ignoring the lithological development of the beds; by this means will be brought into prominence those zones which, through the constant and exclusive occurrence of certain species, mark themselves off from their neighbours as distinct horizons. In this way is obtained an ideal profile, of which the component parts of the same age in the various districts are characterised always by the same species" (translation in Hancock, 1977, p. 12).

The search for the "ideal profile" became the aim of all biostratigraphers who followed.

LOWER TRIASSIC CONODONT ZONATION

Early Zonations

Müller (1956) first suggested the possibility of establishing a time-significant, conodont biostratigraphic succession within the Triassic, and Clark (1960), Mosher and Clark (1965), and Mosher (1968) identified preliminary sequences. The first extensive Lower Triassic zonal scheme based on

LOWER TRIASSIC	SPATHIAN	9 Neospathodus timorensis
		8 Neogondolella jubata
	SMITHIAN	7 Neospathodus waageni
	DIENERIAN	6 Neospathodus pakistanensis
		5 Neospathodus cristagalli
		4 Neospathodus dieneri
		3 Neospathodus kummeli
	GRIESBACHIAN	2 Neogondolella carinata
		1 Anchignathodus typicalis

Fig. 4. Lower Triassic conodont zonation of Sweet (1970), based on specimens from the Salt and Trans-Indus ranges of West Pakistan.

SERIES		STAGE
LOWER TRIASSIC	SCYTHIAN	SPATHIAN
		SMITHIAN
		DIENERIAN
		GRIESBACHIAN

Fig. 5. Lower Triassic stage names for North America.

LOWER TRIASSIC	SPATHIAN	13 Neospathodus timorensis	GREAT BASIN
		12 Neogondolella jubata	
		11 Neospathodus n. sp. G	
		10 Platyvillosus	
	SMITHIAN	9 Neogondolella milleri	
		8 Neospathodus conservativus	
		7 Parachirognathus-Furnishius	
	DIENERIAN	6 Neospathodus pakistanensis	PAKISTAN
		5 Neospathodus cristagalli	
		4 Neospathodus dieneri	
		3 Neospathodus kummeli	
	GRIESBACHIAN	2 Neogondolella carinata	
		1 Anchignathodus typicalis	

Fig. 6. Lower Triassic conodont zonation of Sweet and others (1971), combining data from West Pakistan and the Great Basin of the western United States.

conodonts was provided by Sweet (1970) from the uppermost Permian and Lower Triassic of West Pakistan (Fig. 4). The Lower Triassic was divided into nine zones based on the vertical distribution of six genera, with the oldest zone spanning the Permian-Triassic boundary (Sweet, 1970). Five of the zones were also represented in Triassic collections from Europe and North America, but four were of utility only in West Pakistan. Figure 5 provides series and stage names for the Lower Triassic.

A cooperative effort by North American conodont workers led to the development of a biostratigraphic zonation for the entire Triassic System (Sweet and others, 1971) (Fig. 6). Thirteen Lower Triassic conodont zones were established, and correlated with the ten North American ammonoid zones of Silberling and Tozer (1968). The type strata for the lower Scythian zones are in the Salt and Trans-Indus ranges of West Pakistan. Type localities for all but the topmost upper Scythian zones are in the Great Basin of the western United States (Sweet and others, 1971).

Continuity between the Pakistan and Great Basin portions was not immediately confirmed, although some conodont species were common to both regions. Diagnostic Salt Range forms, such as *Neospathodus pakistanensis* of zone 6, underlying the suture, had not been found in the Great Basin, while *Neospathodus waageni* of zone 7 was not yet reported from the *Parachirognathus-Furnishius* Zone of North America (Figs. 4 and 6) (Sweet and others, 1971).

The *Parachirognathus-Furnishius* interval of Sweet and others (1971) was based on work in Utah and Nevada, and it forms the lowest zone of the North American part of the combined zonation (Fig. 6). This dual assignment was based on the suspicion that, "there may be a facies relationship between *Furnishius*- and *Parachirognathus*-bearing strata" (Sweet and others, 1971, p. 452). To evaluate this concern, *Parachirognathus-Furnishius* ratio studies were conducted along the margin of the Lower Triassic seaway. The paleoecologic work of Clark and Rosser (1976) assumed a basin to shelf transect from the deeper parts of the Cordilleran geosyncline on the west to progressively shallower marine environments to the east, where terrigenous red beds intertongue with marine sediments. Regional stratigraphic work (Koch, 1976; Collinson and Hasenmueller, 1978; Paull, 1980; Carr and Paull, 1983), however, established that the geographic distribution of sections sampled by Clark and Rosser (1976) was biased toward the shelf (shallow transitional) environment (Fig. 7). Although their western sections are thicker than those to the east, this did not mean deeper water, and a true basin to shelf survey was not made.

The upper Scythian conodont biostratigraphy reported by Solien (1979) from Fort Douglas, Utah, was in the same relative basin to shelf position and had a depositional environment similar to the sections used by Clark and Rosser (1976). Progressive changes in the vertical distribution of *Furnishius* and *Parachirognathus* in this single section were included in a modified zonation proposed by Clark and others (1979) (Fig. 8).

Solien (1979) recovered *Neospathodus pakistanensis* from the lower part of his sequence, finally forging the link between Pakistan and the Great Basin. *N. pakistanensis* was also conditionally reported by Clark and others (1979) from southern Idaho. Solien's study, was well as the work of Collinson and Hasenmueller (1978), also confirmed the occurrence of *Neospathodus waageni* with the *Parachirognathus-Furnishius* fauna of western North America (Fig. 4 and 6).

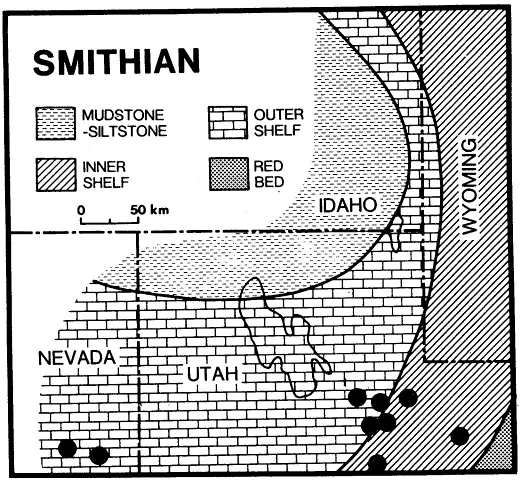

Fig. 7. Lithofacies map of the Lower Triassic during the Smithian Stage. Dots represent study localities of Clark and Rosser (1976) and Solien (1979).

COMPARISON OF LOWER AND MIDDLE SCYTHIAN CONODONT ZONATIONS					
STAGE	FROM: SWEET, 1970	FROM: SWEET AND OTHERS, 1971	FROM: CLARK AND OTHERS,1979	FROM: COLLINSON AND HASENMUELLER, 1978	THIS PAPER
SMITHIAN	NEOSPATHODUS WAAGENI	NEOGONDOLELLA MILLERI NEOSPATHODUS CONSERVATIVUS PARACHIROGNATHUS-FURNISHIUS	NEOGONDOLELLA MILLERI PARACHIROGNATHUS ETHINGTONI PARACHIROGNATHUS-FURNISHIUS FURNISHIUS TRISERRATUS	NEOSPATHODUS WAAGENI FURNISHIUS TRISERRATUS	NEOSPATHODUS WAAGENI
DIENERIAN	NEOSPATHODUS PAKISTANENSIS N. CRISTAGALLI N. DIENERI N. KUMMELI	NEOSPATHODUS PAKISTANENSIS N. CRISTAGALLI N. DIENERI N. KUMMELI	NEOSPATHODUS SPP. NEOSPATHODUS PECULIARIS	NEOSPATHODUS DIENERI NEOSPATHODUS KUMMELI	NEOSPATHODUS DIENERI NEOSPATHODUS KUMMELI
GRIESBACHIAN	NEOGONDOLELLA CARINATA ANCHIGNATHODUS TYPICALIS	NEOGONDOLELLA CARINATA ANCHIGNATHODUS TYPICALIS	NEOGONDOLELLA CARINATA ANCHIGNATHODUS TYPICALIS	HINDEODUS TYPICALIS	HINDEODUS TYPICALIS

Fig. 8. Comparison of Lower and Middle Scythian conodont zonations.

It is instructive to compare the three zonations at this point (Fig. 8). The initial scheme of Sweet (1970) utilizes a single Smithian zone, and six lower Scythian intervals. With the compilation of the 1971 biostratigraphy, the lower zones were retained. However, the Smithian was subdivided and tailored to the Great Basin, where the stratigraphic value of *Neospathodus waageni* had not yet been realized.

The zonation of Clark and others (1979) reflects Smithian conodont distributions in transitional despositional environments (Fig. 8). Dienerian biozones, although still based on neospathodids, were reduced in number, when compared to the scheme of Sweet and others (1971). This change reflects the limited abundances and diversity of conodont faunas from the Lower Triassic Dinwoody Formation.

Paleoecologic Influences

Most early workers believed that the conodont animal was nearly independent of depositional facies. Yet, as additional distributional data were collected, it became apparent that at least some conodont taxa were prone to ecologic control. Recognition of paleoecologic patterns led to a symposium focused on conodont paleoecology, and two opposing models of marine lifestyle were proposed. Seddon and Sweet (1971) envisioned a depth-stratified, pelagic existence, while Barnes and Fahraeus (1975) suggested lateral variation of biofacies reflected a nektobenthic or benthic habit. However, a cautionary note was introduced by Klapper and Barrick (1978), who found that distributional data alone were not definitive of a pelagic or a benthic habit for these extinct organisms. Development of parallel zonations for major Triassic facies was suggested as a way to avoid some paleoecologic pitfalls (Sweet and Bergström, 1981; Clark, 1981b). This would allow the use of two or more semi-"ideal profiles."

The sedimentological history of the upper, or Dienerian, part of the Dinwoody Formation was one of progressive progradation from a shelf region to the east (McKee and others, 1959). As terrigenous sediments encroached basinward, the environment was not favorable to the conodont animal. Also, the rate of Dienerian sedimentation was probably rapid. Observations indicate that conodont numbers, as well as general faunal abundance, decrease with increasing rates of sedimentation (Lindström, 1964; Kidwell, 1981). Other factors adversely affecting the presence and diversity of conodonts during this time include evolution, extinction, and migration. All of these items influence current attempts to refine the zonation of the Dienerian Stage in the western United States.

Paleoenvironmental work supported by quantitative efforts continues. Two recent studies of the spatial distribution of conodonts in the Lower Triassic Thaynes Formation of the western Cordillera distinguished three discrete biofacies (Carr, 1981; Carr, Paull, and Clark, 1983). As a result, conodont species with little facies dependence, and more temporal significance, were identified. Amalgamation of this type of research with stratigraphic distribution studies should enhance the biostratigraphic utility of conodonts, and improve further zonal subdivisions.

Proposed Zonation

Continued biostratigraphic and petrographic work in the western Cordillera resulted in increased understanding of Early Triassic depositional history and paleogeography, and the conodont biozonation was again modified. Collinson and Hasenmueller (1978) suggested a zonation reminiscent of Sweet's original (1970) version (Fig. 8). Additional regional studies (Paull, 1980; Carr and Paull, 1980; Carr, 1981; Paull, 1982; Carr and Paull, 1983) established a workable zonation from basin to shelf that resulted in additional reduction in biozones (Fig. 8).

With this simplified zonation, what was done in the name of *refinement?* The philosophy behind Shaw's (1964) graphic method, which has the potential for a detailed and more quantitative correlation, may provide some insight. In order to arrive at a composite standard reference section, the technique seeks the maximum stratigraphic range for each taxon used, despite local environmental influence or poor preservation (Miller, 1977).

Refinements in correlation may proceed in one of two directions as additional studies are conducted. If the fauna is large and diverse, the result should be a sequence with greater resolving power and a corresponding increase in significant biozones. If the fauna is modest and of limited diversity, biostratigraphic refinement consists of extending the local stratigraphic ranges of faunal elements toward their maximum values. As a result, zonal units may be eliminated (Fig. 9).

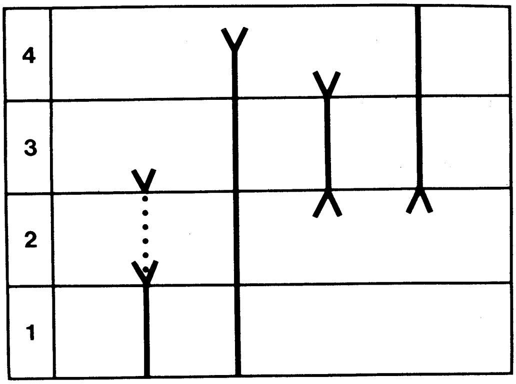

Fig. 9. Extension of range, depicted by dotted line, results in deletion of zone 2, previously a partial range zone.

This latter situation describes the evolution of Lower Triassic conodont zonation. Extension of the local ranges of species resulted in the deletion of the *Neogondolella*

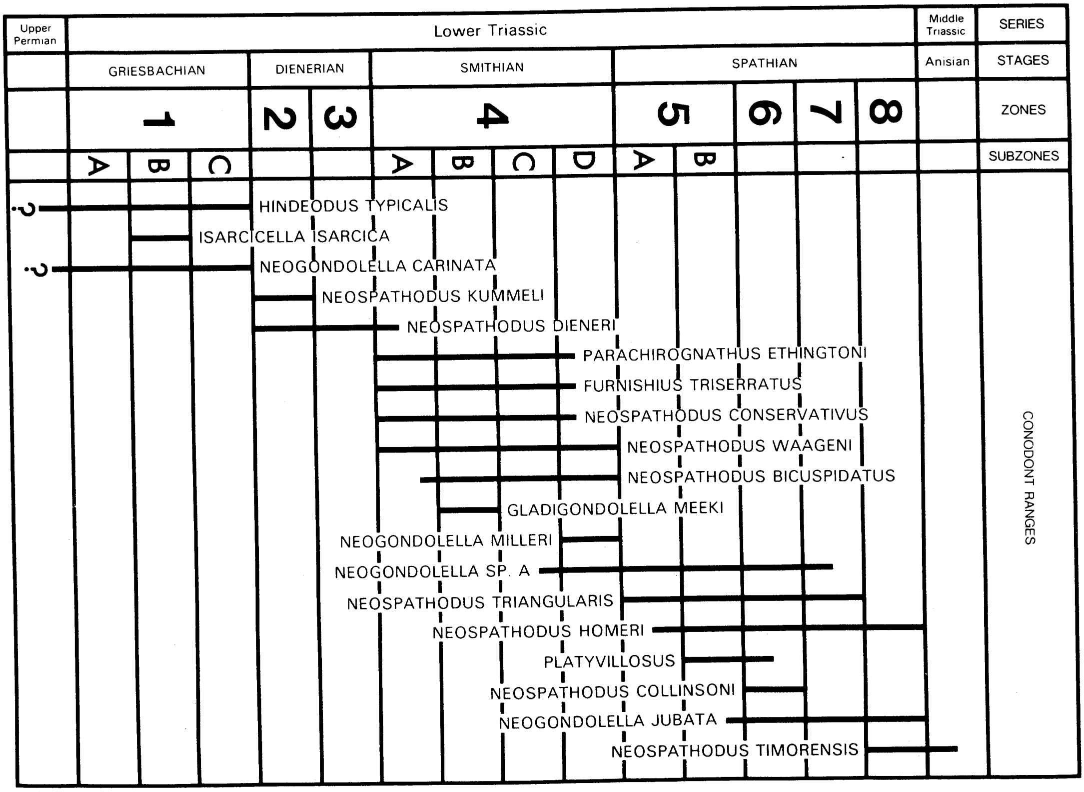

Fig. 10. Lower Triassic conodont zonation of Carr and Paull (1983).

carinata Zone (Sweet, 1973, 1979; Collinson and Hasenmueller, 1978), the *Neospathodus conservativus* Zone (Collinson and Hasenmueller, 1978; Solien, 1979), the *Parachirognathus ethingtoni* Zone (Collinson and Hasenmueller, 1978), and the *Furnishius triserratus* Zone (Paull, 1980, 1982) (Fig. 8). Solien (1979) and Clark and others (1979) recommended expansion of the *Parachirognathus-Furnishius* Zone of Sweet and others (1971), but retained these conodonts as zonal indicators (Fig. 8).

In conclusion, the zonation proposed in Figure 10 is a progress report, and the following facts suggest that the biozones will change again.

1) *Gladigondolella,* a stranger to North America, makes a Smithian appearance. This genus was previously known only from the Middle and Upper Triassic of Europe and Asia (Paull, 1982, 1983) (Fig. 10).
2) *Platyvillosus costatus,* a lower Spathian indicator, is reported with Smithian forms (Goel, 1979; Wang, 1980; Paull, in prep.) (Fig. 10).

With these observations in mind, and others that undoubtedly will be made, one is impressed with the wisdom often attributed to Mark Twain, when he noted: "Researchers have already cast much darkness on the subject, and if they continue their investigations, we shall soon know nothing at all about it." Nevertheless, the search for the ultimate Lower Triassic zonation goes on.

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CONODONTS AND BIOSTRATIGRAPHY OF THE MUSCATATUCK GROUP (MIDDLE DEVONIAN), SOUTH-CENTRAL INDIANA AND NORTH-CENTRAL KENTUCKY

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Abstract

Eighty-two samples were collected and processed for conodonts from strata of the Middle Devonian Muscatatuck Group of south-central Indiana and north-central Kentucky. In this region, the Muscatatuck Group consists of two formations, the Jeffersonville Limestone and the overlying North Vernon Limestone. Although conodonts are abundant (over 20,000 specimens were recovered), diversity is relatively low. *Icriodus* and *Polygnathus* are the dominant faunal elements. Nineteen conodont species and subspecies are recognized including one new subspecies, *Icriodus angustus obliquus*. Few of the recognized species are diagnostic of the standard Middle Devonian conodont zones, making long-distance correlations uncertain. Consequently, a zonation consisting of three local zones and one standard subzone is adopted. These are, in ascending order, the *Icriodus latericrescens robustus* Zone, the *Icriodus angustus angustus* Zone, the *Polygnathus pseudofoliatus* Zone, and the Lower *Polygnathus varcus* Subzone. Examination of the conodont faunas suggests an Eifelian age for the lower part of the Muscatatuck Group and a Givetian age for the upper part.

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INTRODUCTION

Since 1820, over 175 papers have been published on the Devonian stratigraphy and paleontology of the Falls of the Ohio and surrounding area. Relatively few publications, however, have included a detailed discussion of the conodont faunas and biostratigraphy. One of the earliest papers to report Middle Devonian conodonts from the Falls of the Ohio was that of Branson and Mehl (1938), which included the description of a new species, *Icriodus latericrescens*. A number of other papers (e.g., Rexroad and Orr, 1967; Orr and Pollock, 1968; Klapper et al., 1971) mention the occurrence of conodonts in these strata but do not include illustrations of specimens. Only a few publications include both discussion and illustrations of the Middle Devonian conodonts of south-central Indiana and north-central Kentucky (e.g., Orr and Klapper, 1968; Klapper, Philip and Jackson, 1970; Klapper and Johnson, 1980). By far the most important paper on this subject is

Orr's (1946b) unpublished M.A. thesis. Although the stress of this thesis is on the Middle Devonian conodonts of southern Illinois, four sections in south-central Indiana were also included. Conodont faunas are well illustrated, and a local zonal scheme of six conodont zones was established. Since the writing of Orr's thesis, the understanding of Middle Devonian conodont faunas and biostratigraphy has been considerably refined. The main purpose of the present paper is to examine, in greater detail, the conodont faunas of the Middle Devonian Muscatatuck Group of south-central Indiana and north-central Kentucky and to provide an updated biostratigraphy based on these faunas.

Procedures

Eighty-three samples were collected from eight Middle Devonian sections in south-central Indiana and north-central Kentucky. The eight localities lie along a nearly north-south trending line from Jennings County, Indiana to Jefferson County, Kentucky (see Figs. 1 & 2). An effort was made to visit type localities of the lithostratigraphic units under consideration; when not possible, nearby alternate localities were substituted. See the Appendix for detailed location of sections. Samples were generally collected from major beds with spacing no more than 1 meter apart, and with individual samples including no more than 10 cm of vertical section. When possible, one kilogram of each sample was processed for conodonts using standard acidizing procedures with formic acid. In the case of particularly argillaceous samples, the acidizing procedure was supplemented with Stoddard's solvent treatment as described by Collinson (1963). Residues were washed through three nested sieves of 20, 120, and 230 U.S. standard mesh. Only the residue retained on the 120 mesh sieve was picked for conodonts. All specimens that retained the basal cavity were picked to guarantee that only individual elements were collected. In the case of some particularly large samples, only part of the residue was picked. The conodonts illustrated in this paper were photographed on the JEOL JSM-35C scanning electron microscope at The University of Iowa, Iowa City. Lithologic nature of the samples was determined by examination of hand samples, polished slabs, insoluble residues, and, in most instances, thin sections.

LITHOSTRATIGRAPHY

The stratigraphic terminology employed herein is primarily that in use by the Indiana Geological Survey as set forth by Shaver et al. (1970) and modified by Perkins (1963), Shaver (1974), and Droste and Shaver (1975). The Muscatatuck Group, proposed by Shaver (1974, p. 3), in south-central Indiana and north-central Kentucky includes two formations, the Jeffersonville Limestone and the overlying North Vernon Limestone.

The Jeffersonville Limestone was named by Kindle (1899, p. 8) for the "limestone lying between the Sellersburg beds and the *Catenipora* beds of the Niagara" as exposed at the Falls of the Ohio between Jeffersonville, Indiana, and the mouth of Silver Creek. Droste and Shaver (1975) considered the Jeffersonville Limestone to include three members in generally ascending order: the Dutch Creek Sandstone, Geneva Dolomite, and Vernon Fork Members. They considererd the Dutch Creek Sandstone Member to be equivalent to the basal Jeffersonville of the southern Indiana outcrop. This sandstone has a discontinuous distribution and was not encountered in any of the sections examined in this study.

The Geneva and Vernon Fork Members are considered to be northern facies equivalents of the type Jeffersonville Limestone. Of these two members, only the Vernon Fork was sampled for conodonts in this study. Orr (1964b), however, examined samples from the Geneva Member for conodonts, but found them to be nonproductive.

The Vernon Fork Member was examined,

for this paper, only at its principal reference section, the Berry Materials Corp. Quarry (BMQ) (see Droste and Shaver, 1975, p. 405). The sampled strata consist of light yellowish- to brownish-gray, slightly calcitic, sandy, "dolomicrite." Birdseye structures, laminations, and intraclasts also occur in this unit. The term "dolomicrite," as used above, refers only to the fine-grained nature of these dolostones and does not necessarily imply a primary origin for the dolomite.

Of greater concern to this study is the southern facies of the Jeffersonville Limestone. This formation, as exposed at its type locality at the Falls of the Ohio, has not been subdivided into members, as it has in its more northerly occurrences. Several schemes, however, have been proposed to subdivide the formation based on faunal content (see, e.g., Kindle, 1901; Patton and Dawson, 1955; Perkins, 1963; Conkin and Conkin, 1976). To facilitate the discussion of the Jeffersonville Limestone, the zonal scheme as proposed by Perkins (1963, p. 1338) has been adopted. He recognized five zones which are, in ascending order: (1) coral zone; (2) *Amphipora* Zone; (3) *Brevispirifer gregarius* Zone; (4) fenestrate bryozoan-brachiopod zone; (5) *Paraspirifer acuminatus* Zone (Fig. 2). A detailed description of each of these zones and the associated lithologies can be found in Perkins (1963).

The Jeffersonville Limestone is overlain by the North Vernon Limestone (= Sellersburg Limestone of authors). This unit was named by Borden (1876, p. 160-161) for strata occurring at North Vernon, Jennings County, Indiana, and lying "at the horizon of the hydraulic limestone" (Silver Creek Member) of Clark County, Indiana. In Borden's concept, the North Vernon Limestone was overlain by gray, crystalline, commonly crinoidal limestone (= Beechwood Member of present usage). Kindle (1899, p. 8, 20) proposed the name Sellersburg beds for the strata underlying the New Albany Shale down to the lowest beds worked by the cement quarries. As used in this sense, the Sellersburg beds include the Beechwood and Silver Creek Members only. More detailed discussions of the nomenclatural history of these strata can be found in papers by Patton and Dawson (1955, p. 39-43) and Burger and Patton, *in* Shaver et al. (1970, p. 120-122). Through time, usage of the names North Vernon Limestone and Sellersburg Limestone has come to be nearly synonymous, referring to the strata underlying the New Albany Shale and overlying the Jeffersonville Limestone. In this paper, North Vernon Limestone is used in this sense. Three members are recognized in the North Vernon Limestone. These are, in ascending order: the Speeds, Silver Creek, and Beechwood Members.

Sutton and Sutton (1937, p. 326) proposed the name Speeds Member for an 18-inch thick, shaly limestone below the cement rock (= Silver Creek Member) in the Speeds Quarry, near Sellersburg, Indiana. In thin section, the Speeds is a slightly- to highly-dolomitic, packed biomicrosparrudite.

Campbell (1942, p. 1060) considered the Speeds to be of formational status, overlain by the Deputy Formation, a blue to gray limestone weathering light gray. He designated the quarry 3/4 mile south of Deputy, Jefferson County, Indiana, as the type locality. According to Campbell, the Deputy is difficult to distinguish from the Speeds in fresh material, except by the fossil content. In thin section, the Deputy at the type locality is a slightly- to moderately-dolomitic biomicrosparite to biosparite. The Deputy is only locally developed and is considered herein as a facies of the Speeds Member.

The overlying Silver Creek Member was originally proposed by Siebenthal (1901, p. 345-346) for "a homogeneous, fine-grained, bluish to drab, argillaceous, magnesian limestone, the calcined form of which has the property of hydraulicity." This unit is typically exposed in the vicinity of Silver Creek in Clark County, Indiana. Siebenthal originally considered the Silver Creek to be of formational status. Butts (1915, p. 118) reduced it to the rank of member, as it is considered herein. Thin section examination shows the Silver Creek to vary from highly dolomitic, argillaceous biomicrite to fossiliferous, argillaceous "dolomicrite." The Silver Creek Member thins northward from its maximum thickness in Clark County, Indiana. At the same time, the underlying Speeds Member shows a corresponding thickening. Based on stratigraphic position and the inclusion of lentils or tongues of one lithology in the other, the two members have been considered to be contemporaneous facies (see e.g., Patton and Dawson, 1955, p. 42).

The Beechwood Member is the youngest member of the North Vernon Limestone. The name was proposed by Butts (1915, p. 120) for a gray, thick-bedded, coarsely crystalline crinoidal limestone containing black phosphatic pebbles in the basal few inches. Butts named this unit for exposures near Beechwood Station, Jefferson County, Kentucky, but did not establish a type section. Orr and Pollock (1968, p. 2258) proposed a principal reference section for the Beechwood Member, about 4.5 miles west of the old Beechwood Station in Louisville, Jefferson County, Kentucky. In thin section, the Beechwood varies from echinoderm biosparite to biosparrudite. Dolomitization is generally minimal to moderate but may be extensive in some beds. Phosphate pebbles and flattened, phosphatic ooids(?) are frequently encountered at the base of the unit.

BIOSTRATIGRAPHY

The conodont faunas of the Muscatatuck Group in south-central Indiana and north-central Kentucky include few diagnostic species common to the standard zonation, which is reviewed, for example, by Klapper and Johnson (1980). The local zonal scheme proposed by Orr (1964b) and modified by Orr (1971) is further modified and used in this paper (Fig. 3).

Conodonts were not recovered from the Jeffersonville Limestone below the *Brevispirifer gregarius* Zone. Oliver (1976, Fig. 3) considered these lower strata to be of late Emsian to early Eifelian age, as determined from the coral faunas.

Icriodus latericrescens robustus Zone

This, the lowest conodont zone recognized in the study area, corresponds to the *Icriodux latericrescens* n. subsp. Zone of Orr (1964b, p. 36-37). The lower limit of this zone is defined by the lowest occurrence of *I. l. robustus,* and the upper limit by the lowest occurrence of *I. a. angustus. Polygnathus* cf. *P. angusticostatus, I.* sp. A, and *I.* n. sp. E of Weddige first occur near the top of the *Brevispirifer gregarius* Zone below the lowest occurrence of *P. c. costatus* (see Fig. 4). This association suggests that the *I. l. robustus* Zone, of the study area, may be equivalent, in part, to the *P. costatus patulus* Zone of the standard zonation. For ranges of the above-mentioned forms in the standard zonation, the reader is referred to Klapper and Johnson (1980, p. 420-422).

Icriodus angustus angustus Zone

The lower boundary of this zone is defined by the lowest occurrence of *I. a. angustus.* The upper boundary is defined by the lowest occurrence of *Polygnathus pseudofoliatus. Polygnathus c. costatus* and *P. l. linguiformis* first occur in the *I. a. angustus* Zone. In the examined sections, the *I. a. angustus* Zone is recognized in the fenestrate bryozoan-brachiopod zone and the *Paraspirifer acuminatus* Zone of the Jeffersonville Limestone. Correlation of the *I. a. angustus* Zone with the *P. c. costatus* Zone of the standard zonation is suggested.

Polygnathus pseudofoliatus Zone

The base of the *P. pseudofoliatus* Zone is defined by the lowest occurrence of the nominal species. The top is defined, in the study area, by the lowest occurrence of *P. timorensis. Icriodus* n. sp. E of Weddige

(1977), *I.* sp. A, and *I. retrodepressus* show their maximum development in this zone. Below this zone *I. retrodepressus* is represented only by tentatively identified specimens. *Icriodus angustus obliquus* first occurs at the base of the *P. pseudofoliatus* Zone. Faunas characteristic of the *P. pseudofoliatus* Zone were recovered from the Speeds (including the Deputy facies) and Silver Creek Members of the North Vernon Limestone.

A single, apparently weathered specimen of *Polygnathus timorensis* was recovered from a sample (SSQ-5) at the top of the Silver Creek Member. In another sample (OGQ-4), from the top of this member, several fragmentary specimens of *Icriodus l. latericrescens* were recovered below the first occurrence of *P. timorensis* in the overlying Beechwood Member. Also recovered from this sample were a number of flattened phosphatic ooids(?) like those typical of the basal part of the Beechwood Member. The presence of these ooids(?) and the weathered appearance of the specimen of *P. timorensis* suggest the possibility of stratigraphic leak. Orr and Pollock (1968, p. 2261) also reported *I. l. latericrescens* from a fauna without "*P. varcus*" from the top of the Silver Creek Member at the Atkins Quarry, in Clark County, Indiana. On evidence of that occurrence, Orr (1971, p. 17) considered the upper part of the Silver Creek Member to belong to his *I. l. latericrescens* Zone. This zone, however, cannot be recognized with any confidence in the present study.

The relationships of the *Polygnathus pseudofoliatus* Zone with the standard conodont zonation are far from straightforward. Correlation of this zone with part or all of the sequence from the *Tortodus kockelianus australis* Zone (Eifelian) through the *Polygnathus xylus ensensis* Zone (Eifelian-Givetian, Weddige, 1977) is possible.

Lower *Polygnathus varcus* Subzone

The Lower *Polygnathus varcus* Subzone of Ziegler, Klapper and Johnson (1976, p. 113) is recognized in the Beechwood Member of the North Vernon Limestone. *Polygnathus timorensis, P. linguiformis weddigei* and *P. linguiformis klapperi* make their first appearance at the base of this member. Several species, for example *Icriodus angustus angustus, Icriodus angustus obliquus* and *Icriodus retrodepressus,* range upward into the lower *P. varcus* Subzone (see Fig. 4). These forms are not known to occur at this level outside of the study area and many represent reworked elements in the present collections.

One sample (SSQ-1) from the thin limestone at the base of the New Albany Shale Group was also processed for conodonts. A diverse fauna including *Polygnathus cristatus* was recovered from this sample but, because of stratigraphic position, is considered beyond the scope of this paper and will not be discussed further herein. For a detailed description of this fauna, the reader is referred to the paper by Orr and Klapper (1968).

Conodont-based correlations of the Muscatatuck Group with Middle Devonian strata in surrounding areas are shown in Fig. 5.

SYSTEMATIC PALEONTOLOGY

Nineteen conodont species and subspecies were recognized from among the 22,154 specimens recovered in this study. For distribution of species see Figs. 6 and 7. Emphasis is placed on platform and some coniform elements. Multielement reconstructions have generally not been attempted owing to the poor preservation of most nonplatform elements. General associations, however, are noted. Figured specimens are reposited at the University of Iowa (SUI).

Belodella cf. *B. resima* (Philip, 1965)
Fig. 12 G,L

cf. *Belodus resimus* Philip, 1965, p. 98, Pl. 8, Figs. 15-17, 19.

Remarks.—Proclined to erect, denticulate coniform elements have been recovered from several samples in south-central Indiana and north-central Kentucky. These forms are comparable in shape, denticulation, and the development of anterolateral flanges, to *Belodella resima* (Philip, 1965). In *B. resima,* however, the cross-sectional shape is a narrow isosceles triangle whereas in the present material it is a narrow right triangle. Also, the anterolateral flanges of *B. resima* appear to be smooth whereas in the material at hand they are made up of minute, confluent denticles similar to those of the posterior keel. Uyeno, *in* Uyeno, Telford, and Sanford (1982, Pl. 5, Figs. 30-32) illustrated three specimens of *Belodella* sp. which also appear to have denticulated anterolateral flanges.

Material.—39 specimens

Occurrence.—Fenestrate bryozoan-brachiopod zone and *Paraspirifer acuminatus* Zone of the Jeffersonville Limestone and upper Speeds, Silver Creek and Beechwood Members of the North Vernon Limestone.

Coelocerodontus cf. *C. biconvexus*
Bultynck, 1970
Fig. 12 H-K, M-O

cf. *Coelocerodontus biconvexus* Bultynck, 1970, p. 94, Pl. 27, Figs. 13-15.

Remarks.—Erect to slightly recurved coniform elements comparable to *Coelocerodontus biconvexus* are common in the Middle Devonian strata of south-central Indiana and north-central Kentucky. The present material differs, however, from Bultynck's specimens in that the cross-sectional outline of the Indiana and Kentucky specimens varies from biconvex to triangular to concavo-convex, and none of these specimens has a denticulated posterior keel, although denticulation of the anterolateral costa is commonly well-developed. *Paltodus* sp. of Orr (1964a, p. 13, Pl. 2, Figs. 4, 7) and *Coelocerodontus* sp. of Uyeno, *in* Uyeno, Telford, and Sanford (1982, p. 34, Pl. 5, Figs. 25-29) are apparently conspecific with the present form.

Material.—686 specimens.

Occurrence.—Brevispirifer gregarius Zone, fenestrate bryozoan-brachiopod zone, *Paraspirifer acuminatus* Zone, and Vernon Fork Member of the Jeffersonville Limestone; Speeds, Silver Creek, and Beechwood Members and Deputy facies of the North Vernon Limestone.

Icriodus angustus angustus
Stewart and Sweet, 1956
Fig. 8 A-F

Icriodus angustus Stewart and Sweet, 1956, p. 267, Pl. 33, Figs. 4, 5, 11, 15; Klapper and Ziegler, 1967, Pl. 10, Figs. 1,?2, 3; Klapper, *in* Ziegler, 1975, p. 75-76, *Icriodus*—Pl. 2, Figs. 6, 7; Klapper and Johnson, 1980, p. 447, Pl. 3, Figs. 3-6; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 31, Pl. 3, Figs. 1-4.

Remarks.—The specimens herein assigned to *Icriodus angustus angustus* agree well with those described by Stewart and Sweet (1956, p. 267, Pl. 33, Figs. 4, 5, 11, 15). See also Klapper, *in* Ziegler (1975, p. 75-76) for additional comments and relations. For comparison with *Icriodus angustus obliquus,* see remarks for that taxon.

Material.—280 specimens.

Occurrence.—Fenestrate bryozoan-brachiopod zone and *Paraspirifer acuminatus* Zone of the Jeffersonville Limestone; Speeds, Silver Creek, and Beechwood Members of the North Vernon Limestone. For further discussion of occurrence, see section on Biostratigraphy.

Icriodus angustus obliquus n. subsp.
Fig. 8 G-L

Derivation of name.—obliquus, Latin, sloping; referring to the upper margin of the bladelike extension.

Holotype.—SUI 49334, the specimen illustrated on Fig. 8 J-L; from the Sellersburg Stone Company Quarry, sample SSQ-14, 0-10 cm above the base of the Speeds Member.

Diagnosis.—A subspecies of *Icriodus angustus* with a segminiscaphate element in which the posterior extension of the middle row of denticles is bladelike and is made up of about four to six laterally compressed bluntly to acutely pointed denticles. Of these, the anterior two to four denticles are relatively slender and subequal to gradually increasing in height posteriorly. The posteriormost one or two denticles are larger and gradually to distinctly higher than the preceding denticles of the bladelike extension. This extension begins near midlength of the element.

Remarks.—Icriodus angustus angustus is distinguished from the new subspecies by a segminiscaphate element in which the posterior extension of the middle row of denticles is made up of one to four subequal denticles which, in most specimens, are abruptly higher than all other denticles on the platform. In some specimens, however, the denticles of the posterior extension increase gradually in height posteriorly as in one of the paratypes (Stewart and Sweet, 1956, Pl. 33, Fig. 4; also illustrated by Klapper, *in* Ziegler, 1975, *Icriodus*—Pl. 2, Fig. 6). In such specimens, however, the denticles of the posterior extension of the middle row are subequal in the anteroposterior dimension and are fewer in number than in the new subspecies.

Elements of *Icriodus obliquimarginatus* have posterior bladelike extension of the middle row of denticles similar to that of *I. angustus obliquus.* They can be distinguished from the new subspecies, however, by the outline of the basal cavity. In *I. angustus obliquus* the outline is like that of *I. angustus angustus,* in which the inner margin extends farther posteriorly than the outer margin and the two are connected by a diagonally oriented posterior margin. The outline of the basal cavity of *I. obliquimarginatus* is rounder and more expanded posteriorly than in the new subspecies. In addition, the posterior margin of elements of *I. angustus obliquus* is not inclined as strongly posteriorly, in lateral view, as in *I. obliquimarginatus,* and it may be vertical to inclined anteriorly as well.

One specimen assigned to the new subspecies from a sample from the Sellersburg Stone Company Quarry (SSQ-14) shows characteristics intermediate between *Icriodus angustus obliquus* and the nominal subspecies. It possesses a posterior extension of the middle row of denticles in which the anterior two dentiles are slender and subequal, as in *I. angustus obliquus,* but are followed by four abruptly larger denticles similar to those of *I. a. angustus.* Most of the other specimens of *I. angustus* recovered from this sample, however, clearly belong to the new subspecies.

Material.—23 specimens.

Occurrence.—North Vernon Limestone (all members). For further discussion of occurrence, see section on Biostratigraphy.

Icriodus brevis Stauffer, 1940
Fig. 12 P-R

Icriodus brevis Stauffer, 1940, p. 424, Pl. 60, Figs. 36, 43, 44, 52; Klapper, *in* Ziegler, 1975, p. 89-90, *Icriodus*—Pl. 3, Figs. 1-3; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 31-32, Pl. 5, Figs. 10-16, 21, 22 [see further synonymy].

Icriodus cymbiformis Branson and Mehl. Orr, 1964b, p. 70-71, Pl. 2, Fig. 5; Orr, 1971, p. 33-34, Pl. 2, Figs. 1-6.

Icriodus eslaensis Adrichem Boogaert, 1967, Pl. 1, Figs. 9-12; Norris and Uyeno, 1972, Pl. 3. Fig. 9; Huddle, 1981, p. B22, Pl. 4, Figs. 1-29 [see further synonymy].

Remarks.—Segminiscaphate elements assigned to *Icriodus brevis* are characterized by an extension of the middle row of denticles posteriorly beyond the lateral rows. The denticles of this extension stand at approximately the same height as the other denticles on the platform. Some specimens in the present collections have a longitudinal axis that is apparently more curved than that of the type material (Fig. 12 P-R) but are similar in other respects. See Klapper, *in* Ziegler (1975, p. 89) for further discussion of this species.

Material.—5 specimens.

Occurrence.—Beechwood Member, North Vernon Limestone.

Icriodus latericrescens latericrescens
Branson and Mehl, 1938
Fig. 8 V-AD

Icriodus latericrescens Branson and Mehl, 1938, p. 164-165, Pl. 26, Figs. 30-32, 34, 35 (only).

Icriodus latericrescens latericrescens Branson and Mehl. Klapper and Ziegler, 1967, p. 74-75, Pl. 10, Figs. 4-9, Pl. 11, Figs. 1-5 [see further synonymy]; Huddle, 1981, p. B22-B23, Pl. 5, Figs. 1-6; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 32, Pl. 4, Figs. 27-30 [see further synonymy].

Remarks.—This subspecies includes a scaphate pectiniform element, the diagnostic characteristics of which were given by Klapper and Ziegler (1967, p. 75). It is distinguished from the comparable element of *I. l. robustus* in that the main process tends to be slightly bowed with a more or less concave inner side and convex outer side. In *I. l. robustus,* the main process is generally straighter with a straight to convex inner side and convex outer side. The denticulation of the main process in the nominal subspecies consists of three longitudinal rows. The lateral rows are composed of discrete, round nodes, whereas the middle row nodes vary from subround to elongate to an irregular, discontinuous ridge. In *I. l. robustus,* the middle row nodes tend to be more nearly round, although in some specimens they are slightly elongate longitudinally. The lateral row nodes of *I. l. robustus* are generally round but tend to be more robust than those of the nominal subspecies. In some specimens, they appear crowded together, commonly becoming somewhat laterally elongate. In some large specimens of both subspecies, the middle row denticles may be much reduced or absent, in which case the distinction between the two subspecies is more difficult and must be based on the shape of the main process and the lateral row nodes.

Material.—151 specimens.

Occurrence.—Beechwood and upper part of the Silver Creek Members of the North Vernon Limestone.

Icriodus latericrescens robustus Orr, 1971
Fig. 8 M-U

Icriodus latericrescens robustus Orr, 1971, p. 37-38, Pl. 2, Figs. 14-17 [see further synonymy]; Uyeno, *in* Uyeno, Telford and Sanford, 1982, p. 32, Pl. 4, Figs. 1-6, 8-15, 19-22, 25, 26 31-38 (I elements) [see further synonymy].

Remarks—For diagnosis and description see Orr (1971, p. 37-38) and remarks for *Icriodus l. latericrescens* herein. Some of the specimens from the *Brevispirifer gregarius* Zone from the Falls of the Ohio (FOS) and Oak and Vine (OVS) localities have middle row denticles that are longitudinally elongate (e.g., Fig. 8 T). Although this feature is most characteristic of *I. l. latericrescens,* other features of these specimens are typical of *I. l. robustus,* and they are assigned to the latter subspecies. One specimen, which is complete except for the anterior tip, is typical of *I. l. robustus* but occurs in the highest sample of the Beechwood Member from the Sellersburg Stone Company Quarry (SSQ-2). Other latericrescid *Icriodus* from this sample belong to *I. l. latericrescens.*

Material.—530 specimens.

Occurrence.—*Brevispirifer gregarius* Zone, fenestrate bryozoan-brachiopod zone, *Paraspirifer acuminatus* Zone of the Jeffersonville Limestone and ?Beechwood Member of the North Vernon Limestone.

Icriodus retrodepressus Bultynck, 1970
Fig. 9 A-F

Icriodus retrodepressus Bultynck, 1970, p. 110-111, Pl. 30, Figs. 1-6; Ziegler, *in* Ziegler, 1975, p. 143-144, *Icriodus*—Pl. 8, Figs. 4, 5.

Icriodus nodosus (Huddle). Schumacher, 1971, p. 93-95, Pl. 9, Figs. 4-6 (only).

Icriodus corniger retrodepressus Bultynck. Weddige, 1977, p. 290-291, Pl. 1, Figs. 10, 11, ?12.

Icriodus aff. *I. retrodepressus* Bultynck. Uyeno, *in* Uyeno, Telford and Sanford, 1982, p. 33, Pl. 3, Figs. 16-18, 25-27 (only).

Remarks.—Icriodus retrodepressus is characterized by a segminiscaphate element with reduced or absent middle row denticles in the posterior part of the main process resulting in a distinct depression immediately anterior to the posteriormost middle row denticle. For further remarks and diagnosis see Bultynck (1970) and Ziegler, *in* Ziegler (1975). Uyeno, *in* Uyeno, Telford, and Sanford (1982), reported specimens of *Icriodus* with a posterior depression of the middle row denticles. He referred to these specimens as *I.* aff. *I. retrodepressus* and distinguished his material from *I. retrodepressus* sensu stricto by the more uniform longitudinal spacing of the lateral row nodes in the latter species. According to Klapper and Barrick (MS), some specimens of *I. retrodepressus* from the Couvinian Eau Noire sequence above and below the type stratum show greater longitudinal spacing of the lateral row denticles anteriorly than posteriorly. Specimens in the present collection may also show this feature and are considered within the range of variation of *I. retrodepressus*. See also *I.* sp. A, herein, for the distinction from *I. retrodepressus.*

Material.—46 specimens. (mature forms only.)

Occurrence.—North Vernon Limestone (all members). For further discussion of occurrence, see section on Biostratigraphy.

Icriodus n. sp. E. of Weddige, 1977
Fig. 9 G-I, cf. J-L

Icriodus n. sp. E Weddige, 1977, p. 299-300, Pl. 2, Figs. 23-25 [see further synonymy].

Remarks.—For diagnosis and remarks, see Weddige (1977). See also remarks for *Icriodus* sp. A, herein, for comparison of *I.* n. sp. E and *I. retrodepressus.*

Material.—280 specimens (mature forms only).

Occurrence.—Upper part of the *Brevispirifer gregarius* Zone of the Jeffersonville Limestone and all members of the North Vernon Limestone.

Icriodus sp. A
Fig. 9 cf. M-O, S-X

Icriodus nodosus (Huddle). Orr, 1964b, p. 77-78, Pl. 2, Fig. 16?, 24-26; Orr, 1971, p. 38-39, Pl. 2, Figs. 20-23; Schumacher, 1971, p. 93-95, Pl. 9, Figs. 1-3, 7-9?, 10-13, 15, 16 (only).

Icriodus sp. aff. *I. retrodepressus* Bultynck. Klapper and Johnson, 1980, p. 448, Pl. 3, Figs. 19-21, 22?, 23?

Icriodus aff. *I. retrodepressus* Bultynck. Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 33, Pl. 3, Figs. 19?, 23.

Remarks.—This species is to be described and named by Klapper and Barrick (MS). In upper view, the segminiscaphate element of this species is similar to that of *I.* n. sp. E of Weddige (1977), and *I. retrodepressus. I.* sp. A includes two morphotypes; one has a posterior depression of the middle row denticles as in *I. retrodepressus;* the other lacks such a depression and is similar to *I.* n. sp. E. *I.* sp. A, however, possesses a broader basal cavity posteriorly than either *I.* n. sp. E or *I. retrodepressus.* In the present collections, specimens considered intermediate between the three species have also been recognized. In addition, specimens have been recovered that have lateral row denticles that are rounder than is apparently typical of the above-mentioned species. These forms may also have two or three more or less well-developed middle row denticles posterior to the lateral rows, as opposed to the more typical, single, large, triangular denticle of the other forms. In other respects, these specimens are comparable to the three species discussed above (see Fig. 9 J-O). The rounder lateral row denticles and the two to three posterior middle row denticles are generally best developed in the smaller, possibly juvenile forms. If these are juvenile, it is often difficult or impossible to determine with which of the three mature forms they are associated. Faunas made up entirely of these smaller forms are common in the study material and have a stratigraphic range greater than that of the larger specimens. For the distribution of these "juvenile" forms relative to that of the mature forms, refer to Figs. 6 and 7.

Material.—347 specimens (mature forms only).

Occurrence.—Upper part of the *Brevispirifer gregarius* Zone of the Jeffersonville Limestone and all members of the North Vernon Limestone.

Icriodus? sp. B
Fig. 12 S-X

Remarks.—The specimens treated here in open nomenclature include scaphate elements with a narrow anterior primary process consisting of a single row of denticles that are round to laterally compressed in upper view. The denticles are numerous, subequal, discrete to fused, and bluntly pointed to round in lateral view. An outer lateral process extends at right angles to or is directed slightly posteriorly to the posterior end of the anterior primary process. The outer lateral process may have a narrow ridge running along its upper surface or may be weakly denticulate. A less well-developed inner lateral process or spur is also present. In lower view, the basal cavity is broadly flared posteriorly, becoming narrower anteriorly and pinching out slightly posterior of the anterior tip of the element.

The specimens considered herein are morphologically intermediate between *Icriodus* and *Pelekysgnathus*. Unfortunately, few specimens were recovered and all are fragmentary. A tentative assignment to *Icriodus* is based on the following considerations: (1) specimens of *Icriodus*? sp. B are notably similar in lower view to *Icriodus latericrescens latericrescens* with which this form co-occurs; (2) no specimens definitely assignable to *Pelekysgnathus* were recovered from any of the samples in this study; (3) Bultynck (1970, p. 111-112) reported a similar situation for *Icriodus regularicrescens*. In his faunas, he found specimens with well-developed lateral rows, with reduced lateral rows, and with only the middle row of nodes. In the present study, however, no forms were found showing any development of lateral rows of nodes. In addition, the denticulation of the anterior primary process of *Icriodus*? sp. B is unlike that of *Icriodus l. latericrescens* in both the shape and number of denticles. Definitive treatment of the form in question must await recovery of larger and better preserved faunas.

Material.—7 specimens.

Occurrence.—Beechwood Member of the North Vernon Limestone.

Polygnathus cf. *P. angusticostatus*
Wittekindt, 1966
Fig. 10 A-C, G-I

cf. *Polygnathus angusticostatus* Wittekindt, 1966, p. 631, Pl. 1, Figs. 15-18.

Remarks.—The specimens under consideration are all fragmentary carminiplanate elements, which are missing part or all of the free blade. Although platform development and ornamentation is apparently not as well developed as in the type specimen of *P. angusticostatus,* the present material appears closer to that species than to the similar and probably intergradational *P. angustipennatus.* Smaller specimens (see Fig. 10 A-C) tend to have more restricted platforms and appear to be closer to *P. angustipennatus.* For more detailed discussions on the similarities and differences between *P. angusticostatus* and *P. angustipennatus* the reader is referred to the papers by Klapper (1971, p. 65), Weddige (1977, p. 307), and Sparling (1981, p. 309-312).

Material.—21 specimens.

Occurrence.—*Brevispirifer gregarius* and *Paraspirifer acuminatus* Zones of the Jeffersonville Limestone and the Speeds and basal

Silver Creek Members of the North Vernon Limestone.

Polygnathus? caelatus Bryant, 1921
Fig. 10 S-U, cf. V, W

Polygnathus caelatus Bryant, 1921, p. 27, Pl. 13, Figs. 1-6, 8, 12, 13 (not Figs. 7, 9-11 = *Polygnathus collieri* Huddle, 1981).

not *Polygnathus caelata* Bryant. Bischoff and Ziegler, 1957, p. 86, Pl. 18, Figs. 18, 19.

Polygnathus beckmanni Bischoff and Ziegler, 1957, p. 86, Pl. 15, Fig. 25; Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson, 1976, Pl. 4, Figs. 22, 23; Bultynck and Hollard, 1981, p. 42, Pl. 8, Fig. 9.

Polygnathus aff. *P. beckmanni* Bischoff and Ziegler, Bultynck and Hollard, 1981, p. 42, Pl. 8, Fig. 1.

Polygnathus? caelatus Bryant. Huddle, 1981, p. B27, Pl. 11, Figs. 15-18, Pl. 12, Figs. 12-18, 22-24 (only), Pl. 13, Figs. 1-6, 12, 13.

Remarks.—Huddle (1981, p. B27) considered Bryant's original concept of *Polygnathus caelatus* to include two species. Specimens with an elongate, asymmetrical platform, ornamented by irregular ridges, and with little or no free blade, were referred to *Polygnathus? caelatus,* whereas the remainder of Bryant's specimens, characterized by a large free blade and smaller basal pit, were included in *Polygnathus collieri.* Huddle (1981, Pl. 13, Figs. 1-6, 12, 13) reillustrated several of Bryant's original specimens and designated the specimen illustrated on Pl. 13, Figs. 6, 12, 13 (= Bryant, 1921, Pl. 13, Fig. 2) to be lectotype of *P.? caelatus.* In addition, he considered *P. beckmanni* and *P.? variabilis,* both of Bischoff and Ziegler, as junior synonyms of *P.? caelatus.*

Bischoff and Ziegler (1957, Pl. 15, Fig. 25 a,b) illustrated only an upper and lateral view of the holotype of *P. beckmanni. P.? caelatus* shows considerable variation in nature and strength of ornamentation and in shape of the platform in upper and lateral views. In this respect, the holotype of *P. beckmanni,* as well as the material in the present study, appears to be within this range of variation and assignment to *P.? caelatus* sensu Huddle, 1981, is adopted herein.

Material.—1 nearly complete and 10 fragmentary specimens.

Occurrence.—Beechwood and upper part of the Silver Creek Members of the North Vernon Limestone.

Polygnathus costatus costatus Klapper, 1971
Fig. 10 D-F, J-L

Polygnathus sp. nov. B Philip, 1967, p. 158-159, Pl. 2, Figs. 4, ?5, 8.

Polygnathus costatus costatus Klapper, 1971, p. 63, Pl. 1, Figs. 30-36, Pl. 2, Figs. 1-7; Klapper, *in* Ziegler, 1973, p. 347-348, *Polygnathus*—Pl. 1, Fig. 3 [see further synonymy]; Bultynck and Hollard, 1981, p. 42, Pl. 3, Figs. 7, 8; Klapper, *in* Johnson, Klapper, and Trojan, 1980, Pl. 4, Figs. 14, 15, 17; Sparling, 1981, p. 312-313, Pl. 1, Figs. 25-27 [P element] [see further synonymy]; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 28-29, Pl. 1, Figs. 11-13, 24, 25 [Pa element] [see further synonymy].

Remarks.—The specimens considered herein agree well with typical specimens of *Polygnathus costatus costatus.* For diagnosis and relations of *P. c. costatus,* see Klapper (1971, p. 63) and Klapper, *in* Ziegler (1973, p. 347-348).

Material.—79 specimens.

Occurrence.—Specimens confidently identified as *P. c. costatus* have been recovered, in this study, only from the *Paraspirifer acuminatus* Zone of the Jeffersonville Limestone at the Sellersburg Stone Company Quarry (SSQ) and from the Berry Materials Corporation Quarry (BMQ).

Polygnathus linguiformis klapperi
Clausen, Leuteritz, and Ziegler, 1979
Fig. 11 R-T

Polygnathus linguiformis linguiformis Hinde, epsilon morphotype Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson, 1976, p. 123-124, Pl. 4, Figs. 3, 12, 14, 24; Klapper, *in* Ziegler, 1977, p. 465, *Polygnathus*—Pl. 10, Figs. 5, 9, 10 [see further synonymy]; Bultynck and Hollard, 1981, p. 44, Pl. 7, Figs. 2-7, 9.

Polygnathus linguiformis klapperi Clausen, Leuteritz, and Ziegler, 1979, p. 32, Pl. 1, Figs. 7, 8.

Remarks.—Polygnathus linguiformis klapperi has a carminiplanate element with a flatter outer platform margin than that of the nominal subspecies. It can also be distinguished from *P. l. weddigei* by the poorer development of the tongue in the carminiplanate element of the latter subspecies. For a complete diagnosis and remarks, see Clausen, Leuteritz, and Ziegler (1979) or Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson (1976).

Material.—9 specimens.

Occurrence.—Basal Beechwood Member of North Vernon Limestone.

Polygnathus linguiformis linguiformis
Hinde, 1879
Fig. 11 O-Q

Polygnathus linguiformis Hinde, 1879, p. 367, Pl. 17, Fig. 15.

Polygnathus linguiformis linguiformis Hinde gamma forma nova Bultynck, 1970, p. 126-127, Pl. 11, Figs. 1-6, Pl. 12, Figs. 1-6.

Polygnathus linguiformis linguiformis Hinde. Weddige, 1977, p. 315-316, Pl. 5, Figs. 80-82; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 29-30, Pl. 2, Figs. 26-31 (Pa elements) [see further synonymy].

Polygnathus linguiformis linguiformis Hinde gamma morphotype Bultynck. Klapper, *in* Ziegler, 1977, p. 463-464, *Polygnathus*—Pl. 10, Fig. 2, *Polygnathus*—Pl. 11, Figs. 4, 7 (P element) [see further synonymy]; Bultynck and Hollard, 1981, p. 43-44, Pl. 7, Fig. 1.

Remarks.—Polygnathus linguiformis linguiformis has been divided into several morphotypes (Bultynck, 1970; Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson, 1976, p. 122-124; Klapper, *in* Johnson, Klapper, and Trojan, 1980, p. 102; Huddle, 1981, p. B30-B31). Most of these have since been treated as subspecies of *Polygnathus linguiformis* (Weddige, 1977, p. 312-316; Clausen, Leuteritz, and Ziegler, 1979, p. 30-33). Weddige (1977, p. 312-316) considered the gamma morphotype synonymous with the nominal subspecies and this opinion is followed in the present paper. Detailed diagnoses and descriptions of this form can be found in Weddige (1977); Klapper *in* Ziegler (1977), and Bultynck (1970).

Material.—943 specimens.

Occurrence.—Fenestrate bryozoan-brachiopod zone and *Paraspirifer acuminatus* Zone of the Jeffersonville Limestone and all members of the North Vernon Limestone.

Polygnathus linguiformis weddigei Clausen
Leuteritz, and Ziegler, 1979
Fig. 11 L-N

Polygnathus linguiformis linguiformis Hinde. Wittekindt, 1966, p. 635-636, Pl. 2, Fig. 11.

Polygnathus linguiformis linguiformis Hinde, delta morphotype, Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson, 1976, p. 123, Pl. 4, Figs. 4-8; Klapper, *in* Ziegler, 1977, p. 464-465, *Polygnathus*—Pl. 10, Figs. 1, 3; Bultynck and Hollard, 1981, p. 44, Pl. 7, Fig. 8.

Polygnathus linguiformis Hinde, delta morphotype, Ziegler and Klapper. Orchard, 1978, p. 944, Pl. 110, Figs. ?9, ?10, 21, 23, ?28, ?30.

Polygnathus linguiformis weddigei Clausen, Leuteritz, and Ziegler, 1979, p. 30-32, Pl. 1, Figs. 4, 9-12.

not *Polygnathus linguiformis linguiformis* Hinde, form delta Huddle, 1981, p. B30-B31, Pl. 15, Figs. 1-8.

(Text continues on page 108)

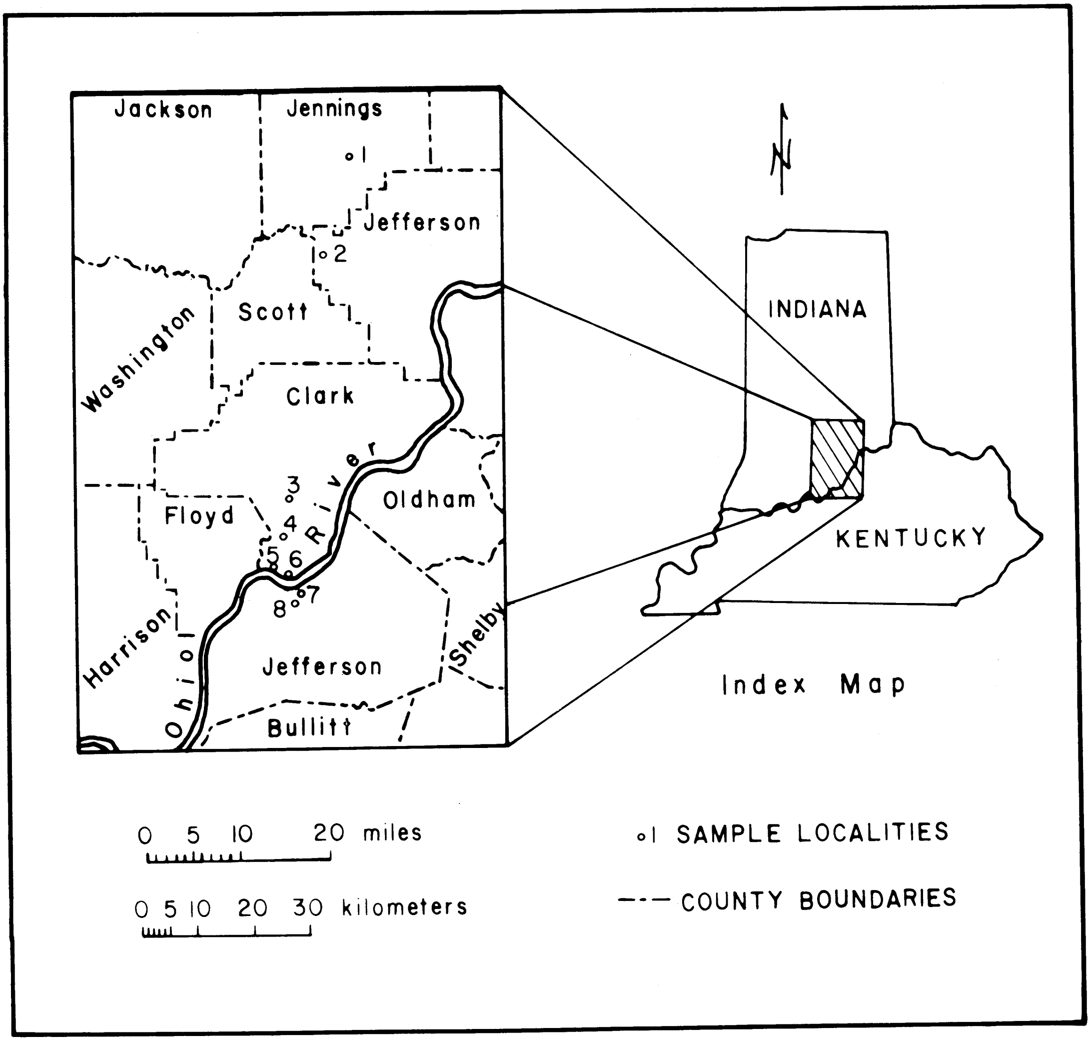


Fig. 1. Locality map for measured sections (see Appendix of Localities for precise locations).

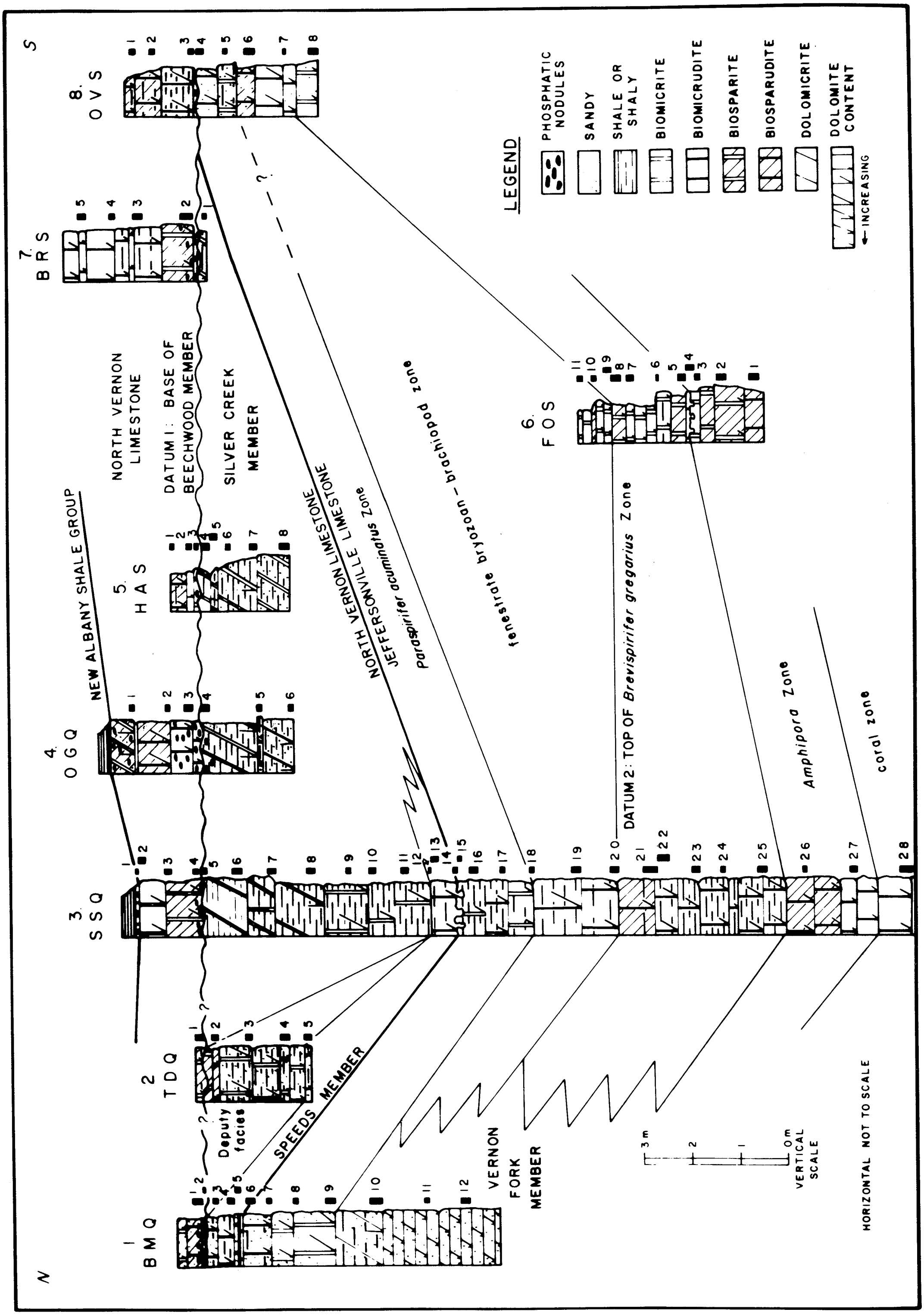
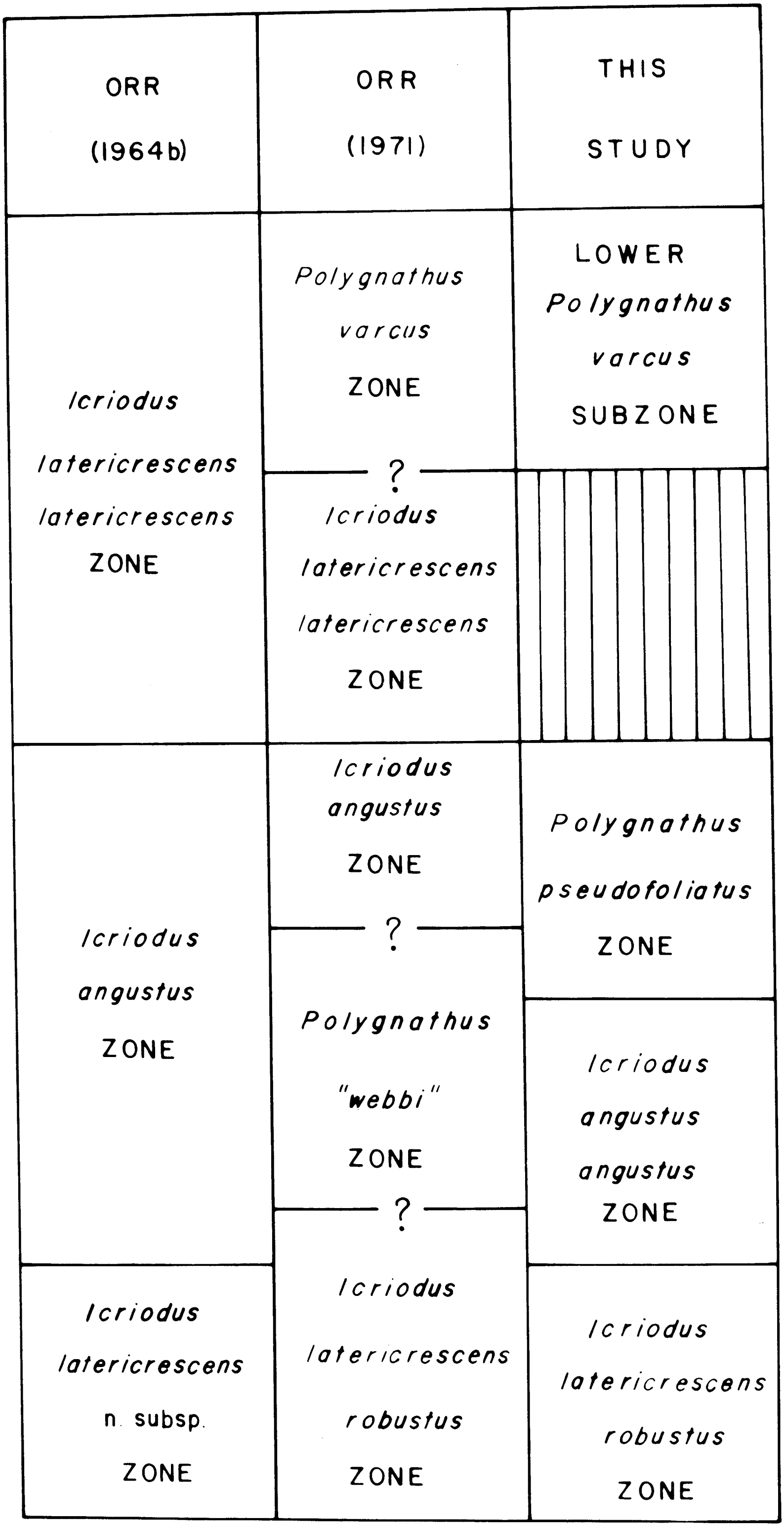


Fig. 2. Stratigraphy and conodont sample locations (numbered black rectangles) in the Muscatatuck Group, south-central Indiana and north-central Kentucky.



ORR (1964b)	ORR (1971)	THIS STUDY
Icriodus latericrescens latericrescens ZONE	*Polygnathus varcus* ZONE	LOWER *Polygnathus varcus* SUBZONE
	? *Icriodus latericrescens latericrescens* ZONE	▥
Icriodus angustus ZONE	*Icriodus angustus* ZONE	*Polygnathus pseudofoliatus* ZONE
	? *Polygnathus "webbi"* ZONE	
		Icriodus angustus angustus ZONE
	? *Icriodus latericrescens robustus* ZONE	
Icriodus latericrescens n. subsp. ZONE		*Icriodus latericrescens robustus* ZONE

Fig. 3. Comparison of the conodont zonations of Orr (1964b), Orr (1971), and that of the present study.

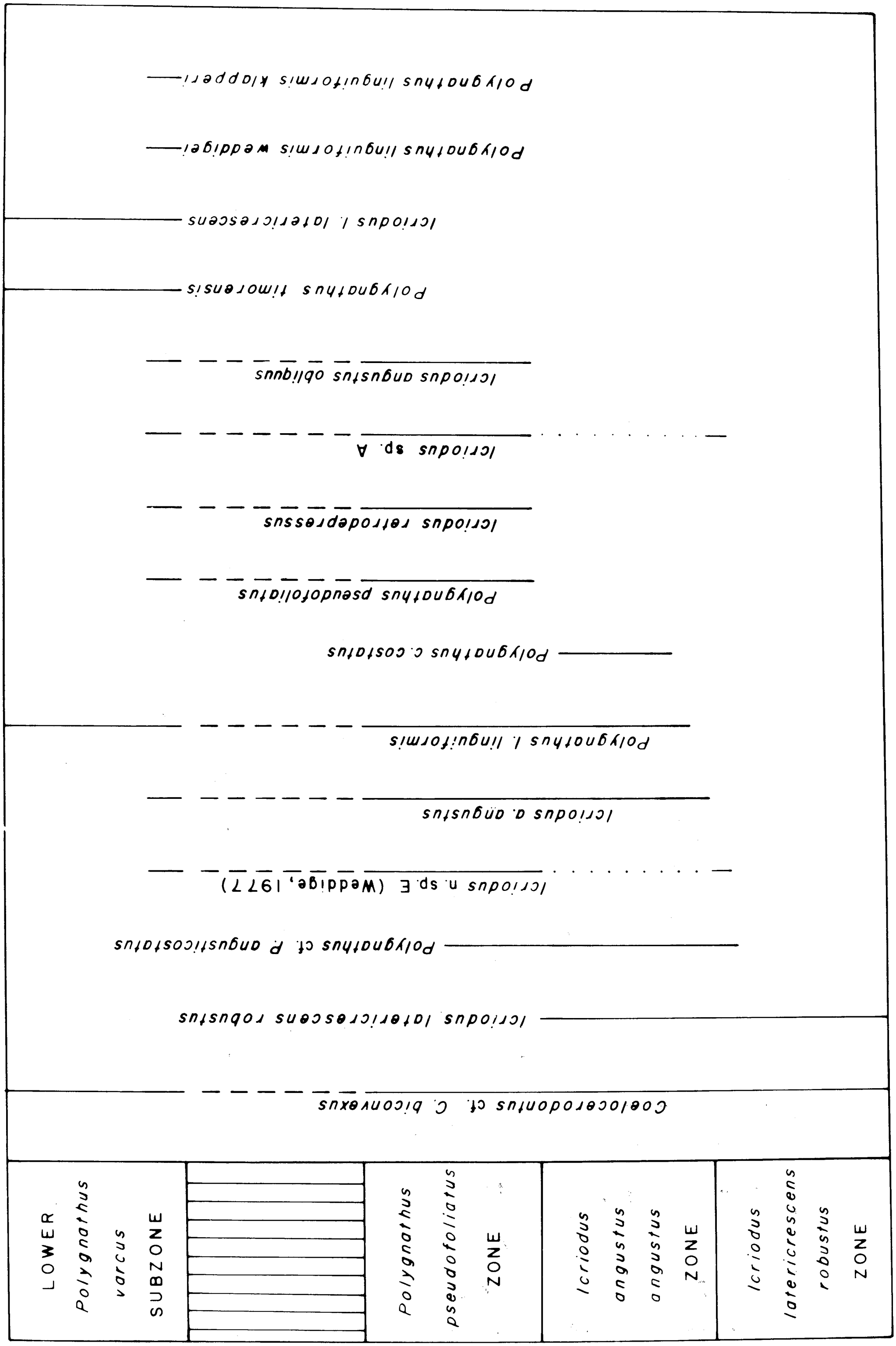


Fig. 4. Ranges of important conodont taxa in the Muscatatuck Group of south-central Indiana and north-central Kentucky.

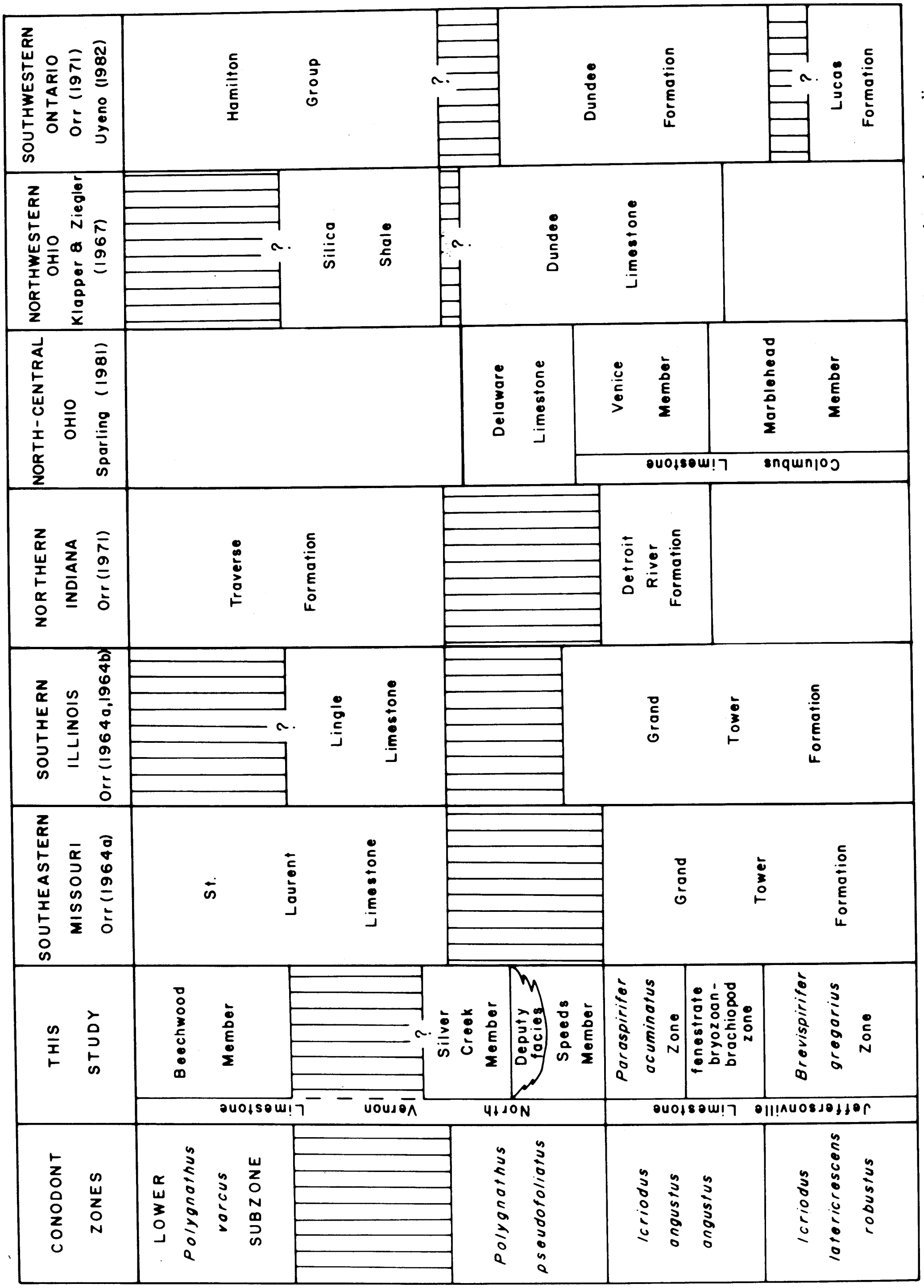


Fig. 5. Biostratigraphic correlations of Middle Devonian conodont zones in south-central Indiana, north-central Kentucky and surrounding areas.

CONODONTS SAMPLE NUMBER	*Belodella* cf. *B. resima*	*Coelocerodontus* cf. *C. biconvexus*	*Icriodus angustus angustus*	*I. angustus obliquus*	*I. brevis*	*I. latericrescens latericrescens*	*I. latericrescens robustus*	*I. retrodepressus*	*I.* n. sp. E of Weddige (1977)	*I.* sp. A	*I.?* sp. B	*Polygnathus* cf. *P. angusticostatus*	*P.? caelatus*	*P. costatus costatus*	*P. linguiformis klapperi*	*P. linguiformis linguiformis*	*P. linguiformis weddigei*	*P. pseudofoliatus*	*P. timorensis*	*Icriodus* "juveniles"	*Icriodus* sp. indeterminate	*Polygnathus* sp. indeterminate	genus & species indeterminate	alate elements	angulate elements	bipennate elements	cones (circular)	cones (compressed)	dolabrate elements	indeterminate ramiforms
SSQ-2	5	5				35	1cf.				4					2			25		76	3				2	3	3		2
SSQ-3		11				14															22		2				4	12		
SSQ-4	1	7				10							1cf.		1cf.	15		2	14	8	156	153	1	2	5	13	1	10	6	158
SSQ-5		17											1cf.			9			1	22	6					3	1	3	1	7
SSQ-6		24														9				36	6	8			2	6	3	18	5	11
SSQ-7		6														1				5				1		1	1	2		4
SSQ-8																1										1				1
SSQ-9																2				2						2				1
SSQ-10																														
SSQ-11		1														2				1								1		
SSQ-12	8	17	7	1				2	33	83		1				118		8		705	642	240		2	9	33	161	286	9	266
SSQ-13	6	10	1cf.					1	1	13										14	3						17	18		
*SSQ-14	1	11	2	15				8	20	94						115				452	184	57			3	7	48	47	4	47
*SSQ-15		2	7	1cf.				8	27	78						42		11		401	373	64			2	4	5	29	2	36
SSQ-16		14					37									20				90	18	17		2		12	20	47	7	30
SSQ-17	2	41					18							23		11				33	37	25		2	3	15	58	131	3	59
SSQ-18	2	51	9				147							34		72				186	146	14				9	228	182	7	75
SSQ-19	1	7					16									2				20	22					2	8	40	1	6
SSQ-20			1				1													1	11							1		
SSQ-21							1		2											2	10									
SSQ-22		1					5		1cf.											13	15						1	7		
SSQ-23		3					8													2	5						1	8		
SSQ-24			1cf.				9													10	16						2	6		
SSQ-25		2					6													3	5							1		
SSQ-26																														
SSQ-27																														
SSQ-28																														
OGQ-1	1	11			2	1							4			25			93	10	110	289			5	18	3	13	55	320
OGQ-2	1	6				16										2			6		37			1				8		
OGQ-3		2																			3	1								1
OGQ-4		3				1										4		1cf.		15	11	6			6	4		1	2	7
OGQ-5		6			2											6				15	4	3		2	5	4		3	4	6
OGQ-6	2	14			5											27				19	4	7		4	11	18	1	1	9	18
OVS-1	1																				5									
OVS-2						1																								1
OVS-3	4	2				3										4					3	1				1				1
OVS-4		26					11									9				23	12	8		1		4	9	22	7	13
OVS-5		15	1				30									32				83	58	5		1	1	9	2	15	4	12
OVS-6		19					45									19				46	17	5			3	7	1	25	2	8
OVS-7		5					27													9	12					1		8		1
OVS-8		1	1cf.				5		2	4										14	3							3		

Fig. 6. Distribution of conodonts in the Sellersburg Stone Company Quarry (SSQ), Old Gheen's Quarry (OGQ) and Oak and Vine Streets (OVS) sections. For discussion of *Icriodus* "juveniles," refer to remarks on *Icriodus* sp. A. Sample numbers preceded by an asterisk (*) indicate partial picking.

CONODONTS SAMPLE NUMBER	*Belodella* cf. *B. resima*	*Coelocerodontus* cf. *C. biconvexus*	*Icriodus angustus angustus*	*I. angustus obliquus*	*I. brevis*	*I. latericrescens latericrescens*	*I. latericrescens robustus*	*I. retrodepressus*	*I.* n. sp. E of Weddige (1977)	*I.* sp. A	*I.?* sp. B	*Polygnathus* cf. *P. angusticostatus*	*P.? caelatus*	*P. costatus costatus*	*P. linguiformis klapperi*	*P. linguiformis linguiformis*	*P. linguiformis weddigei*	*P. pseudofoliatus*	*P. timorensis*	*Icriodus* "juveniles"	*Icriodus* sp. indeterminate	*Polygnathus* sp. indeterminate	genus & species indeterminate	alate elements	angulate elements	bipennate elements	cones (circular)	cones (compressed)	dolabrate elements	indeterminate ramiforms
BMQ-1		5	5	3		10			3cf.							9		2cf.		40	260	50			5	1	1	12	3	52
*BMQ-2		2	18	1		19		5	6	10					4	38		2cf.	3	263	803	149		2	3	2	3	41	3	135
BMQ-3		3	9					2	5	3										177	29					2	48	61		6
BMQ-4		17	68					10	5	13		5				4				543	330	21		4	3	5	56	175	4	50
BMQ-5		10	21					7	2	12						4				136	85	13			2	1	20	42		19
BMQ-6		16	1cf.													4				108	44					4		9		9
BMQ-7		31	11				17							1		15				231	199	8		2	1	6	17	34	1	30
BMQ-8		36	3				18					3				2cf.				136	97			2		2	23	52		14
*BMQ-9		39	27				36							21		13				645	639	32		1	2	4	83	46	4	35
BMQ-10																														
BMQ-11																														
BMQ-12																														
TDQ-1		63						1	6	10										31		1					39	34		9
TDQ-2		13						1	6	10										9	9						1	16		
TDQ-3		16																		7	5	1					8	12		2
TDQ-4		17	2cf.																	32	17						21	35		2
TDQ-5		11	83	2				1	26	15						68		4		476	289	42		1	3	22	12	109	8	40
HAS-1																					2							1		
HAS-2		1																												
HAS-3		8				23			139	2			5cf.		4	132	4	12	18	120	927	452		7	2	29		28	38	129
HAS-4		3														3				4	2	2			1	2		1	2	8
HAS-5		3														13				19	2			1	4	7		2	2	13
HAS-6		16														42				67	19	12				21	2	5	16	45
HAS-7																														1
HAS-8																1				2	1							3		1
FOS-11	1	5					25									10				58	42	1				7	2	20	1	11
FOS-10		15	3				28									5				55	19	1		2		3		24		2
FOS-9		1					5							1cf.						1	7					1		5		
FOS-8		3					5													2	7							2		
FOS-7		1					2					1								3	4	1				1		2		
FOS-6		2					13													6	4							1		
FOS-5		10					15			2cf.										4	5							3		
FOS-4																														
FOS-3																														
FOS-2																														
FOS-1																														
BRS-5	5	1				3															4						4	6		
BRS-4																														
BRS-3																														
BRS-2	1	9				15			1cf.							31	1	2cf.	1	3cf	38	47		1	3	7	3	16	2	37
BRS-1																2					1	1								4

Fig. 7. Distribution of conodonts in the Berry Materials Corporation Quarry (BMQ), Type Deputy Quarry (TDQ), Harrison Avenue (HAS), Falls of the Ohio (FOS) and Beechwood Reference (BRS) sections. For discussion of *Icriodus* "juveniles," refer to remarks on *Icriodus* sp. A. Sample numbers preceded by an asterisk (*) indicate partial picking.

Fig. 8. Conodonts from the Muscatatuck Group of south-central Indiana and north-central Kentucky. All figures approximately X40.

A-F *Icriodus angustus angustus* Stewart and Sweet, 1956. A, B, C, upper, lower and lateral views of SUI 49331, TDQ-5. D, E. F, upper, lower, and lateral views of SUI 49332, BMQ-4.

G-L *Icriodus angustus obliquus* n. subsp. G, H, I, upper, lower, and lateral views of paratype SUI 49333, TDQ-5. J, K, L, upper, lower, and lateral views of holotype SUI 49334, SSQ-14.

M-U *Icriodus latericrescens robustus* Orr, 1971. M, N, O, lower, upper, and lateral views of SUI 49335, FOS-6. P, Q, R, upper, lower and lateral views of SUI 49336, OVS-6. S, T, U, lower, upper, and lateral views of SUI 49337, OVS-6.

V-AD *Icriodus latericrescens latericrescens* Branson and Mehl, 1938. V, W, X, lower, upper, and lateral views of SUI 49338, BRS-2, Y, Z, AA, upper, lower, and lateral views of SUI 49339, OGQ-2. AB, AC, AD, lower, upper, and lateral views of SUI 49340, BRS-2.

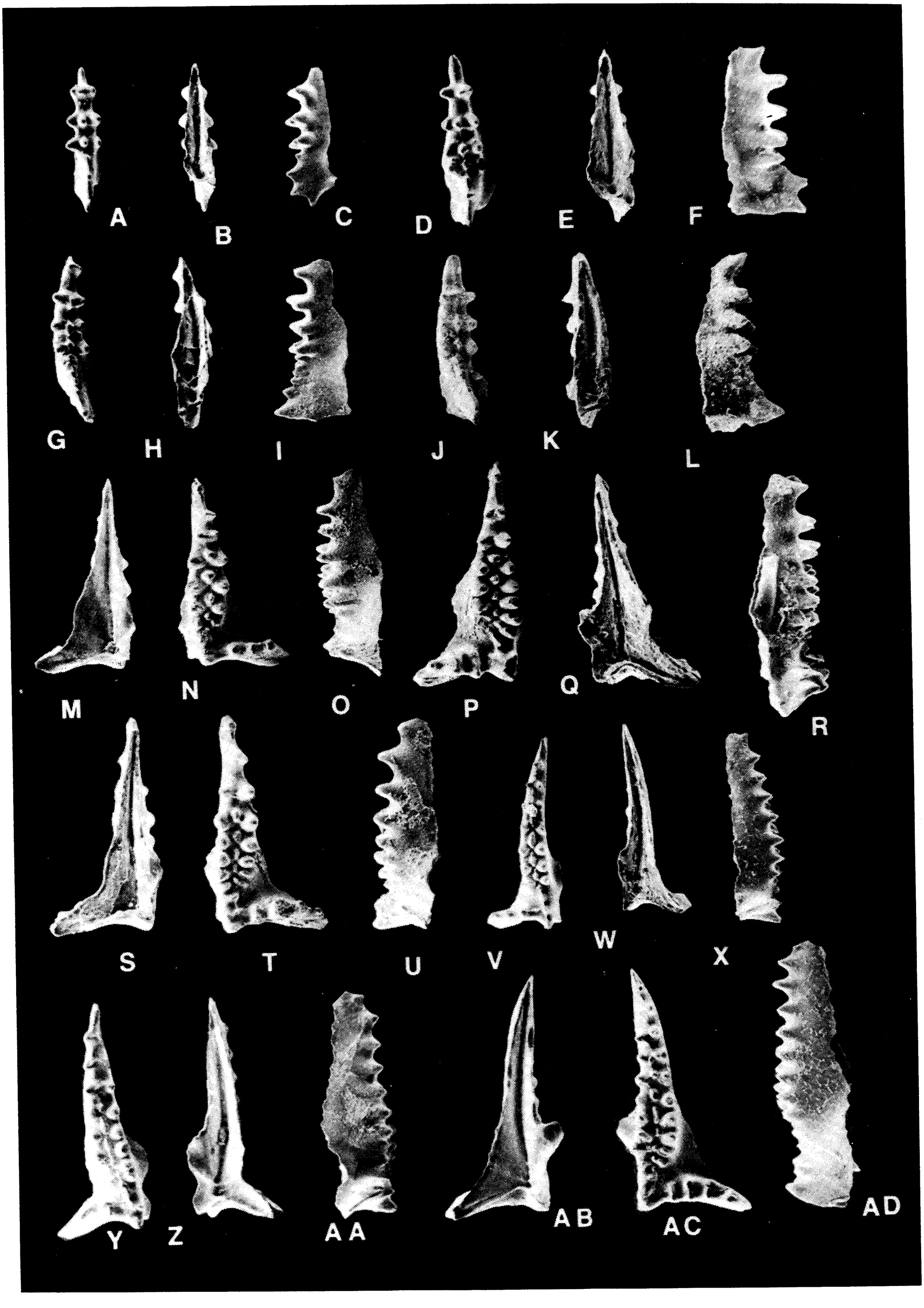

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Fig. 9 Conodonts from the Muscatatuck Group of south-central Indiana and north-central Kentucky. All figures approximately X40.

A-F *Icriodus retrodepressus* Bultynck, 1970. A, B, C, upper, lower, and lateral views of SUI 49341, BMQ-4. D, E, F, upper, lower, and lateral views of SUI 49342, BMQ-4.

G-I *Icriodus* n. sp. E of Weddige, 1977. Upper, lower, and lateral views of SUI 49343, BMQ-2.

J-L *Icriodus* cf. *I.* n. sp. E of Weddige, 1977. Upper, lower, and lateral views of SUI 49344, OVS-6.

M-O *Icriodus* cf. *I.* sp. A. Upper, lower, and lateral views of SUI 49345, FOS-5.

P-R *Icriodus* n. sp. E of Weddige, 1977 → *Icriodus* sp. A. Upper, lower, and lateral views of SUI 49346, BMQ-4.

S-X *Icriodus* sp. A. S, T, U, upper, lower, and lateral views of SUI 49347, TDQ-5. V, W, X, upper, lower, and lateral views of SUI 49348, BMQ-4.

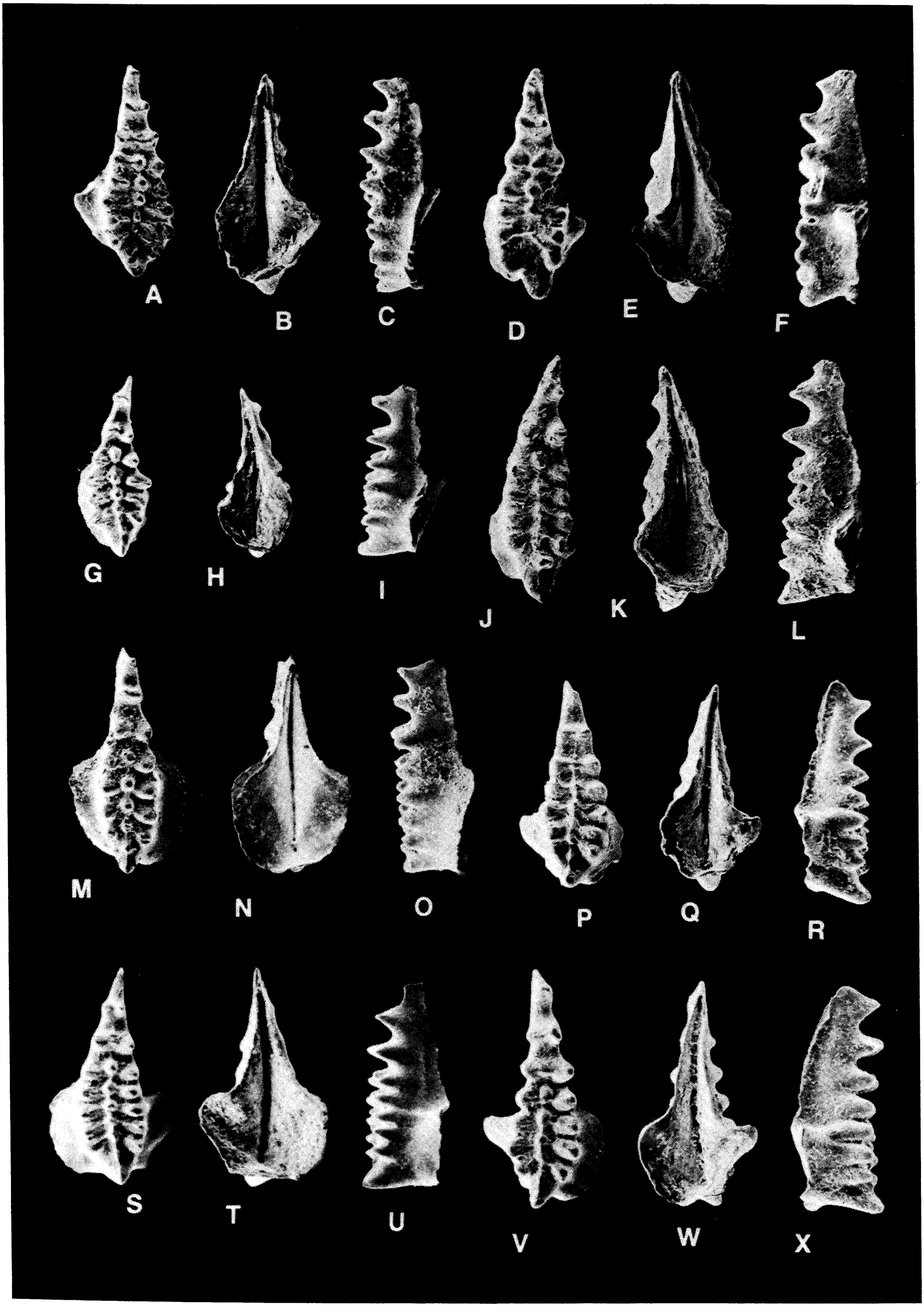
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Fig. 10. Conodonts from the Muscatatuck Group of south-central Indiana and north-central Kentucky. All figures approximately X40.

A-C *Polygnathus* cf. *P. angusticostatus* Wittekindt, 1966. Upper, lower, and lateral views of SUI 49349, BMQ-1. Specimen missing most of free blade.

D-F *Polygnathus costatus costatus* Klapper, 1971. Upper, lower, and lateral views of SUI 49350, SSQ-17.

G-I *Polygnathus* cf. *P. angusticostatus* Wittekindt, 1966. Upper, lower, and lateral views of SUI 49351, SSQ-15. Specimen missing free blade.

J-L *Polygnathus costatus costatus* Klapper, 1971. Upper, lower, and lateral views of SUI 49352, SSQ-18.

M-R *Polygnathus pseudofoliatus* Wittekindt, 1966. M, N, O, upper, lower, and laterial views of SUI 49353, SSQ-15. P, Q, R, upper, lower, and lateral views of SUI 49354, SSQ-15. Specimen missing most of free blade.

S-U *Polygnathus? caelatus* Bryant, 1921. Upper, lower, and lateral views of SUI 49355, OGQ-1. Specimen missing anterior tip.

V,W *Polygnathus?* cf. *P.? caelatus* Bryant, 1921. Upper and lower views of SUI 49356, HAS-3. Fragmentary specimen missing anterior portion and posterior tip.

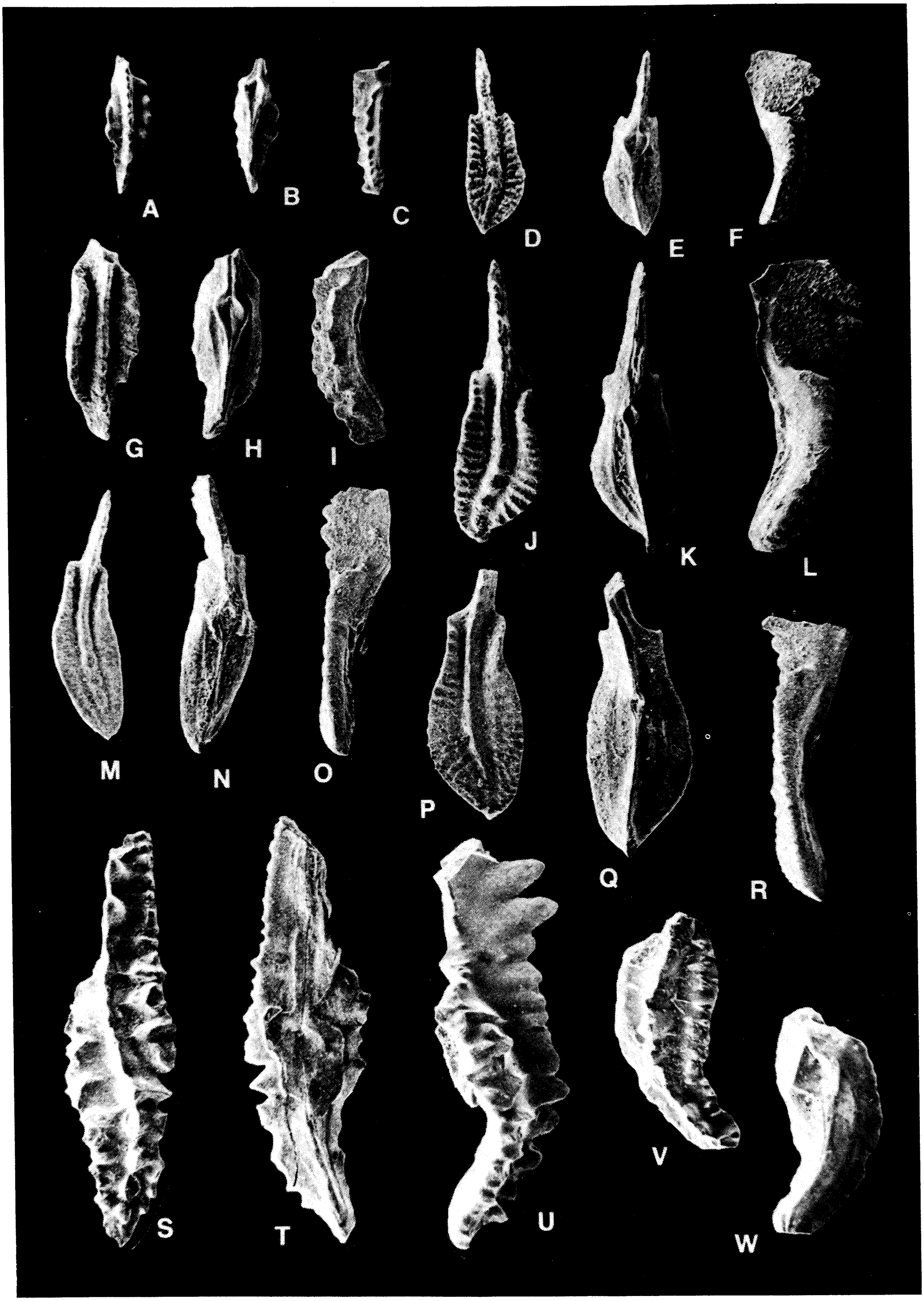
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Fig. 11 Conodonts from the Muscatatuck Group of South-central Indiana and north-central Kentucky. All figures approximately X40.

A Bipennate element. Inner lateral view of fragmentary specimen, SUI 49357, FOS-10.

B-E Dolabrate elements. B, inner lateral view of SUI 49358, OGQ-1. C, D, E, inner lateral, outer lateral, and lower views of SUI 49359, HAS-5.

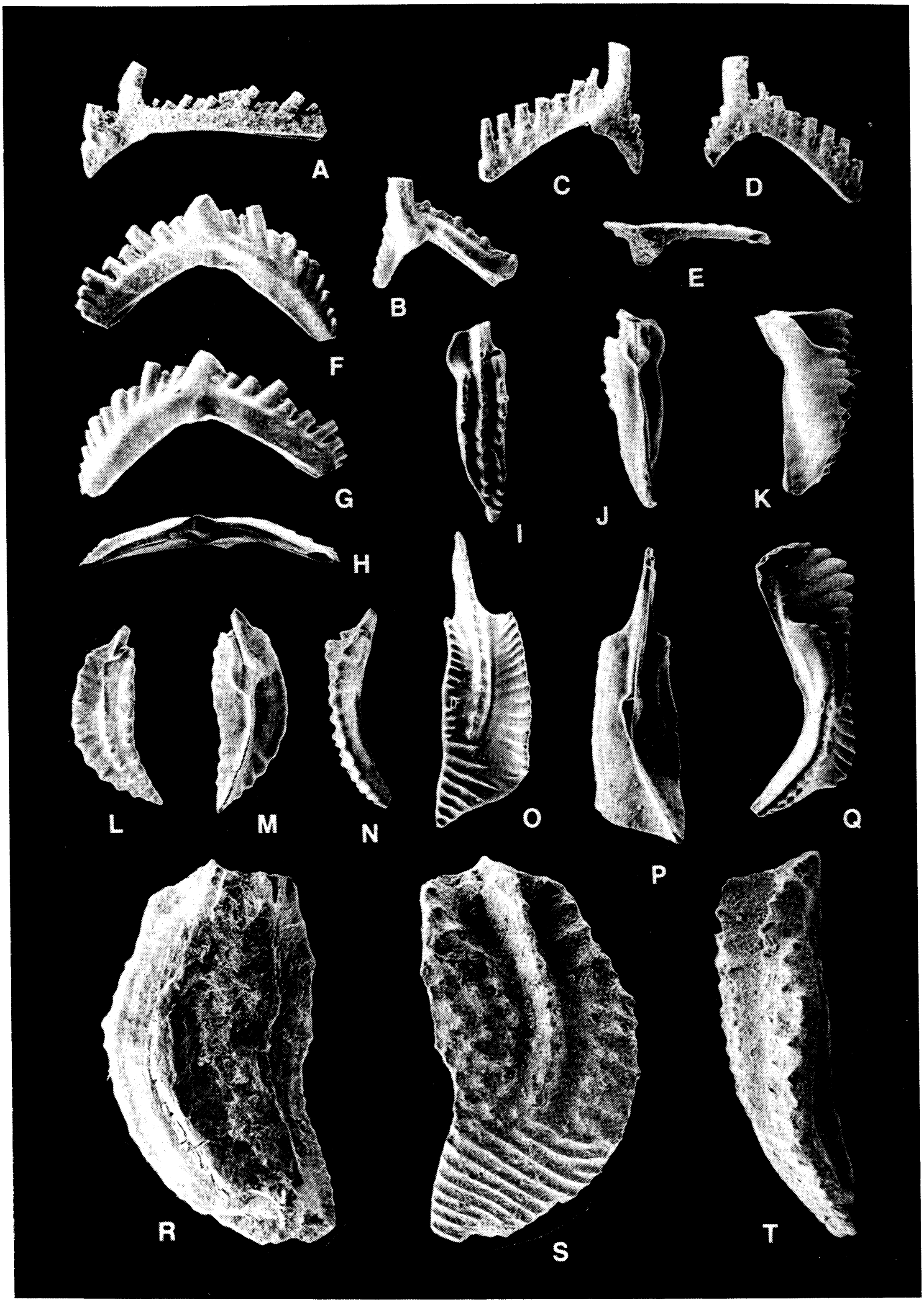
F-H Angulate element. Inner lateral, outer lateral, and lower views of SUI 49360, TDQ-5.

I-K *Polygnathus timorensis* Klapper, Philip, and Jackson, 1970. Upper, lower, and lateral views of SUI 49361, OGQ-1.

L-N *Polygnathus linguiformis weddigei* Clausen, Leuteritz, and Ziegler, 1979. Upper, lower, and lateral views of SUI 49362, BRS-2.

O-Q *Polygnathus linguiformis linguiformis* Hinde, 1879. Upper, lower, and lateral views of SUI 49363, SSQ-4.

R-T *Polygnathus linguiformis klapperi* Clausen, Leuteritz, and Ziegler, 1979. Lower, upper, and lateral views of SUI 49364, BMQ-2.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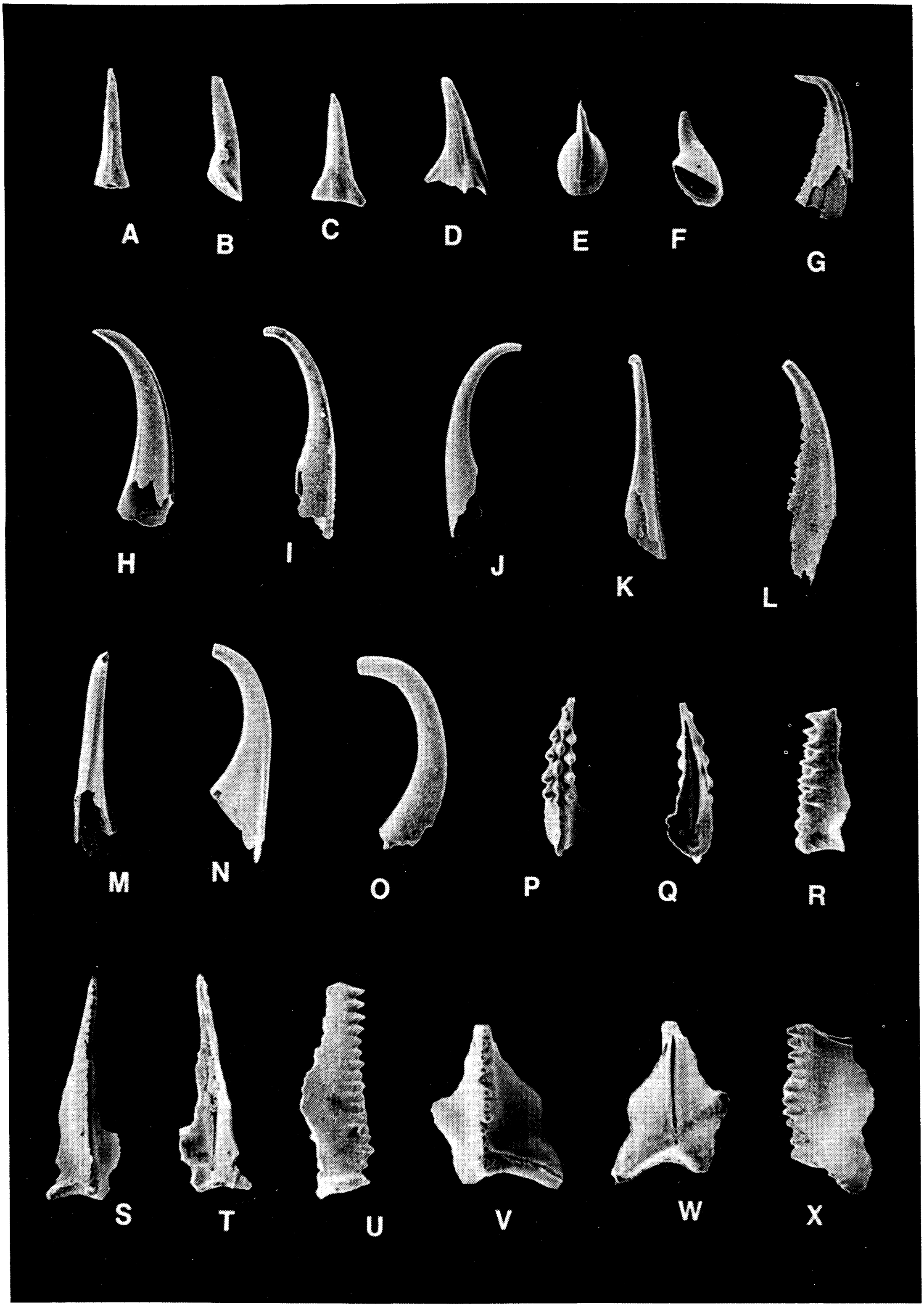
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Fig. 12 Conodonts from the Muscatatuck Group of south-central Indiana and north-central Kentucky. All figures approximately X40.

A-D Coniform elements. A, SUI 49365, OGQ-1; B, SUI 49366, TDQ-5; C, SUI 49367, BRS-2; D, SUI 49368, SSQ-3.

E,F Genus and species indeterminate. Upper and lateral views of SUI 49369, SSQ-4.

G *Belodella* cf. *B. resima* (Philip, 1965). Lateral view of SUI 49370. OVS-3.

H-K *Coelocerodontus* cf. *C. biconvexus* Bultynck, 1970. H, posterolateral view of SUI 49371, SSQ-3; I, J, K, inner lateral, outer lateral, and posterolateral view of SUI 49372, TDQ-5.

L *Belodella* cf. *B. resima* (Philip, 1965). Lateral view of SUI 49373, SSQ-4.

M-O *Coelocerodontus* cf. *C. biconvexus* Bultynck, 1970. M, N, posterior and lateral views of SUI 49374, SSQ-3. O, lateral view of SUI 49375, OGQ-1.

P-R *Icriodus brevis* Stauffer, 1940. Upper, lower, and lateral views of SUI 49376, OGQ-1.

S-X *Icriodus?* sp. B. S, T, U, upper, lower, and lateral views of SUI 49377, SSQ-2. V, W, X, upper, lower, and lateral views of SUI 49378, GHE-2.

Remarks.—*Polygnathus linguiformis weddigei* is distinguished from the nominal subspecies by the flatter platform, the poorly developed tongue, and a carina that extends to, or nearly to, the posterior tip in the former. For a detailed diagnosis, see Clausen, Leuteritz, and Ziegler (1979) or Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson (1976). *P. l. weddigei* is a rare form in the present faunas and was recovered from only two samples.

Material.—5 specimens.

Occurrence.—Basal part of the Beechwood Member of the North Vernon Limestone.

Polygnathus pseudofoliatus
Wittekindt, 1966
Fig. 10 M-R

Polygnathus n. sp. Ziegler. Flajs, 1966, p. 232-233, Pl. 23, Figs. 5-7.

Polygnathus pseudofoliata Wittekindt, 1966, p. 637-638, Pl. 2, Figs. 20-23 [non Fig. 19 = *P. eiflius*].

Polygnathus pseudofoliatus Wittekindt. Klapper, 1971, p. 63-64, Pl. 2, Figs. 8-13 [see further synomymy]; Klapper, *in* Ziegler, 1973, p. 375-376, *Polygnathus*—Pl. 1, Figs. 8, 9 [see further synonymy]; Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson, 1976, Pl. 3, Figs. 2, 3, 12, 13; Weddige, 1977, p. 317-318, Pl. 4, Figs. 68-70 [see further synonymy]; Bultynck and Hollard, 1981, p. 45, Pl. 5, Figs. 13, 14.

Polygnathus cf. *P. pseudofoliatus* Wittekindt. Pedder, Jackson, and Ellenor, 1970, Pl. 15, Fig. 26.

Remarks.—For diagnosis and description of *Polygnathus pseudofoliatus,* see Wittekindt (1966, p. 637-638). For amended diagnosis see Klapper, *in* Ziegler (1973, p. 375). *P. pseudofoliatus* includes a carminiplanate element that may have a platform outline similar to that of *P. c. costatus.* In *P. pseudofoliatus,* however, the platform tends to be shallower with shallower adcarinal troughs, especially in the posterior part of the platform. The ornamentation of *P. pseudofoliatus* is less strongly developed than in *P. c. costatus* and consists of transverse rows of nodes to weakly developed to broken transverse ridges. Rare specimens in the present study have unusually elongate platforms (see Fig. 10, M-O) but otherwise agree with specimens considered herein as *P. pseudofoliatus.*

Material.—44 specimens.

Occurrence.—North Vernon Limestone (all members).

Polygnathus timorensis
Klapper, Philip, and Jackson, 1970
Fig. 11 I-K

Polygnathus varca Stauffer. Bischoff and Ziegler, 1957, Pl. 18, Fig. 34 (only).

Polygnathus varcus Stauffer. Kirchgasser, 1970, p. 351-352, Pl. 66, Figs. 9-11; Orr, 1971, p. 53-54, Pl. 5, Figs. 4-8.

Polygnathus cf. *decorosa* Stauffer. Matthews, 1970, Pl. 1, Fig. 10.

Polygnathus timorensis Klapper, Philip, and Jackson, 1970, p. 655-656, Pl. 1, Figs. 1-3, 7-10; Klapper, *in* Ziegler, 1973, p. 385-386, *Polygnathus*—Pl. 2, Fig. 3; Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson, 1976, p. 125, Pl. 2, Figs. 27-32; Orchard, 1978, p. 949, Pl. 112, Figs. 13-15, 17, 18, 25, 28, 32, 35; Bultynck and Hollard, 1981, p. 45, Pl. 6, Figs. 8-14; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 30, Pl. 2, Figs. 7, 8, 13-16 (Pa elements).

Polygnathus rhenanus marijae Huddle, 1981, p. B32, Pl. 17, Figs. 10-12, 19-27 (only), Pl. 18, Figs. 1, 2, 5 (only).

Remarks.—For diagnosis and remarks, see Klapper, Philip, and Jackson (1970) and Ziegler and Klapper, *in* Ziegler, Klapper, and Johnson (1976).

Material.—161 specimens.

Occurrence.—Uppermost part of the Silver Creek Member, and the Beechwood Member of the North Vernon Limestone. See section on Biostratigraphy for comments on occurrence in the Silver Creek Member.

Genus and species indeterminate
Fig. 12 E, F

Remarks.—Three, slightly asymmetrical, nongeniculate coniform elements of uncertain affinities have been recovered from two of the examined samples. These elements have a broad, circular to elliptical basal margin. The thin-walled base occupies the lower three-fourths to four-fifths of the specimen. The cusp is proclined, oval in cross-section, and bluntly pointed apically. A low, narrow keel runs along the anterior margin from the apex to the basal margin; otherwise, the elements are smooth. These specimens bear some resemblance to *Coelocerodontus* cf. *C. biconvexus* in the development of the deep, thin-walled base. Paucity of material and restricted distribution, however, obscure the relationship, if any, with that species.

Material.—3 specimens

Occurrence.—Beechwood Member, North Vernon Limestone.

Coniform Elements
Fig. 12 A-D

Remarks.—Proclined coniform elements that are generally either compressed or nearly circular in cross-section are common to abundant in many of the examined samples. Similar coniform elements have been included in multielement reconstructions of species of *Icriodus* (see, e.g., Klapper and Philip, 1971, p. 446; Johnson and Klapper, 1981, p. 1242; Clark et al., 1981, p. W125; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, p. 32). The comparable distributions of the segminiscaphate elements of *Icriodus* and of the simple cones, in the present study, support those reconstructions (refer to Figs. 6 and 7). No similar reconstructions are attempted in this paper, however, because of the diversity of the simple cones and of species of *Icriodus*.

Material.—Compressed: 1,955; circular: 978.

Occurrence.—*Brevispirifer gregarius* Zone; fenestrate bryozoan-brachiopod zone; *Paraspirifer acuminatus* Zone and Vernon Fork Member of the Jeffersonville Limestone; Speeds, Silver Creek and Beechwood Members and Deputy facies of the North Vernon Limestone.

Ramiform and Angulate Elements
Fig. 11 A-H

Remarks.—Ramiform and angulate elements are common constituents of many of the conodont faunas examined. Preservation tends to be poor, however, with most specimens being fragmentary. Whenever possible, specimens were placed into the various shape categories (alate, bipennate, dolabrate, and angulate). Elements belonging to these shape categories have been included in reconstruction of species of *Polygnathus* (see, e.g., Klapper and Philip, 1971, p. 431-433; Sparling, 1981, p. 308-309; Clark et al., 1981, p. W162-W164; Uyeno, *in* Uyeno, Telford, and Sanford, 1982, Pl. 2). The comparable distribution of the carminiplanate elements of *Polygnathus* and the ramiform and angulate elements in the present study support these reconstructions.

Material.—Alate elements: 51; bipennate elements: 367; dolabrate elements: 235; angulate elements: 117.

Occurrence.—Brevispirifer gregarius Zone; fenestrate bryozoan-brachiopod zone; *Paraspirifer acuminatus* Zone and Vernon Fork Member of the Jeffersonville Limestone; Speeds, Silver Creek and Beechwood Members and Deputy facies of the North Vernon Limestone.

CONCLUSIONS

Conodont faunas from the Middle Devonian Muscatatuck Group of south-central Indiana and north-central Kentucky contain few species diagnostic of the standard conodont zonation. Consequently, a zonation consisting of three local zones and one standard subzone has been adopted. By means of this local zonal scheme, a correlation of the Middle Devonian strata of the study area and surrounding areas can be established. A late Emsian to early Givetian age is suggested for the Muscatatuck Group

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APPENDIX

LOCALITIES

Three distinct methods (Federal System of Rectangular Surveys, Clark Military Grants, and Carter Coordinates) have been used to survey the land in the study area. For the sake of consistency, locations are given in terms of latitude and longitude.

1) Berry Materials Corporation Quarry (BMQ), Lat. 39°00′53″ N, Long. 85°37′07″ W, Butlerville 7.5′ Quadrangle, Jennings County, Indiana (type locality of North Vernon Limestone).
2) Deputy Quarry (TDQ), Lat. 38°46′50″ N, Long. 85°38′18″ W, Deputy 7.5′ Quadrangle, Jefferson County, Indiana (type locality of Deputy Limestone of Campbell, 1942).
3) Sellersburg Stone Company Quarry (SSQ), Lat. 38°23′24″ N, 85°46′54″ W, Charlestown 7.5′ Quadrangle, Clark County, Indiana.
4) Old Gheen's Quarry (OGQ), Lat. 38° 21′27″ N, Long. 85°44′30″ W, Jeffersonville 7.5′ Quadrangle, Clark County, Indiana (type area of Silver Creek Member).
5) Harrison Avenue Section (HAS), Lat. 38°17′17″ N, Long. 85°46′39″ W, New Albany 7.5′ Quadrangle, Clark County, Indiana.
6) Falls of the Ohio Section (FOS), Lat. 38° 16′20″ N, Long. 85°45′45″ W, New Albany 7.5′ Quadrangle, Clark County, Indiana (type locality of Jeffersonville Limestone).
7) Beechwood Reference Section (BRS), Lat. 38°15′13″ N, Long. 85°42′53″ W, Jeffersonville 7.5′ Quadrangle, Jefferson County, Kentucky (reference section of Beechwood Member).
8) Oak and Vine Streets Section (OVS), Lat. 38°14′08″ N, Long. 85°43′46″ W, Louisville East 7.5′ Quadrangle, Jefferson County, Kentucky.

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